THEME SECTION

Individual variability in seabird foraging and migration

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This Theme Section showcases the latest research on individual variability in foraging and migration in seabirds. The studies thus contribute to our understanding of the causes and consequences of movement, dietary and habitat variability among individuals, using a range of methods for quantification and analysis. These studies provide fundamental insights into key factors such as individual specialisation, plasticity in response to environmental change and seasonal carry-over effects.

Eleven foraging trips tracked with GPS devices on the same Cory's shearwater during the incubation period over 5 consecutive years

Image: Jose Manuel Reyes-González

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Contribution to the Theme Section 'Individual variability in seabird foraging and migration'

INTRODUCTION: REVIEW

Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds

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ABSTRACT: Technological advances in recent years have seen an explosion of tracking and stable isotope studies of seabirds, often involving repeated measures from the same individuals. This wealth of new information has allowed the examination of the extensive variation among and within individuals in foraging and migration strategies (movements, habitat use, feeding behaviour, trophic status, etc.) in unprecedented detail. Variation is underpinned by key life-history or state variables such as sex, age, breeding stage and residual differences among individuals (termed 'individual specialization'). This variation has major implications for our understanding of seabird ecology, because it affects the use of resources, level of intra-specific competition and niche partitioning. In addition, it determines the responses of individuals and populations to the environment and the susceptibility to major anthropogenic threats. Here we review the effects of season (breeding vs. nonbreeding periods), breeding stage, breeding status, age, sex and individual specialization on foraging and migration strategies, as well as the consequences for population dynamics and conservation.

KEY WORDS: Individual specialization · Consistency · Sexual segregation · Age effects · Central-place constraint · Intrinsic variation · State dependence · Life-history

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INTRODUCTION

The burgeoning of tracking and stable isotope studies of seabirds and other marine predators since the 1990s has provided a wealth of information on numerous aspects of their ecology and life-history, including the striking variation in movement patterns and foraging behaviour of individuals (Phillips et al. 2008, Wakefield et al. 2009a). Until relatively recently, this variation was examined largely by testing for effects of factors such as species, colony, sex, age, year, season (breeding vs. nonbreeding period), breeding phase or breeding status. Much less attention was paid to the residual variation among individuals after accounting for these group effects. This residual variation was considered to define 'individual specialization' in the seminal review by Bolnick et al. (2003) and is also the focus of research on 'behavioural syndromes' or 'animal personalities' in the field of animal behaviour (Dall et al. 2012). Research on individual variation has burgeoned in the last decade, spurred partly by reductions in cost and mass of tracking devices, allowing larger sample sizes, and by the increasing use of more powerful statistical techniques (Carneiro et al. 2017, this Theme Section).

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Most seabirds show striking changes in distribution associated with stage of the annual cycle. Many species are migratory, making directed movements from breeding to nonbreeding grounds to exploit seasonal peaks in prey abundance or to avoid inclement weather, with implications for survival and subsequent fecundity (Daunt et al. 2014, Reiertsen et al. 2014). The changing degree of central-place constraint during the breeding period — from pre-laying through incubation, brood-guard and later chick-rearing (post-guard) — can lead to major shifts in distribution, activity patterns or diet within individuals (Hedd et al. 2014, Quillfeldt et al. 2014). There may be within-breeding-season (date-related) differences in distribution or diet, which reflect extrinsic changes in the environment (Phillips et al. 2009b). In addition, some seabirds (particularly albatrosses and petrels) adopt a bimodal (or dual) foraging strategy during chick-rearing, in which adults alternate between foraging close to the colony and increasing feeding frequency for the benefit of the chick, and foraging further afield to recover their own body condition (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994).

There is mounting evidence that movements and distributions of seabirds are influenced by age and breeding status. Failed breeders often depart on their migration sooner than successful ones (Phillips et al. 2005, Bogdanova et al. 2011, Hedd et al. 2012), and they may spend the late breeding season in the same areas as deferring (sabbatical) breeders, but be partially or completely segregated from active breeders (Phillips et al. 2005, González-Solís et al. 2007, Reid et al. 2014). In this way, nonbreeders (failed or deferring) may be avoiding competition with breeders (Clay et al. 2016). Juvenile and immature seabirds avoid competition with adults — possibly to compensate for poorer foraging skills — by using less productive habitats and increasing their foraging time (Daunt et al. 2007b, Fayet et al. 2015). Their distributions frequently differ from those of adults, often markedly so during the nonbreeding period even though adults are no longer limited by the central-place foraging constraint (but see Péron & Grémillet 2013, Gutowsky et al. 2014, de Grissac et al. 2016).

Age effects on foraging ability are often apparent amongst breeders: younger or less experienced birds may forage less efficiently, with implications for breeding success (Daunt et al. 2007b, Limmer & Becker 2009, Harris et al. 2014a, Le Vaillant et al. 2016), or feed at lower trophic levels (Le Vaillant et al. 2013). Inferior foraging success among younger individuals is thought to reflect the poorer skills in identifying or catching prey or in selecting suitable locations, weaker motor control or physiological fitness (e.g. cardiovascular or muscular performance) of young birds or the selective disappearance of poor phenotypes among the adult population. Although there is evidence that foraging ability can decline in old age (Catry et al. 2006), changes in behaviour may not be detectable — despite physiological ageing (Elliott et al. 2015) — or are apparent only in particular environments (Lecomte et al. 2010, Froy et al. 2015). Moreover, differences between old and young animals can be difficult to interpret, because lower activity (e.g. more time on the water recorded by a leg-mounted immersion logger) might indicate either inferior physiological function or greater efficiency allowing more discretionary time to be spent resting (Catry et al. 2011).

Sexual segregation and other between-sex differences in foraging behaviour are apparent in many seabirds. This may reflect habitat specialization or avoidance of competition in sexually dimorphic species and sex role specialization or sex-specific nutrient requirements in monomorphic or dimorphic species (Lewis et al. 2002, Phillips et al. 2004, 2011). Sex differences in distribution and behaviour of seabirds tend to be more apparent during particular periods, for example during pre-laying (presumably related to sex-role partitioning of nest defense), affecting attendance patterns (Hedd et al. 2014, Quillfeldt et al. 2014). However, such effects are far from universal; despite a degree of spatial segregation, activity patterns of male and female albatrosses are comparable during the breeding and nonbreeding periods, suggesting little difference in prey type or foraging method (Mackley et al. 2011, Phalan et al. 2007). Similarly, in the 2 recent studies that recorded sex differences in the proportions of residents and migrants, the effects were in opposite directions (Pérez et al. 2014, Weimerskirch et al. 2015).

Variation among and within individuals in foraging distribution and behaviour has major implications for our understanding of seabird ecology because it affects the use of resources, level of intra-specific competition and niche partitioning (Phillips et al. 2004, de Grissac et al. 2016). In addition, it determines the responses of individuals and populations to environmental drivers (including climatic change) and the overlap with, and hence susceptibility to major anthropogenic threats, including fisheries and pollutants (Phillips et al. 2009a, Granadeiro et al. 2014, Patrick et al. 2015). Individual variation is also at the root of carry-over effects, whereby processes in one season have consequences in subsequent seasons (Harrison et al. 2011). Surprisingly, however, there are rarely demonstrable life-history consequences of individual consistency in foraging strategies *per se* despite the many studies of adult quality (consistent individual differences in breeding performance) in seabirds (Lescroël et al. 2009, Crossin et al. 2014, but see Patrick & Weimerskirch 2017).

Here we review the intrinsic group effects underlying individual variation in foraging and migration patterns of seabirds, including breeding stage, season (breeding vs. nonbreeding period), breeding status, age, sex and — after those have been accounted for — the incidence, causes and consequences of the individual effects that remain. We consider these last, residual effects to be synonymous with individual specialization sensu Bolnick et al. (2003) and expect specialists to show repeatability or consistency in foraging distribution, behaviour or diet. We do not review effects of colony, as these may reflect differences in resource availability or habitat accessibility, nor effects of date or year *per se*, as these reflect environmental variation and are extrinsic to individual decisions and trade-offs. We explore whether the degree of variation among and within individuals (i.e. both groups effects and specialization) depends on phylogeny, biogeography or other factors and focus on the consequences for life-histories and population dynamics and the implications for seabird conservation. The impetus for this review and for this Theme Section on 'Individual variability in seabird foraging and migration' in *Marine Ecology Progress Series* was the session on 'Individual variation in movement strategies' at the 2nd World Seabird Conference in Cape Town, South Africa, 27–30 October, 2015.

EFFECTS OF THE ANNUAL CYCLE

Breeding stage and season (breeding vs. nonbreeding period)

Changes in seabird diet across the annual cycle, particularly over different stages of the breeding period, have been studied for several decades (Barrett et al. 2007), but until the advent of suitable tracking technologies, information on year-round foraging behaviour of seabirds was scarce. Subsequently, many studies have recorded foraging distribution and behaviour of individuals over extended periods, showing that these vary markedly throughout the annual cycle; some of these changes reflect differences in food availability or the underlying biophysical environment, and others are directly related to changes in reproductive demands and central-place foraging (Phillips et al. 2008, González-Solís & Shaffer 2009). Energy requirements and breeding duties change across the annual cycle, limiting foraging in time and space (including to the most productive habitats) to different extents.

During pre-laying, birds visit the colony frequently or remain there for a prolonged period for pair bonding and nest defence, but they are still free from parental duties and may have time available for long trips. Although the constraints for males and females may differ, individuals typically forage further from the colony and in more productive waters than in later stages (Phillips et al. 2006, Paiva et al. 2008, Pinet et al. 2012, Hedd et al. 2014). During incubation, most seabirds alternate incubation bouts, with one parent incubating the clutch while the other is at sea. In penguins, albatrosses, petrels and alcids, birds may fast for several weeks on the nest while the partner engages in foraging trips that are longer and further afield than during chick rearing (Hull 2000, Phalan et al. 2007, Ito et al. 2010, Péron et al. 2010, Hedd et al. 2014). Nevertheless, trips usually shorten when hatching approaches, allowing the chick to be fed within a few days (Weimerskirch et al. 1997, González-Solís 2004). In gulls and skuas, however, incubation bouts are relatively short, and the foraging range during that phase can be similar or shorter than during chick rearing (Carneiro et al. 2014, Camphuysen et al. 2015).

During brooding, the parents alternate foraging with guarding the chicks, which are rarely left unattended in order to reduce exposure to the elements or predators. In pelagic seabirds, this is often regarded as the period with the greatest energy requirements, since an adult must forage both to meet its own demands during the subsequent brooding stint and those of the chicks (Ricklefs 1983). In some species (including albatrosses, petrels and penguins), parents are forced to forage closer to the colony than in any other stage (Hull 2000, Charrassin & Bost 2001, Phillips et al. 2004, González-Solís et al. 2007), even though the areas visited may not be optimal, leading to progressive deterioration in parental body condition (Weimerskirch & Lys 2000, Green et al. 2009). In addition, the requirements of the chick in terms of prey energetic or nutritional content, size or digestibility may necessitate a change in foraging behaviour of the adult (Davoren & Burger 1999, Isaksson et al. 2016). Several studies have shown that parents feed their chicks with a high-quality diet, for example selecting lipid-rich fishes (Wilson et al. 2004, McLeay et al. 2009, Bugge et al. 2011, Dänhardt et al. 2011), and a failure to do so may reduce chick survival (Annett & Pierotti 1999, Grémillet et al. 2008). Alternatively, selection of high quality prey may reflect the need to maximise net energy gain per unit foraging effort for parents that are unable to carry more than one item in their bill (Wilson et al. 2004). In species delivering mainly undigested food, chicks are limited in terms of the size of prey they can swallow, and parents are typically forced to seek small items, steadily increasing the size with chick age, which may require parents to change prey types and foraging areas over the chick-rearing period (Pedrocchi et al. 1996, Rodway & Montevecchi 1996, McLeay et al. 2009).

In many species there is a post-brooding period (crèche in penguins) when parents leave chicks unattended except when delivering meals so that they can increase trip length. Initially, the foraging range usually remains more constrained than during incubation (Phillips et al. 2004, Saraux et al. 2011, Froy et al. 2015), presumably because chicks have a lower fasting capability than incubating adults until the mid- to late chick-rearing phase (Phillips & Hamer 1999). Trip duration tends to increase and parents forage further away from the colony as the chick-rearing period progresses (Weimerskirch & Lys 2000, Dall'Antonia et al. 2001, Rishworth et al. 2014b). These longer trips are likely prompted by the chicks' increased fasting capability and energetic demand, as well as a deterioration in food availability or an increase in foraging conspecifics enhancing density-dependent competition near the colony (Rishworth et al. 2014b). The ability to increase intervals between feeding is limited by the maximum payload, which is inversely related to adult body mass in Procellariiformes (Phillips & Hamer 2000). Food delivery rates also depend on whether the adults forage in coastal or inshore waters and deliver food that is fresh and carried in the bill (terns and alcids), partially-digested in the stomach (gulls, penguins and other taxa) or further digested to an energy-dense stomach oil in the proventriculus (Procellariiformes; except diving petrels, Pelecanoididae); in this last group, the single chick stores extensive fat reserves, allowing the adults to exploit more remote areas (Ricklefs 1983, Phillips & Hamer 1999). Changes in trip duration during breeding can be detected using stable isotopes, and an increase in foraging range may be associated with an expansion of the isotopic niche (Ceia et al. 2014).

For breeding, seabirds need land that is free of terrestrial predators. Such breeding grounds may be distant from productive foraging sites. One mechanism for coping with low food availability close to the breeding colony is to adopt a so-called 'dual foraging' strategy, when parents alternate between short and long foraging trips to balance their own energetic requirement with that of the chick (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994). During these short trips, parents forage within shorter distances, maximising provisioning rates; however, this apparently reduces their body condition, causing the adult to switch to more distant and more productive waters with predictable food resources (frontal zones, neritic areas, etc.) to restore its own reserves. The dual foraging strategy is seen in many albatrosses, shearwaters and other petrels, but there is a great deal of variability among species and populations, potentially related to differences in foraging strategies and resource distribution around colonies or between years (Granadeiro et al. 1998, Baduini & Hyrenbach 2003, Phillips et al. 2009b). A similar but less flexible strategy has also been postulated for penguins (Ropert-Coudert et al. 2004, Saraux et al. 2011). Dual foraging has also been described in auks (Welcker et al. 2009), possibly because the energetic cost of transit in this group is particularly high (Costa 1991, Thaxter et al. 2010).

Changes in foraging behaviour also occur in the nonbreeding period. After breeding, most species of seabirds migrate to more suitable habitats, avoiding low temperatures, shorter days and reduced food availability around colonies. In some populations, individuals move to a post-breeding, stopover area, presumably offering good foraging opportunities at that time of year, where they may spend considerable time before departing for their main wintering grounds (Anker-Nilssen & Aarvak 2009, Frederiksen et al. 2012, Bogdanova et al. 2017, this Theme Section). Both conventional diet (stomach content analysis) and stable isotope studies indicate that wintering seabirds can change their diet or widen their trophic niche, since individuals are no longer central-place foragers and are free to select their favoured habitat or prey (Cherel et al. 2007, Karnovsky et al. 2008, Hedd et al. 2010, Harris et al. 2015). It is important to note that we lack knowledge for most seabirds of their prey during the winter; although stable isotope studies offer a partial solution, ideally these need to control for changes in isotopic baselines because of the scale of seabird movements (Meier et al. 2017).

Activity levels decrease during part of or the entire nonbreeding period in Procellariiformes (Mackley et al. 2011, 2010, Cherel et al. 2016), sulids (Garthe et al. 2012), skuas (Magnusdottir et al. 2014, Carneiro et al. 2016) and alcids (Mosbech et al. 2012). Reasons for this decrease may include lower energetic demands, freedom from parental care duties and removal of the central-place foraging constraint, higher food availability or lower costs of thermoregulation. In addition, productive nonbreeding grounds may allow for a sit-and-wait foraging strategy that is more energy-efficient, or food availability may be enhanced by the activities of subsurface predators or fisheries (Péron et al. 2010). Seabirds generally, but not always, moult in the nonbreeding period to avoid overlap with other energetically demanding processes, such as reproduction or migration (Bridge 2006, Catry et al. 2013b). This may result in flight impairment, which would explain a decrease in activity levels in the winter in some species (Cherel et al. 2016), or in flightlessness, which may drive movements (particularly by auks) to specific moulting areas (Linnebjerg et al. 2013, Frederiksen et al. 2016).

Lower activity during the nonbreeding period is far from universal, and species that breed in high latitudes, are resident year-round, or have limited capacity to migrate, cope with winter conditions by increasing their activity levels. Indeed, foraging time of cormorants or shags breeding at high latitudes peaks in mid- to late winter, possibly due to reduced prey availability or high energetic costs associated with thermoregulation (Grémillet et al. 2005, Daunt et al. 2006, Lewis et al. 2015), and penguins sometimes dive longer and deeper to exploit less accessible prey during winter (Moore et al. 1999, Charrassin & Bost 2001, Green et al. 2005).

Breeding status

Studies of seabird foraging and movements during the breeding season usually focus on breeding adults because of the relative ease with which they can be caught for logger deployment and retrieval. However, an important component of the breeding population comprises individuals that are not breeding or have failed in their breeding attempt, and an increasing number of studies aim to quantify the foraging dynamics of these groups and to test whether they show different behaviours compared to breeding adults. Much of the attention has been directed at failed breeders, whose failure may have been natural, a consequence of the deployment, or induced as part of a manipulative experiment (Phillips et al. 2005, Bogdanova et al. 2011, Ponchon et al. 2014, 2015). Failed breeders often continue to associate with the colony, operating as central-place foragers but expanding their foraging areas (González-Solís et al. 2007). The spatial overlap with breeders varies among populations; it can be high (Ponchon et al. 2014), moderate (Phillips et al. 2008), or there may be marked segregation (Jaeger et al. 2014, Reid et al. 2014, Clay et al. 2016). Further, failed breeders may make visits to other colonies when breeders are still actively rearing chicks; this behaviour is interpreted as prospecting potential new breeding sites and may be motivated by having failed at the current location (Fijn et al. 2014, Ponchon et al. 2014, 2015). In contrast, successful breeders do not undertake prospecting trips or only do so after breeding is finished (Fijn et al. 2014, Ponchon et al. 2014, 2015).

Quantifying differences in foraging and movements between breeding and nonbreeding individuals (the latter including deferring breeders and older prebreeders, but not failed breeders) during the breeding season is hampered by the difficulty in capturing nonbreeders to deploy data loggers. There is considerable indirect evidence from observations at breeding sites that nonbreeders often attend the colony in the breeding season and act as central-place foragers, suggesting that foraging overlap with breeders would be substantial (Aebischer 1986, Harris & Wanless 1997). This has been confirmed by tracking black-browed albatross *Thalassarche melanophris* at South Georgia (Phillips et al. 2005), but in the same species elsewhere and in Cory's shearwater *Calonectris borealis*, deferring adults segregate isotopically from breeders, indicating differences in their foraging niche (Campioni et al. 2015). Some of the most compelling evidence for spatial segregation based on breeding status during the breeding season is for biennial breeders such as the wandering albatross *Diomedea exulans* and grey-headed albatross *Thalassarche chrysostoma*, in which a proportion of individuals spend the sabbatical period entirely at sea, thousands of kilometres from the colony (Weimerskirch et al. 2015, Clay et al. 2016).

At the end of the breeding season, timing of departure from breeding colonies is strongly dependent on breeding status, with failed and deferred breeders typically leaving significantly earlier than successful breeders (Phillips et al. 2005, 2007, Bogdanova et al. 2011, Hedd et al. 2012, Catry et al. 2013a). Carry-over effects of breeding status on migration may persist into the nonbreeding period, with evidence that failed breeders arrive at wintering grounds early and depart the wintering grounds later or earlier, depending on the study species (Phillips et al. 2005, Catry et al. 2013a, Bogdanova et al. 2017). There may also be differences in migration destination; in black-legged kittiwakes *Rissa tridactyla*, failed breeders wintered further from the breeding colony on average than successful breeders (Bogdanova et al.

2011), and evidence from stable isotope analyses suggested that failed wandering albatrosses differed from successful and deferred breeders in terms of distribution in the following winter (Jaeger et al. 2014). Such differences are not always apparent, however, and high overlap of individuals of differing breeding status during the winter has been observed in other studies (Phillips et al. 2005, 2007, Hedd et al. 2012, Clay et al. 2016).

EFFECTS OF AGE

Age-specific foraging and movements

Comparisons of juveniles and adults

A long-standing theory in avian ecology is that juveniles have reduced survival probability because they have a lower foraging proficiency, resulting from a lack of experience or physical ability; this theory is supported by widespread empirical evidence across many avian species (Marchetti & Price 1989, Wunderle 1991). These are topics of particular interest in seabirds because of their slow maturity, which suggests that the development of foraging is complex and requires an extended period of learning. A list of studies that tested for differences in foraging and migration between juveniles, immatures and adult seabirds is provided in Table 1. Early work on seabirds, based primarily on visual observations of feeding individuals or flocks, provided clear evidence that juveniles had lower foraging success than adults (Orians 1969, Dunn 1972, Burger & Gochfeld 1981, Porter & Sealy 1982, Greig et al. 1983, MacLean 1986). Comparisons of multiple age classes showed progressive improvement in performance in the prebreeding years (Orians 1969, Porter & Sealy 1982, MacLean 1986), and more recent studies indicate that foraging effort and skills develop rapidly after fledging (Yoda et al. 2004, Daunt et al. 2007b, Guo et al. 2010, Orgeret et al. 2016); however, the foraging proficiency of juveniles throughout their first winter remains lower than that of adults, linked to a lower survival probability (Daunt et al. 2007b, Orgeret et al. 2016). Indeed, in terms of survival prospects, the critical period is around independence, which, depending on the species, may occur at fledging or be a gradual process as parents progressively reduce post-fledging provisioning rate (Daunt et al. 2007b, Riotte-Lambert & Weimerskirch 2013, Orgeret et al. 2016).

Biologging and biotelemetry have been instrumental in the study of movements during the juvenile phase (Table 1). It has long been apparent from ringing recoveries that juvenile seabirds often disperse long distances and generally have a wider distribution than adults (Weimerskirch et al. 1985), but attachment of loggers to chicks has enabled the critical months after fledging to be investigated in detail. Fledglings typically undertake rapid and large-scale movements in the first few months and (in flying seabirds) appear to target favourable wind patterns, sometimes delaying departure until these become available (Kooyman et al. 1996, Åkesson & Weimerskirch 2005, Trebilco et al. 2008, Alderman et al. 2010, Riotte-Lambert & Weimerskirch 2013, Blanco et al. 2015, de Grissac et al. 2016, Weimerskirch et al. 2016). Such movements can lead to striking segregation from adults in the nonbreeding period (Kooyman et al. 1996, Jorge et al. 2011, Riotte-Lambert & Weimerskirch 2013). However, this is not universal, and the degree of segregation seems largely to stem from among-species variation in adult movements, with the greatest segregation in species where adults stay close to colonies throughout the year (Grémillet et al. 2015, de Grissac et al. 2016). Juveniles often forage in less productive waters than adults, which may be key to explaining their lower survival probability (Thiebot et al. 2013, Gutowsky et al. 2014, Jaeger et al. 2014).

Detailed analyses suggest that it may take juveniles several months to attain the flight ability of adults (Riotte-Lambert & Weimerskirch 2013). In association with this, the structure of their movements also differs markedly from adults, with evidence of longer, more sinuous pathways in juveniles (Péron & Grémillet 2013, Riotte-Lambert & Weimerskirch 2013, Missagia et al. 2015, de Grissac et al. 2016). There is considerable interest in how individuals are able to navigate during this juvenile period (Guilford et al. 2011, Fayet et al. 2015, de Grissac et al. 2016). However, understanding the mechanisms is challenging because of the lack of information on potential cues (ocean features, presence of conspecifics, etc.), but detailed analyses of movements suggest extensive variation among species in the relative importance of inheritance, cultural mechanisms and acquired memory through exploration (Guilford et al. 2011, Péron & Grémillet 2013, de Grissac et al. 2016).

The immaturity period between the juvenile (first winter) phase and adulthood is also a challenge to study. Device deployments are restricted to the few species where immatures can be captured (generally at colonies), as loggers and transmitters deployed on feathers on the last occasion when these birds were accessible on land (at or before fledging) remain secure only until the first moult, and those attached

Table 1. Studies testing for differences in foraging and migration among juveniles (first year, J), immatures (subsequent sub-adult age classes, I) and adult seabirds (A). Ix = inexperienced; Ex = experienced; Y = yes (effect detected); N = no effect

Taxon	Age classes[a]	Nonbreeding season location	Breeding season location	Foraging effort	Foraging success	Dive characteristics	Flight characteristics	Reference
Charadriiformes								
Herring gull *Larus argentatus*	I, A				Y			Greig et al. (1985)
	J, I, A				Y			MacLean (1986)
Lesser black-backed gull *Larus fuscus*	J, I, A	Y	Y					Jorge et al. (2011)
Bonaparte's gull *Chroicocephalus philadelphia*	J, I, A				Y			MacLean (1986)
Ring-billed gull *Larus delawarensis*	J, I, A				Y			MacLean (1986)
Gull species (*Larus* spp.) × 4	J, I, A				Y			Burger & Gochfeld (1981)
Gull spp. × 6	J, I, A				Y			Porter & Sealy (1982)
Auk spp. × 2	J, I, A				Y			Porter & Sealy (1982)
Sandwich tern *Thalasseus sandvicensis*	J, older				Y			Dunn (1972)
Pelecaniformes								
Brown pelican *Pelecanus occidentalis*	J, A[b]				Y			Orians (1969)
Northern gannet *Morus bassanus*	I, A		Y					Votier et al. (2011)
	J, A	N						Grémillet et al. (2015)
Brown booby *Sula leucogaster*	J			Y			Y	Yoda et al. (2004)
Red-footed booby *Sula sula*	J			Y				Guo et al. (2010)
European shag *Phalacrocorax aristotelis*	J, A			Y				Daunt et al. (2007b)
Procellariiformes								
Wandering albatross *Diomedea exulans*	J	Y					Y	Åkesson & Weimerskirch (2005)
	J, I	Y					Y	Weimerskirch et al. (2006)
	J, I, A	Y		Y			Y	Riotte-Lambert & Weimerskirch (2013)
	I, A	Y	Y					Jaeger et al. (2014)
Shy albatross *Thalassarche cauta*	J	Y						Alderman et al. (2010)
Black-footed albatross *Phoebastria nigripes*	J, A	Y						Gutowsky et al. (2014)
Black-browed albatross *Thalassarche melanophris*	I, A	Y					Y	Petersen et al. (2008)
White-capped albatross *Thalassarche steadi*	I, A	Y					Y	Petersen et al. (2008)
Black-browed albatross *Thalassarche melanophris*	I, A	Y						Campioni et al. (2015)
Northern giant petrel *Macronectes halli*	J, A	Y						Trebilco et al. (2008)
Southern giant petrel *Macronectes giganteus*	J, A	Y					Y	Blanco et al. (2015)
	J, A	Y						Trebilco et al. (2008)
Cory's shearwater *Calonectris borealis*	I, A	Y						Campioni et al. (2015)
	Ix, Ex	Y		Y				Missagia et al. (2015)
Manx shearwater *Puffinus puffinus*	I, A		N		Y			Fayet et al. (2015)
Scopoli's shearwater *Calonectris diomedea*	J, A	N						Grémillet et al. (2015)
	J, I, A	N		Y			Y	Péron & Grémillet (2013)
Sooty shearwater species	J, I, A				Y			Porter & Sealy (1982)
Procellariiformes spp. × 9	J, A	Y/N					Y	de Grissac et al. (2016)
Sphenisciformes								
Emperor penguin *Aptenodytes forsteri*	J	Y						Kooyman et al. (1996)
	J	Y						Thiebot et al. (2013)
King penguin *Aptenodytes patagonicus*	J, A					Y		Orgeret et al. (2016)

[a] Studies restricted to juveniles typically compare with adults based on past work/unpublished data. [b] First winter birds defined as immatures

to leg rings require the individual to be recaptured after return to the colony (Daunt et al. 2007b, de Grissac et al. 2016). Tracking has demonstrated that immatures show limited or no segregation from adults during the nonbreeding season until the point when adults return to colonies in preparation for breeding (Petersen et al. 2008, Péron & Grémillet 2013). Older immatures may also associate with colonies and operate as central-place foragers, although trip structure, trip duration and resource use differ from those of breeding adults (Votier et al. 2011, Riotte-Lambert & Weimerskirch 2013, Campioni et al. 2015). However, immatures also undertake prospecting movements, where they visit multiple colonies either during the breeding season or autumn migration, resulting in seasonal segregation from breeding adults from the same site (Votier et al. 2011, Péron & Grémillet 2013). In addition to these spatial differences associated with key age-specific behaviours, immatures exhibit lower foraging efficiency than adults (Fayet et al. 2015), supporting the theory that the acquisition of foraging skills is a lengthy and complex process in seabirds that may in part explain the long immaturity phase.

Adults

An increase in reproductive success with age is widespread among iteroparous breeders (Clutton-Brock 1988, Newton 1989, Forslund & Pärt 1995). One of the principal mechanisms underpinning this pattern is an improvement in foraging performance with age (Curio 1983). Seabirds show marked changes in foraging performance in early life, and for some species, the immature period may be sufficiently long that individuals have reached full foraging capability by the time they recruit into the breeding population (Weimerskirch et al. 2005). Alternatively, individuals may require additional skills or experience to forage successfully both for themselves and their young (Haug et al. 2015).

Despite growing evidence of differences in foraging performance between young and older breeders (Table 2), there have been few definitive studies of the underpinning mechanisms. Young breeders may be less successful at foraging because they are poorer at locating prey, physically less capable (Curio 1983) or because they are showing restraint because of their higher residual reproductive value (Williams 1966). A further challenge is to establish whether individuals improve their foraging performance with age, and if the higher average performance of older age classes is due to differential survival rates of individuals of differing foraging abilities (Smith 1981, Nol & Smith 1987, Reid et al. 2010). Longitudinal studies are therefore essential to establish the relative importance of within-individual improvements and natural selection (Limmer & Becker 2009). In addition, it has proved difficult to tease apart age from experience, since the two are closely correlated (Pärt 1995). Finally, most seabirds breed seasonally, and younger individuals usually breed later in the year and less successfully; as such, intrinsic performance is potentially confounded by a deterioration in environmental conditions later in the season, and experimental approaches are required to tease these processes apart (Daunt et al. 1999, 2007a).

Habitat use and foraging behaviour and efficiency may vary among different age classes. Although progressive changes in habitat type with age during the nonbreeding season have been detected using stable isotope analyses (Jaeger et al. 2014), in another recent study, there were no significant differences in migration destinations or strategies between adult age classes (Pérez et al. 2014). More attention has focussed on age-related foraging performance during the breeding season (Table 2). In line with theory, young breeders often obtain less food than older breeders (Daunt et al. 2007a, Limmer & Becker 2009, Le Vaillant et al. 2013), and their diet may be of lower quality (Navarro et al. 2010), with impacts on chick growth rates and reproductive success (Daunt et al. 2001, Limmer & Becker 2009). Such patterns may result from age-specific differences in foraging efficiency (Daunt et al. 2007a, Limmer & Becker 2009). Older breeders may have greater experience in locating profitable feeding areas, as shown in Cory's shearwater where site fidelity to productive areas was higher in experienced age classes (Haug et al. 2015). Older individuals may also have physical advantages; for example, Le Vaillant et al. (2012, 2013) showed that they dive deeper, experience reduced underwater drag and undertake more prey pursuits than younger breeders. Older breeders may increase foraging effort to maximise chick provisioning rates, in particular when environmental conditions are poor (Daunt et al. 2007a). Alternatively, they may reduce foraging effort, potentially to maximise time spent on other activities such as resting or guarding the young (Weimerskirch et al. 2005, Zimmer et al. 2011, Harris et al. 2014a, Lewis et al. 2015, Le Vaillant et al. 2016). Young individuals may increase foraging effort to compensate for their reduced efficiency; for example, Weimerskirch et al. (2005) showed that younger and older breeders expended similar foraging effort dur-

Table 2. Studies testing for age-specific differences in foraging and migration among adult seabirds. Age classes: young (Y), middle-aged (M), old (O). +: minimum age. Main comparison classed either as young vs. middle-aged (YM) or middle-aged vs. old (MO)

Taxon	Age classes	Ages	Main comparison	Non-breeding location	Breeding location	Timing of foraging	Foraging effort	Foraging success	Dive charac-teristics	Flight charac-teristics	Reference
Charadriiformes											
Common tern *Sterna hirundo*	Y, M	n/a[a]	YM					Y			Limmer & Becker (2009)
Audouin's gull *Larus audouinii*	Y, M	4–11	YM					Y			Navarro et al. (2010)
Brünnich's guillemot *Uria lomvia*	Y, M, O	3–30	MO						N		Elliott et al. (2015)
Pelecaniformes											
European shag	Y, M	2; >2	YM				Y	Y			Daunt et al. (2007a)
Phalacrocorax aristotelis	Y, M, O	2–3; 4–5; 6–7; 8–9; 10+	YM,MO	N							Grist et al. (2014)
	Y, M, O	2–19	YM,MO				N				Lewis et al. (2015)
Imperial shag *Phalacrocorax atriceps*	Y, M	2–3; min 6–7[b]	YM						Y	Y	Harris et al. (2014a)
Procellariiformes											
Wandering albatross	Y, M	6–11; 12–30	YM			Y	Y				Weimerskirch et al. (2005)
Diomedea exulans	Y, M, O	6–48+	MO		Y		Y				Lecomte et al. (2010)
	Y, M, O	3–11; 7–29; >29	YM, MO	Y	Y						Jaeger et al. (2014)
	Y, O	8–16; 25–37	MO		N						Froy et al. (2015)
	Y, M, O	8–35+	MO		N						Froy et al. (2015)
Grey-headed albatross *Thalassarche chrysostoma*	M, O	<28; 35+[c]	MO				Y	Y			Catry et al. (2006)
Cory's shearwater	M, O	13–20; >26	MO				Y				Catry et al. (2011)
Calonectris borealis	Y, M, O	n/a[d]	YM, MO	N							Pérez et al. (2014)
	Y, M	7–14; >20[b]	YM		Y						Haug et al. (2015)
Sphenisciformes											
King penguin	Y, M	5; 8–9	YM						Y		Le Vaillant et al. (2012)
Aptenodytes patagonicus	Y, M	5; 9	YM				Y	Y	Y		Le Vaillant et al. (2013)
	Y, M	4–11	YM				Y				Le Vaillant et al. (2016)
Little penguin *Eudyptula*	Y, M, O	3–4; 5–10; 11–14	YM, MO						Y		Zimmer et al. (2011)
minor	M, O	5–11; 12–18	MO		Y		N	N			Pelletier et al. (2014)

[a]Categorised as new recruit vs. experienced breeder. [b]Categorised as inexperienced vs. experienced. [c]Middle-aged group, lower boundary = minimum 4 yr of breeding experience. [d]Ages not provided

ing daylight, but younger breeders foraged more at night. However, interpretation of foraging effort is challenging in the absence of data on foraging efficiency (requiring data on energy expenditure, mass and quality of prey, etc.), since it is not clear whether increased effort might be a compensation for poor efficiency or, alternatively, if it maximises energy gain when efficiency is high. Further, such patterns are probably context dependent, with age-specific patterns in foraging effort and efficiency likely to be more pronounced during poor environmental conditions (Daunt et al. 2007a).

Considering the opposite end of the breeding lifespan, there is widespread evidence that senescence leads to a decline in breeding success in the oldest age classes (Froy et al. 2013, Nussey et al. 2013). Although the mechanisms underpinning these patterns are poorly understood, the most frequent explanation is a reduction in foraging performance with age due to physiological declines, reducing the resources that can be allocated to reproduction. Accordingly, studies have shown marked differences in the foraging performance of the oldest breeding age classes in comparison with middle-aged birds (Table 2). Catry et al. (2006) showed that old grey-headed albatrosses undertook longer trips and gained less mass than middle-aged birds. Similarly, old male wandering albatrosses undertook longer trips to remote foraging grounds and showed less foraging activity (Lecomte et al. 2010). In little penguins *Eudyptula minor*, there is spatial segregation between old and middle-aged breeders during foraging, and the oldest age classes show reduced diving effort (Zimmer et al. 2011, Pelletier et al. 2014). Differences in effort were also apparent in a study of Cory's shearwaters, where old individuals undertook fewer take-offs and landings (which are energetically expensive) and spent more time resting on the water (Catry et al. 2011).

Some studies have linked differences in activity budgets and foraging patterns between young and old birds to physiological declines (Catry et al. 2011), but others have found no physiological changes and instead interpreted this variation in terms of differences in foraging efficiency (Lecomte et al. 2010, Weimerskirch et al. 2014). However, for reasons discussed above with regard to comparisons between young and old individuals, interpretation of indices of foraging effort is not straightforward in the absence of information on energy gain. Low foraging effort in old birds may indicate poor physical fitness, resulting from physiological senescence, or may be due to high foraging efficiency, linked to experience (Catry et al. 2011, Froy et al. 2015). Furthermore, age-related declines in foraging performance are not universal; foraging behaviour of old Brünnich's guillemots *Uria lomvia* did not differ from younger adults, despite evidence for physiological senescence (Elliott et al. 2015). Age-related effects can also vary with region; in contrast to results from wandering albatrosses tracked in the Indian Ocean (Lecomte et al. 2010), there was very limited evidence for age-related variation in foraging in the same species in the southwest Atlantic, which was attributed to potential differences in oceanographic conditions (Froy et al. 2015). The ability to tease apart the effects of age from those of extrinsic conditions would be enhanced considerably by longitudinal approaches that examine within-individual changes over time (Limmer & Becker 2009, Daunt et al. 2014).

Implications for population dynamics and conservation

Despite limited evidence to date, age-specific variation in foraging and migration is likely to have important effects on individual fitness. In turn, heterogeneity in fitness among age classes will have profound consequences for population dynamics (Caswell 2001). One important mechanism underpinning these links is the interaction with extrinsic effects, whereby very young or very old individuals may be disproportionately impacted by poor environmental conditions because of lower foraging efficiency (Sydeman et al. 1991). These differences may arise from age-specific variation in susceptibility, or differences in distribution or scheduling of migration of very young or old individuals, leading to heterogeneity in environments experienced. A key factor in quantifying effects on population dynamics is the extent to which age-related variation in foraging and migration is due to ageing effects (longitudinal changes in individuals), or progressive appearance and disappearance of different phenotypes in the population (Limmer & Becker 2009, Reid et al. 2010). Long-term deployments of loggers provide opportunities to distinguish these possibilities (Daunt et al. 2014). Effects of ageing and its interaction with the environment may have important implications for conservation. Age-specific variation in migration destinations could lead to differential exposure to anthropogenic effects such as pollution or fisheries. Equally, marine protection could benefit some age classes more than others. Conservation and management initiatives could potentially target those individuals that make the highest contribution to population growth rate (Moreno 2003).

EFFECTS OF SEX

General patterns and drivers

Sexual segregation of male and female birds during foraging and migration is widespread and occurs at a range of temporal and spatial scales (Catry et al. 2005). One of the earliest studies highlighting sexual segregation in seabirds was on the wandering albatross, based on at-sea distributions of birds sexed by plumage (Weimerskirch & Jouventin 1987); this finding was later confirmed using satellite-telemetry (Prince et al. 1992, Weimerskirch et al. 1993). Sexual segregation can also involve a preference by one sex for a particular microhabitat (Table 3). In many bird families, males winter closer and return sooner to the breeding grounds than females (Cristol et al. 1999, Catry et al. 2005). An extensive, but non-exhaustive review of the recent literature on sex differences in foraging and migration since the review by Phillips et al. (2011) is provided in Table 3. Note that due to the nature of the literature search (where sex, seabirds, foraging or migration were included in the search topic in Web of Science), there may be a bias towards those studies that found positive sex differences.

Male and female seabirds may differ in scheduling of migration. Female black-browed albatrosses began migration 1 to 2 wk earlier than males and wintered further north (Phillips et al. 2005). The same pattern appears to be consistent across years in brown skuas *Stercorarius antarcticus* (Carneiro et al. 2016). In 3 species of crested penguins *Eudyptes* sp., males began migrating back to the breeding colonies earlier than females (Thiebot et al. 2014b). Recent technological advances have facilitated similar studies on smaller seabirds, which usually show a lower degree of sexual size dimorphism or are monomorphic (Table 3).

There are within-pair effects that appear to be unrelated to sex; for example if there is assortative mating of partners with similar strategies according to arrival dates. In the Scopoli's shearwater *Calonectris diomedea*, pair members do not migrate together but spend a similar number of days travelling to and from similar (but not identical) terminal nonbreeding areas (Müller et al. 2015). This was attributed to shared genes, given that pairs breeding in close proximity within the same colony (which were presumed to be more closely-related) also appeared to have similar migration strategies. In addition, paired Kerguelen shags showed some similarity in distribution and behaviour (Camprasse et al. 2017c, this Theme Section). Further, there was pair-wise segregation in wintering niche (spatial and isotopic) in the southern rockhopper penguin *Eudyptes chrysocome* but no clear sexual segregation (Thiebot et al. 2015).

The general consensus is that sexual segregation arises either from social dominance and competitive exclusion by the dominant (often larger) sex, or by habitat or niche specialization due to differences in morphology or reproductive role (Peters & Grubb 1983). Social dominance and competitive exclusion are particularly prevalent in dimorphic species where one sex has an obvious physical advantage, but there is increasing evidence for sex differences in monomorphic species as well (Lewis et al. 2002, Pinet et al. 2012, Hedd et al. 2014). A classic example of social dominance is where larger, male giant petrels *Macronectes* spp. dominate scavenging opportunities at seal and penguin carcasses on land, where interference competition clearly occurs, forcing females to primarily forage at sea (González-Solís et al. 2000). In contrast, male and female black-browed and grey-headed albatrosses are highly segregated during incubation but not during brood-guard or post-chick rearing; given that there were sex-specific differences in flight performance but no obvious role of competitive exclusion by the larger males, the seasonal segregation was attributed to niche divergence (Phillips et al. 2004).

In a recent review exploring the potential drivers or correlates of sexual segregation, stable isotope ratios rarely differed between males and females in monomorphic species, implying a link between sexual size dimorphism and segregation in diet or distribution (Phillips et al. 2011). Also, differences in δ^{13}C (reflecting carbon source) in albatrosses in the Southern Ocean suggested the underlying mechanism was related to habitat specialization, whereas in other size-dimorphic species (both male- and female-biased), sex differences were more commonly in δ^{15}N than δ^{13}C, which is more consistent with size-mediated competitive exclusion or dietary specialization. Mancini et al. (2013) found no correlation between indices of sexual size dimorphism and differences in mean δ^{15}N or δ^{13}C values in males and females for 6 tropical and 5 polar seabird species, yet their review indicated that 70 % of studies on dimorphic seabird species from temperate and polar regions showed some degree of trophic or spatial segregation between sexes, compared to only 20 % of studies on dimorphic species in the tropics. Therefore, sexual size dimorphism appears to facilitate trophic or spatial segregation, particularly in high latitude seabirds (potentially related to more intense competition for resources during the shorter breeding season); however, even in those re-

Table 3 (this and the next page). Studies testing for sex differences in foraging and migration strategies in seabirds since 2011. Dimorphism index = (mean male mass – mean female mass)/(mean male mass + mean female mass), where positive values indicate sexual size dimorphism (SSD), and negative values indicate reverse sexual size dimorphism (RSD). Diet (trophic level)

Taxon	Mean adult mass (kg) of males (females)[a]	Dimorphism index	Wintering location	Timing of migration	Foraging location
Charadriiformes					
Brown skua *Stercorarius antarcticus*	1.765 (1.973) [17]	−0.056	N	Y	
	1.765 (1.973) [17]	−0.056			N
	1.765 (1.973) [17]	−0.056	N	Y	
Audouin's gull *Larus audouinii*	0.580 (0.492) [18]	0.082			Y*
Lesser black-backed gull *Larus fuscus*	0.941 (0.776)	0.096			Y
Black-legged kittiwake *Rissa tridactyla*	0.400 (0.400) [7]	0.000	Y	N	
Brünnich's guillemot *Uria lomvia*	0.990 (1.000) [7]	−0.005			
Atlantic puffin *Fratercula arctica*	0.480 (0.510) [7]	−0.030	Y		
Pelecaniformes					
Christmas Island frigatebird *Fregata andrewsi*	1.400 (1.550) [7]	−0.051			Y**, Y*
Australasian gannet *Morus serrator*	2.600 (2.520) [12]	0.016			N
	2.510 (2.690)	−0.035			Y
	2.600 (2.520) [12]	0.016			
Northern gannet *Morus bassanus*	2.956 (3.209)	−0.041	N		Y*
	2.930 (3.070) [7]	−0.023	N	Y	
	2.810 (3.021)	−0.036			Y
Cape gannet *Morus capensis*	2.705 (2.715) [13]	−0.002			
Masked booby *Sula dactylatra*	2.059 (2.470)	−0.091			
Imperial shag *Phalacrocorax atriceps*	2.810 (2.210)	0.120			Y
	2.285 (1.929) [14]	0.084			Y
	2.285 (1.929)	0.084			
	2.810 (2.210) [15]	0.120			
	2.285 (1.929) [14]	0.084			Y
South Georgia shag *Phalacrocorax georgianus*	2.600 (2.160)	0.092			
Kerguelen shag, *Phalacrocorax verrucosus*	2.429 (2.133)	0.065			N
European shag *Phalacrocorax aristotelis*	1.928 (1.636) [16]	0.082	N		
	1.940 (1.600) [7]	0.096			Y
	1.928 (1.636)	0.082			
Procellariiformes					
Wandering albatross *Diomedea exulans*	9.768 (7.686) [6]	0.119			
	9.768 (7.686) [6]	0.119	Y		
	9.768 (7.686) [6]	0.119			Y
	9.768 (7.686) [6]	0.119			
	9.768 (7.686) [6]	0.119	Y		Y
	9.768 (7.686) [6]	0.119	Y		
	9.768 (7.686) [6]	0.119			Y
	9.768 (7.686) [6]	0.119			Y
Black-browed albatross *Thalassarche melanophris*	3.650 (2.970)	0.103			Y
Southern giant petrel *Macronectes giganteus*	5.190 (3.940) [7]	0.137	Y		Y
Northern giant petrel *Macronectes halli*	5.000 (3.800) [7]	0.136	Y		Y
Barau's petrel *Pterodroma baraui*	0.380 (0.380)	0.000			Y*
Scopoli's shearwater *Calonectris diomedea*	0.676 (0.569) [8]	0.086	Y	Y	
	0.676 (0.569)	0.086	Y		
Cory's shearwater *Calonectris borealis*	0.880 (0.810) [9]	0.041	Y		
	0.880 (0.810) [9]	0.041	Y		
Streaked shearwater *Calonectris leucomelas*	0.549 (0.482) [10]	0.065			Y
	0.549 (0.482) [10]	0.065		Y	
Sooty shearwaters *Ardenna grisea*	0.897 (0.881)	0.009	N		Y*
Balearic shearwater *Puffinus mauretanicus*	0.509 (0.495) [11]	0.014			N
Sphenisciformes					
King penguin *Aptenodytes patagonicus*	13.981 (12.782)	0.045			
Adélie penguin *Pygoscelis adeliae*	5.350 (4.740) [1]	0.060			
Chinstrap penguin *Pygoscelis antarctica*	4.980 (4.470) [1]	0.054			
Gentoo penguin *Pygoscelis papua*	5.500 (5.060) [1]	0.042			
	5.500 (5.060) [1]	0.042			N
Southern rockhopper penguin *Eudyptes c. chrysocome*	3.917 (3.869)	0.006			Y
	3.917 (3.869) [2]	0.006	N	Y	
	3.917 (3.869) [2]	0.006			Y
Eastern rockhopper penguin *Eudyptes chrysocome filholi*	3.050 (2.980) [3]	0.012		Y	
Northern rockhopper penguin *Eudyptes chrysocome moseleyi*	2.960 (3.120) [1]	−0.026			
	2.960 (3.120) [1]	−0.026		Y	
Macaroni penguin *Eudyptes chrysolophus*	4.650 (4.890) [1]	−0.025		Y	
	4.650 (4.890) [1]	−0.025	Y	Y	
African penguin *Spheniscus demersus*	3.452 (2.996)	0.071			Y**
Magellanic penguin *Spheniscus magellanicus*	3.800 (3.000)	0.118			
	4.490 (3.709) [4]	0.095			
	4.490 (3.709) [4]	0.095			N
Humboldt penguin *Spheniscus humboldti*	4.100 (3.200)	0.123			
Little penguin *Eudyptula minor*	1.172 (1.048) [1]	0.056			N
	1.247 (1.119) [5]	0.054			

[a] Mean adult body mass was taken from the reference in the final column (if available); otherwise, it was extracted from the following sources: [1]Borboroglu & Boersma (2015), [2]Ludynia et al. (2013), [3]J.B. Thiebot pers. comm., [4]Forero et al. (2001), [5]Salton et al. (2015), [6]Tickell (1968), [7]Schreiber & Burger (2002), [8]Müller et al. (2015), [9]Ramos et al. (2009), [10]Ochi et al.

based on $\delta^{15}N$, unless indicated otherwise by '~' representing conventional diet analysis. Diet (carbon source) based on $\delta^{13}C$. BR = breeding season; NB = nonbreeding season; NB* = pre-laying. Asterisks after (Y) indicate that sex specific differences only occurred (*) during certain periods of the reproductive stage, (**) in certain years, (***) in some tissues (blood, bones or feathers)

Timing of foraging	Diving	Flight characteristics	Diet (trophic level)	Diet (carbon source)	Breeding stage	No. years in study	Reference
					NB	2	Carneiro et al. (2016)
					BR	1	Carneiro et al. (2014)
		Y			NB	3	Krietsch et al. (2017), this Theme Section
			N	N	BR	1	García-Tarrasón et al. (2015)
					BR	4	Camphuysen et al. (2015)
					NB	1	Bogdanova et al. (2011)
Y	Y*				BR	1	Elliott & Gaston (2015)
					NB	7	Fayet et al. (2016)
					BR	2	Hennicke et al. (2015)
	N	N			BR	3	Machovsky-Capuska et al. (2014)
					BR	1	Wells et al. (2016)
			Y~		BR	3	Machovsky-Capuska et al. (2016)
			Y	Y	NB, BR	3	Stauss et al. (2012)
					NB	2	Fifield et al. (2014)
	Y			Y	BR	3	Cleasby et al. (2015)
Y					BR	2	Rishworth et al. (2014b)
	Y	Y			BR	1	Sommerfeld et al. (2013)
	Y**				BR	3	Quillfeldt et al. (2011)
N	Y	N			BR	1	Quintana et al. (2011)
Y*					NB, BR	1	Harris et al. (2013)
			Y	Y	NB, BR	3	Michalik et al. (2013)
					BR	4	Harris et al. (2014b)
	Y				BR	3	Ratcliffe et al. (2013)
	N		N	N	BR	2	Camprasse et al. (2017a)
					NB	3	Grist et al. (2014)
					BR	3	Soanes et al. (2014)
	Y*				NB, BR	3	Lewis et al. (2015)
			N	Y***	NB, BR	1	Çeia et al. (2012)
					NB	1	Åkesson & Weimerskirch (2014)
					BR	1	Carravieri et al. (2014)
			Y	Y	NB, BR	1	Jaeger et al. (2014)
			Y	Y	NB, BR	24	Weimerskirch et al. (2014)
					NB	15	Weimerskirch et al. (2015)
					BR	6	Cornioley et al. (2016)
					BR	22	Jiménez et al. (2016)
					BR	1	Patrick et al. (2014)
					NB, BR	1	Thiers et al. (2014)
					NB, BR	1	Thiers et al. (2014)
		Y			NB*, BR	3	Pinet et al. (2012)
					NB	3	Müller et al. (2014)
					NB	3	Müller et al. (2015)
					NB	6	Pérez et al. (2014)
					NB	3	Pérez et al. (2016)
					NB*, BR	1	Yamamoto et al. (2011)
					NB	5	Yamamoto et al. (2014)
					NB, BR	1	Hedd et al. (2014)
					BR	4	Meier et al. (2015)
	Y		Y	N	BR	1	Le Vaillant et al. (2013)
			N	N	NB*	3	Gorman et al. (2014)
			Y	N	NB*	3	Gorman et al. (2014)
			Y	N	NB*	3	Gorman et al. (2014)
	N		Y	N	BR	1	Camprasse et al. (2017b), this Theme Section
			Y		BR	1	Ludynia et al. (2013)
			N	N	NB	1	Thiebot et al. (2015)
	Y		Y	Y	BR	3	Rosciano et al. (2016)
					NB	2	Thiebot et al. (2014b)
			Y*	Y*	BR	1	Booth & McQuaid (2013)
					NB	2	Thiebot et al. (2014b)
					NB	2	Thiebot et al. (2014b)
			N	N	NB		Thiebot et al. (2014a)
	Y				BR	2	Pichegru et al. (2013)
	Y				BR	1	Rey et al. (2013)
			N	Y***	NB	1	Silva et al. (2014)
	N		N	N	BR	3	Rosciano et al. (2016)
	Y				BR	1	Rey et al. (2013)
	N		N	N	BR	1	Pelletier et al. (2014)
			N Y~	Y**	BR	9, 17	Chiaradia et al. (2016)

(2010), [11]Genovart et al. (2003), [12]G. E. Machovsky-Capuska pers. comm., [13]Rishworth et al. (2014a), [14]Harris et al. (2013), [15]Quillfeldt et al. (2011), [16]Lewis et al. (2015), [17]Phillips et al. (2002), [18]Ruiz et al. (1998)

gions, this pattern is not ubiquitous (Phillips et al. 2007, Young et al. 2010, Mancini et al. 2013) (Table 3).

Sexes may also segregate by exploiting prey at different depths, as shown in early studies on cormorants or shags *Phalacrocorax* spp., in which males made deeper and longer dives than females (Wanless et al. 1995, Kato et al. 2000). More recently, Quintana et al. (2011) used GPS and dive recorders simultaneously and found that female imperial shags *Phalacrocorax atriceps* foraged in shallow coastal waters, whereas males preferred deeper offshore waters. The authors suggested that this finding reflected the preference by each sex for foraging at depths that maximised their respective foraging efficiencies. In line with this hypothesis, sex differences in foraging behaviour and dive depths in northern gannets *Morus bassanus* appear to indicate sex-specific habitat segregation, but in this case, males foraged mostly in mixed, shallow coastal waters and females in stratified, deeper offshore waters (Lewis et al. 2002, Cleasby et al. 2015).

The sexes may also segregate temporally by undertaking foraging trips at different times of the day. In sexually dimorphic cormorants, males preferentially forage in the afternoon (Wanless et al. 1995, Kato et al. 2000, Harris et al. 2013). Links between time of day and foraging patterns are also evident in monomorphic species, including the Brünnich's guillemot *Uria lomvia*, which exhibits strong sex-specific diurnal schedules, with one sex foraging mostly at night and the other mostly at midday (Jones et al. 2002, Paredes et al. 2008, Elliott et al. 2010). Diurnal patterns of foraging in this species also resulted in spatial segregation, as males (which mostly forage at night) made shallower dives than females (in the late afternoon), presumably because males specialize on shallow prey normally found at night (Elliott & Gaston 2015).

As with effects of age, the effects of sex may be apparent only in some years. Sex differences in foraging location and diving behaviour were detected in one year in the sexually dimorphic Japanese cormorant, *Phalacrocorax capillatus*, but not in the following year when food was abundant, suggesting that segregation is more likely during intense intraspecific competition (Ishikawa & Watanuki 2002). More recently, Quillfeldt et al. (2011) showed in a multi-year study during chick rearing that larger male imperial shags dived deeper than females in some years but not others, though the mechanism was unclear.

Similarly, sex-specific foraging differences may vary with environmental conditions within years. Smaller female European shags, *Phalacrocorax aristotelis*, foraged for longer than males during strong onshore winds, but not at lower wind speeds (Lewis et al. 2015). In contrast, there was no evidence that tide or weather influenced foraging behaviour of either sex in the Brünnich's guillemot (Elliott & Gaston 2015). In other taxa, sexual segregation appears to be related more obviously to sex differences in reproductive roles (see following section).

Interactions between sex and stage of the annual cycle

Although males and females share their breeding duties to a similar extent in most seabirds, intersexual competition for food, differences in energetic or nutritional requirements, or different parental roles can lead to sexual differences in foraging behaviour during specific periods. Sex differences in stable isotope ratios are more likely during the pre-laying and later breeding periods than during the nonbreeding period (Phillips et al. 2011). Tracking studies also show that the sexes may segregate by location (Stauss et al. 2012) or time of day (Harris et al. 2013) during the breeding but not the nonbreeding season. These results imply that sex differences in foraging strategies are more likely when males and females have different reproductive roles and when potential competition and partitioning of resources between sexes are probably higher (but see Silva et al. 2014).

During the pre-laying period, males and females frequently differ in their diet or distribution, as indicated, for example, by sexual differences in isotope ratios (Phillips et al. 2011). Males (which usually perform a greater role in nest defence) often forage more locally and visit the colony more frequently, whereas females often go on a pre-laying exodus, engaging in longer foraging trips in more productive waters to meet energetic or other nutritional requirements for the clutch (Lewis et al. 2002, Yamamoto et al. 2011, Hedd et al. 2014, Quillfeldt et al. 2014, Pistorius et al. 2015). Indeed, changing energetic or nutritional requirements during the breeding cycle would explain why sex differences are apparent only at certain stages in monomorphic species such as Barau's petrel *Pterodroma baraui* (Pinet et al. 2012) or why late-incubation trips by male southern rockhopper penguins are longer, as they do all the early chick-guarding (Ludynia et al. 2013). In theory, such differences seem less likely if the male courtship feeds the female, potentially contributing substantially to clutch formation as in terns, gulls and skuas (Becker

& Ludwigs 2004), but this does not seem to be the case in the brown skua, as a higher proportion of females than males undertake a pre-laying exodus (Carneiro et al. 2016). In contrast, in some species (including gadfly petrels), males perform longer foraging trips than females, perhaps to prepare themselves for the typically-long fasting bout post-laying (Pinet et al. 2011, Rayner et al. 2012), and in the black-legged kittiwake, males are more likely than females to perform a pre-laying excursion, although the reason for this is unclear (Bogdanova et al. 2011).

Sexual differences in foraging patterns may extend into the incubation period, possibly due to the requirement for females to replenish the energy, essential nutrients or minerals spent in clutch formation. Hence, females may perform particularly long or distant foraging trips after laying (Lewis et al. 2002, Phillips et al. 2004). The emperor penguin *Aptenodytes forsteri* is an extreme example; the male incubates the egg until hatching (60–70 d), while the female forages to recover from egg formation and to gather food to feed the chick just after hatching (Williams 1995). After hatching in some penguins and alcids, males brood the chick while the females forage to provide meals for the offspring (Clarke et al. 1998, Tremblay & Cherel 2003, Paredes et al. 2006, Green et al. 2009); the reverse occurs in some terns (Becker & Ludwigs 2004).

During chick-rearing, some species show sexual differences in chick provisioning rates. Usually, these differences involve more frequent visits or larger meals from the male (Catry et al. 2005, Thaxter et al. 2009, Welcker et al. 2009), perhaps reflecting deferred costs of egg production in females or sex-specific allocation of foraging effort between parents and offspring (Monaghan et al. 1998, Thaxter et al. 2009). In Cape gannets *Morus capensis*, females undertake a greater proportion of long trips than males (Pistorius et al. 2015). In the Manx shearwater *Puffinus puffinus*, only females adopt the dual foraging strategy, whereas males perform short foraging trips and provision chicks at a higher rate (Gray & Hamer 2001). In several alcids, the role of males in provisioning chicks increases during later rearing or in the post-fledging period, when males forage closer to the colony, dive longer and deeper per day and are forced to forage at lower-quality prey patches than females (Harding et al. 2004, Thaxter et al. 2009, Elliott et al. 2010, Burke et al. 2015). Although sex differences usually decrease or disappear after the breeding period, with males and females showing similar distribution and foraging behaviour, in some species, sexual segregation in trophic niches persists year-round (Phillips et al. 2005, 2011). Males and females can differ in moulting strategies (Hunter 1984, Weimerskirch 1991), which in theory might result in different dietary needs or foraging behaviour, but this has not been investigated so far.

Interactions between sex and other factors

Sex-specific patterns of migration and foraging may involve interactions with various other intrinsic factors. For example, trip duration in the common guillemot *Uria aalge* during incubation was longer in low-quality females, i.e. those with consistently lower long-term breeding success (Lewis et al. 2006). There can also be interactions with age; older female king penguins *Aptenodytes patagonicus* conducted shorter trips, dived deeper and performed more prey pursuits during the chick rearing phase and also had higher blood δ^{15}N than younger females (Le Vaillant et al. 2013). As adults, male but not female wandering albatrosses forage progressively farther south with increasing age (Lecomte et al. 2010, Jaeger et al. 2014).

Implications for population dynamics and conservation

If sexual segregation in foraging or migration behaviour has fitness consequences and if such behaviour is heritable, there may be important evolutionary consequences (Grémillet & Charmantier 2010). However, as far as we are aware, no seabird study has determined the heritability of sex-specific foraging and migration strategies. Sexual segregation can have important implications for population dynamics and conservation if there are fitness costs associated with foraging location. One principal mechanism is that segregation leads to differing foraging efficiencies, with demographic consequences (Jaeger et al. 2014). Sex-specific variation in demographic rates could also arise from differential association with anthropogenic factors that have impacts on survival rates. Sexual segregation of wandering and other albatrosses affects the relative vulnerability of males and females to bycatch by pelagic longline fleets (Bugoni et al. 2011, Jiménez et al. 2014, Gianuca et al. 2017). Sexual segregation can also affect the relative risk of exposure to organic contaminants (Carravieri et al. 2014).

INDIVIDUAL SPECIALIZATION

Patterns of individual specialization: incidence and types

Individual specialization is generally regarded as the variation among individuals, in terms of distribution, behaviour, diet or other aspects of resource acquisition, that remains after accounting for the group effects outlined above (Bolnick et al. 2003, Dall et al. 2012). Specialization is often used to describe consistency in some aspect of the behaviour of an individual, but there is no consensus as to the minimum period over which that has to be maintained or the extent to which it may just reflect stability in the environment. The advantages and disadvantages of different approaches commonly used to detect and quantify individual specialization using conventional diet, stable isotope or tracking data are reviewed by Carneiro et al. (2017). To illustrate the diversity of research and to explore taxonomic, biogeographic and other patterns, we carried out a non-exhaustive review of studies that tested for individual specialization (Table 4). This expands on a previous review by Ceia & Ramos (2015) and includes studies examining fidelity to foraging sites, staging areas or routes during the breeding or nonbreeding seasons, and consistency in breeding-season trip characteristics, migration schedules, diving patterns and other aspects of at-sea activity, habitat use, diet or trophic level in the short or long term (Table 4).

Prior to the last decade, statistical analyses of characteristics that might reflect individual specialization were rare, although a number of studies documented consistent spatial segregation among individuals that were tracked for a sufficient length of time during the breeding (Irons 1998, Hedd et al. 2001) or nonbreeding seasons (Croxall et al. 2005). For example, in a study on grey-headed albatrosses, all were successful breeders from the same subcolony but showed diverse movement strategies during the 16 mo nonbreeding period, from largely resident in the southwest Atlantic Ocean to repeated use of the southwest Indian Ocean or more distant regions in successive winters (Croxall et al. 2005). As devices have become smaller and cheaper, many more seabird studies have shown that individuals repeatedly use the same foraging areas (i.e. show high site fidelity) in successive trips during the breeding season or in multiple nonbreeding seasons, or show consistency in departure bearing or other trip characteristics (Table 4). High nonbreeding site fidelity at a fine scale has also been determined using colour-ring resightings (Grist et al. 2014). Few studies have examined site fidelity among rather than within breeding seasons (but see Wakefield et al. 2015, Patrick & Weimerskirch 2017). During the nonbreeding season, individuals of most species tracked to date (15 of 20; see Table 4) showed a very high degree of foraging site fidelity at the regional level, with the notable exceptions of a small proportion of Cory's shearwaters, sooty shearwaters *Ardenna grisea*, long-tailed skuas *Stercorarius longicaudus* and 2 species of guillemots (Dias et al. 2011, Hedd et al. 2012, McFarlane Tranquilla et al. 2014, van Bemmelen et al. 2017, this Theme Section).

Site fidelity is usually considered to arise in seabirds either through a 'win-stay, lose-shift' strategy that is optimal if there is high spatio-temporal correlation in resource availability or through the benefit of site familiarity (Irons 1998, Wakefield et al. 2015). The incidence of site fidelity appears to be lower in the breeding than in the nonbreeding season (Table 4), but this is at least partly an issue of spatial scale and accuracy of different tracking devices: GPS loggers or satellite-transmitters for breeding birds and geolocators for nonbreeding birds. In around half of the species tracked in multiple years, site fidelity of nonbreeding birds was much lower at the mesoscale than the regional level, and there was often little or no consistency in the use of staging areas and migration routes (Table 4). Black-browed albatrosses from South Georgia were consistent in the centroid of their terminal wintering area, but not in the use of staging sites (Phillips et al. 2005); Scopoli's shearwaters showed significant repeatability in wintering region and some (but not all) aspects of migration schedule but not in the most westerly longitude reached during the return journey (Müller et al. 2014); long-tailed skuas were generally faithful to staging and wintering area and to migration routes, but as the winter progressed, a small but increasing number of individuals began to deviate from their route in previous years (van Bemmelen et al. 2017). Migration schedules (i.e. timing of departure and return to the colony and timing of major movements during the winter) were usually consistent within individuals across years, having excluded the influence of changes in breeding success or status (see Table 4). Migration timing can be affected by extrinsic factors; relative consistency in date of arrival at the colony among individual Desertas petrels *Pterodroma deserta* was attributed to potential delays because unfavourable winds increased return time from more distant regions or because birds waited for a bright moonlight night before departing (Ramirez et al. 2016).

All studies that tested for individual consistency in foraging behaviour have found evidence for this in terms of diving depth, diving or flight bout duration, proportion of daylight and darkness spent in flight, landing rate, etc. (Table 4). However, this may reflect a positive publication bias. The degree of individual variability can also change seasonally; in the imperial shag, there is an effect of photoperiod (and hence daylight available for foraging) and degree of constraint associated with breeding or moulting, on the relative consistency in the time that foraging begins and ends each day (Harris et al. 2013, 2014b). Results from conventional stomach contents or stable isotope ratios indicate significant consistency within individuals in many species in habitat use, prey type or trophic level in the short or long term (days to weeks, between the breeding and nonbreeding seasons or annual); however, there were exceptions, particularly among the albatrosses and petrels (Table 4).

Drivers of individual specialization: influence of species and sex

Individual specialization in some form has been recorded in all orders of seabirds (Sphenisciformes, Procellariiformes, Pelecaniformes and Charadriiformes) but only half of the families (Spheniscidae, Diomedeidae, Procellariidae, Sulidae, Phlacrocoracidae, Stercorariidae and Laridae, but not Pelecanoididae, Hydrobatidae, Fregatidae, Phaethontidae, Sternidae and Rhynchopidae) (Table 4). This likely reflects a research bias, with fewer studies on tropical seabirds and less tracking of smaller species because of the greater impacts of devices on these birds. The correspondence between the presence or absence of individual specialization and phylogeny or region is therefore unclear; nevertheless, all 10 studies to date that tested for individual specialization in diverse aspects of movement and foraging behaviour of cormorants and shags have found evidence for its existence, suggesting that it is the dominant pattern in those taxa (Table 4).

Several studies have compared the degree of site fidelity or behavioural consistency between males and females, but results do not show a clear pattern. Long-term consistency in habitat use was greater in male than in female wandering albatrosses, possibly because females shift distribution to the north to reduce competition with males in the nonbreeding period (Ceia et al. 2012). Female imperial shags were less variable in the timing of foraging and other trip characteristics, attributed to the lower costs of foraging in males and hence their greater discretionary time for accommodating the female, which typically takes the first foraging shift each day (Harris et al. 2013, 2014b). In Kerguelen shags *Phalacrocorax verrucosus*, males were less specialized in diving behaviour than females (Camprasse et al. 2017a). Similarly, males showed more variability in dive depths in South Georgia shags *Phalacrocorax georgianus*, possibly because maximum dive depth is more closely correlated with body mass in females (Ratcliffe et al. 2013). Female Audouin's gulls *Larus audouinii* foraged at sea throughout the week, whereas males switched from foraging at sea during weekdays to inland coastal habitats (rice fields) on weekends, when fisheries discards were unavailable (García-Tarrasón et al. 2015). In other studies, there were no differences in behavioural consistency or wintering site fidelity between sexes (Grist et al. 2014, Potier et al. 2015), or there were sex differences in consistency, but the direction depended on the parameter (Müller et al. 2014).

Extrinsic explanations for individual specialization: influence of prey predictability

Individual specialization appears to be widespread in cormorants and shags (Table 4). This seems likely to be related to their exploitation of benthic prey, which may be constrained in terms of seabed habitat. Such habitats contain numerous static features, enabling foraging birds to memorize topographic cues to improve encounter rate. Differing degrees of spatial and temporal predictability of resources might also explain relative fidelity to foraging sites in more pelagic seabirds, as particular areas (shelf, shelf breaks, fronts, etc.) reliably hold more prey resources, and individuals return there in successive trips. Indeed, this was the suggested explanation for consistent differences in trip bearings and repeatability in travel distances of individual northern gannets only at the Bass Rock and not Great Saltee, UK, on the basis that predictability of resources was higher in the North Sea than in the Irish Sea (Hamer et al. 2001). However, specialization does not always relate to resource predictability; black-browed albatross, shy albatross *Thalassarche cauta* and razorbill *Alca torda* were not consistent in site or habitat use although they all fed in neritic waters (Hedd et al. 2001, Granadeiro et al. 2014, Shoji et al. 2016). In addition, although it is intuitive that specialization would be less likely in tropical waters, given the

Table 4 (this and the next 3 pages). Evidence for significant individual specialization in distribution, movements, activity or diet of seabirds. √: significant effect; (√): some evidence but with exceptions; X: study tested explicitly for specialization but found no evidence; W: within breeding season; B: between breeding seasons; N: nonbreeding site; R/S: route or staging area; Dep: at departure; Dur: during; Ret: at return; ST: short-term (days to weeks); LT: between seasons or annual

Species	Breeding colony	Foraging site fidelity within or between breeding seasons	Foraging trip bearing or distance (breeding season)	Fidelity to nonbreeding site, route or staging area[a]
King penguin *Aptenodytes patagonicus*	Falklands	W - X	√	
Macaroni penguin *Eudyptes chrysolophus*	South Georgia			
Southern rockhopper penguin *Eudyptes c. chrysocome*	Falklands			
Adélie penguin *Pygoscelis adeliae*	Syowa Station, Antarctica	W - (√)		
Little penguin *Eudyptula minor*	Penguin Island, Australia			
Yellow-eyed penguin *Megadyptes antipodes*	Oamaru, New Zealand	W - √		
Black-browed albatross *Thalassarche melanophris*	South Georgia			N - √, R/S - X
	Falklands			
	Kerguelen	W - (√), B - (√)	√	
Grey-headed albatross *Thalassarche chrysostoma*	South Georgia			N - √
Shy albatross *Thalassarche cauta*	Tasmania	W - X, B - X	√	
Light-mantled albatross *Phoebetria palpebrata*	South Georgia			
Wandering albatross *Diomedea exulans*	South Georgia			
	Crozet			N - √
White-chinned petrel *Procellaria aequinoctialis*	South Georgia			
Yelkouan shearwater *Puffinus yelkouan*	Malta			N - √
Short-tailed shearwater *Ardenna tenuirostris*	Tasmania			N - √
Sooty shearwater *Ardenna grisea*	Kidney Island (Falklands)			N - (√), R/S - (√)
Streaked shearwater *Calonectris leucomelas*	Sangan, Mikura, Awa Islands, Japan			N - √, R/S - √
Cory's shearwater *Calonectris borealis*	Selvagem Grande (Madeira)			N - (√), R/S - X
	Berlenga (Portugal)			
	Canary Islands	W - √		
Scopoli's shearwater *Calonectris diomedea*	Sicily (Italy)			N - √, R/S - X
Desertas petrel *Pterodroma deserta*	Madeira			N - √
Thin-billed prion *Pachyptila belcheri*	New Island, Falklands			
Broad-billed prion *Pachyptila vittata*	Rangatira, Chatham Islands			
Northern gannet *Morus bassanus*	Bass Rock (UK)	W - √, B - √	√	
	Great Saltee (UK)	W - X	X	
	Grassholm (UK) and Brittany (France)	W - √	√	
	Alderney	W - X	√	
	Various colonies, Canada			N - √
	North Norway	W - X	(√)	

Consistent migration schedule[b]	Consistent activity or diving pattern	Consistent habitat use[c] in short- or long-term	Consistent diet or trophic level[d] in short- or long-term	Reference
				Baylis et al. (2015)
	√	LT - √		Green et al. (2005), Horswill et al. (2016)
		LT - √	LT - √	Dehnhard et al. (2016)
				Watanuki et al. (2003)
	√			Ropert-Coudert et al. (2003)
				Mattern et al. (2007)
Dur - √, Ret - √	√			Phillips et al. (2005), Mackley et al. (2010)
		ST - X	ST - X	Granadeiro et al. (2014)
		ST - √		Patrick & Weimerskirch (2014b, 2017)
	√			Croxall et al. (2005), Mackley et al. (2010)
				Hedd et al. (2001)
	√			Mackley et al. (2010)
	√	ST - √, LT - √	ST - √, LT - X	Mackley et al. (2010), Ceia et al. (2012)
				Weimerskirch et al. (2015)
	√			Mackley et al. (2011)
Dep - √, Dur - √, Ret - √				Raine et al. (2013)
				Yamamoto et al. (2015)
Dep - (√), Dur - (√)				Hedd et al. (2012)
Dep - √, Dur - √				Yamamoto et al. (2014)
Dep - √, Dur - √, Ret - √				Dias et al. (2011), Dias et al. (2013)
		ST - (√)	ST - (√)	Ceia et al. (2014)
				Navarro & González-Solís (2009)
Dep - X, Dur - √, Ret - X				Müller et al. (2014)
Dep - √, Ret - √		LT - √	LT - √	Ramirez et al. (2016)
		ST - √, LT - X	ST - √, LT - X	Quillfeldt et al. (2008)
		LT - X	LT - X	Grecian et al. (2016)
	√	ST- √, LT - √	ST - √, LT- √	Hamer et al. (2001, 2007), Wakefield et al. (2015)
				Hamer et al. (2001)
	√	ST - √	ST - √	Votier et al. (2010), Patrick et al. (2014)
				Soanes et al. (2013)
Dur - √, Ret - √				Fifield et al. (2014)
				Pettex et al. (2012)

(table continued on next 2 pages)

(Table 4 continued)

Species	Breeding colony	Foraging site fidelity within or between breeding seasons	Foraging trip bearing or distance (breeding season)	Fidelity to nonbreeding site, route or staging area[a]
Great cormorant *Phalacrocorax carbo*	Chausey Islands, France	W - √, B - √		
European shag *Phalacrocorax aristotelis*	Isle of May (UK)			
Imperial shag *Phalacrocorax atriceps*	Argentina	W - √	√	
South Georgia shag *Phalacrororax georgianus*	South Georgia			
Kerguelen shag *Phalacrocorax verrucosus*	Kerguelen	W - √	√	
Crozet shags *Phalacrocorax melanogenis*	Possession Island, Crozet			
King cormorant *Phalacrocorax purpurascens*	Macquarie Island			
Pelagic cormorant *Phalacrocorax pelagicus*	Gulf of Alaska	W - √		
Double-crested Cormorant *Phalacrocorax auritus*	Oneida Lake, New York, USA	W - √		
Japanese cormorants *Phalacrocorax capillatus*	Teuri Island, Japan	W - √	√	
Razorbill *Alca torda*	Skomer (UK)	W - X	X	
Atlantic puffin *Fratercula arctica*	Skomer			N - √, R/S - √
Great skua	Bjørnøya			N - √
Stercorarius skua	Shetland, UK	W - √		
Brown skua	South Georgia			
Stercorarius lonnbergi	South Shetland Islands			N - √
South polar skua *Stercorarius maccormicki*	King George Island			N - √
Long-tailed skua *Stercorarius longicaudus*	Sweden, Svalbard, and Greenland			N - (√), R/S - (√)
Lesser black-backed gull *Larus fuscus*	North Norway			N - √
Yellow-legged gull *Larus michahellis*	Gulf of Cadiz, Spain			
Dolphin gull *Leucophaeus scoresbii*	Falkland Islands	W - √		
Black-legged Kittiwake *Rissa tridactyla*	Prince William Sound, Alaska	W - √		
	Pribilof Islands			N - (√), R/S - (√)
Pigeon guillemot *Cepphus columba*	Prince William Sound, Alaska			
Brünnich's guillemot *Uria lomvia*	Various colonies, Canada			N - (√)
	Nunavut, Canada			
Common guillemot	Various colonies, Canada			N - (√)
Uria aalge	Newfoundland, Canada	W - √	√	

[a]Studies only included if 2 or more individuals tracked in multiple years. [b]Where possible, studies were excluded that did not control for differences in breeding success between years. [c]Includes results from tracking and stable isotope studies. [d]Includes conventional diet and stable isotope studies

greater variability and patchiness of resources (Weimerskirch 2007), streaked shearwaters *Calonectris leucomelas*, which migrate to tropical waters, showed a high degree of fidelity to nonbreeding destination and migration route (Yamamoto et al. 2014). Availability and predictability can also vary over time in the same habitats, which might partly explain why the degree of consistency in diet or isotopic niche in the same species can depend on breeding stage and year (Ceia et al. 2014).

Consistent migration schedule[b]	Consistent activity or diving pattern	Consistent habitat use[c] in short- or long-term	Consistent diet or trophic level[d] in short- or long-term	Reference
	√			Grémillet et al. (1999), Potier et al. (2015)
	√			Daunt et al. (2014)
	√			Harris et al. (2013, 2014b)
	√	LT - √	LT - √	Bearhop et al. (2006), Ratcliffe et al. (2013)
	√	ST - √, LT - √	ST - √, LT - √	Bearhop et al. (2006), Camprasse et al. (2017a)
	√			Cook et al. (2006)
	√			Kato et al. (2000)
	√			Kotzerka et al. (2011)
				Coleman et al. (2005)
	√			Ishikawa & Watanuki (2002)
				Shoji et al. (2016)
Dur - √				Guilford et al. (2011), Fayet et al. (2016)
			ST - √, LT - √	Magnusdottir et al. (2012) Votier et al. (2004)
Dep - √, Ret - √	√	LT - √	LT - √	Phillips et al. (2007) Krietsch et al. (2017), this Theme Section
				Kopp et al. (2011)
				van Bemmelen et al. (2017), this Theme Section
				Helberg et al. (2009)
		√		Navarro et al. (2017), this Theme Section
			ST - √	Masello et al. (2013)
				Irons (1998)
				Orben et al. (2015b)
			LT - √	Golet et al. (2000)
Dep - X, Ret - X	√			McFarlane Tranquilla et al. (2014)
	√	ST - √	ST - √, LT - √	Woo et al. (2008), Elliott et al. (2009)
Dep - (√), Ret - √	√			McFarlane Tranquilla et al. (2014)
				Regular et al. (2013)

Development of individual specialization: the role of learning

Individual specialization is expected to offer a selective advantage where resources are to some extent predictable; under these circumstances, birds can increase foraging efficiency by reducing search times or develop proficiency in locating or handling particular types of prey. Specialization, particularly site fidelity, likely develops largely from experience gained (learned) when seabirds are immature. During these formative years, individuals show high variability in dispersal and movement patterns (Thiers et al. 2014, de Grissac et al. 2016), in which the roles of genetics and experience are not well understood. Whether individual wandering albatrosses are partial or full migrants does not appear to be heritable (Weimerskirch et al. 2015). However, because fledgling seabirds migrate for the first time without parents, initial dispersal direction — and potentially the distance travelled — may be heritable as in other birds (Piersma et al. 2005).

Although intrinsic factors will also play a role, in the absence of a central-place foraging constraint, the subsequent timing of movements and areas visited by immatures is probably dictated to a considerable extent by local conditions (including weather) and the availability, patchiness and predictability of prey (Mueller & Fagan 2008). Individual migration pattern probably becomes fixed according to experience (Guilford et al. 2011, Péron & Grémillet 2013, de Grissac et al. 2016). There is no effect of age *per se* on the nonbreeding strategy in the wandering albatross (Weimerskirch et al. 2015) nor on the likelihood of an adult shifting its winter destination in the Cory's shearwater (Dias et al. 2011). Indeed, Cory's shearwaters may switch back and forth between different regions (Dias et al. 2013), and long-tailed skuas may switch between different routes in successive migrations (van Bemmelen et al. 2017), indicating that these changes are not the result of accidental displacement by severe weather conditions. Hence, knowledge of the previous experience of the individual is key to understanding the navigation process, and the development of individual specialization in movements in general.

Learning may also be responsible for development of individual specializations in diving behaviour, particularly as benthic feeders such as shags and cormorants would benefit from local knowledge of bottom topography and currents (Table 4). Learning could also explain consistency in at-sea activity patterns (including in flights and landings), trophic level or diet, even in pelagic species, as individuals may specialize in locating or handling particular types of prey (Table 4). Indeed, learning seems the likeliest explanation for dietary specializations in highly opportunistic species with diverse diets, such as great skua *Stercorarius skua*, brown skua and dolphin gull *Leucophaeus scoresbii*, which presumably need to develop particular skills to successfully pursue different foraging modes, whether that is kleptoparasitism, predation of selected species or scavenging, etc. (Votier et al. 2004, Phillips et al. 2007, Masello et al. 2013).

Implications of individual specialization

Links to physiology and life-history

Many studies have related differences between individuals in distribution, timing, foraging success, etc. to body condition, past experience or future breeding performance (Bogdanova et al. 2011, Orben et al. 2015a). By comparison, only a few studies have examined the physiological correlates of specialization or the energetic or life-history consequences. Specialization should in theory be advantageous if an individual has fixed on a particular strategy that is more profitable than the alternatives. Positive evidence for an advantage of specialization is particularly apparent among predatory seabirds. Specialist western gulls *Larus occidentalis* that maintained feeding territories within colonies of other seabirds had higher reproductive success and similar or higher survival rates compared to non-specialists (Spear 1993). Pairs of slaty-backed gulls *Larus schistisagus* that delivered more depredated seabird chicks raised more fledglings, and their chicks grew faster than those of pairs that mainly delivered fish, possibly because of the differences in energy value of the meals (Watanuki 1992). Individual specialization has also been linked to potential fitness advantages in other seabirds. There were significant relationships between repeatability in some dive characteristics of great cormorants *Phalacrocorax carbo* and foraging efficiency (Potier et al. 2015). In the black-browed albatross, foraging trip characteristics were less variable in successful than unsuccessful male breeders and in females that were more faithful to foraging sites but not necessarily to habitat (water depth) had higher reproductive success (Patrick & Weimerskirch 2014a, 2017). Pairs of pigeon guillemots *Cepphus columba* that were dietary specialists fledged more chicks than the diet generalists, apparently because they delivered larger individual prey items (Golet et al. 2000).

Individual specialization has been linked to carry-over effects in a number of studies. Individual European shags showed consistent differences in daily foraging times during winter, and the shorter foraging times were associated with earlier and more successful breeding, demonstrating a clear carry-over effect (Daunt et al. 2014). In this context, it is important to note that carry-over effects may be evident in only a proportion of colonies (Bogdanova et al. 2017); it is also often hard to exclude the possibility that a cross-seasonal correlation is unrelated to specialization and instead due to stable within-individual performance, i.e.

consistently good or poor performance or decision-making year-round (Harrison et al. 2011). The mechanisms underlying carry-over effects are not always clear, but it seems that stress (reflected in feather corticosterone levels) affects energy or nutrient acquisition and hence physiological condition, which has impacts on behaviour and performance in the subsequent season (Young et al. 2017, this Theme Section).

Intuitively, consequences of individual specializations might be most obvious when examining effects of migration distance, as those individuals that travel the furthest incur greater energy or time costs, reducing the time available for feeding and resting en route or delaying the return to the colony. Late return has repercussions for nest defence, mating opportunities or re-establishment of the pair bonds and, ultimately, timing of laying, which is typically closely correlated with breeding performance. Yet, 2 studies did not find evidence of a substantial energetic advantage for individuals that remained closer to the colony, having accounted for flight time to and within alternative wintering areas and for thermoregulatory costs associated with resting on the water (Garthe et al. 2012, Fort et al. 2013). Similarly, Ramirez et al. (2016) did not detect differences in the level of individual repeatability in at-sea activity patterns of Desertas petrels that migrated to different wintering areas. In theory, the choice of a short- or long-distance migration strategy may be neutral, reflect individual optima or vary in terms of advantages or disadvantages for survival or reproduction depending on the year. If so, individual specialization in the form of high nonbreeding-site fidelity may not affect subsequent body condition, survival or fitness unless there is a major deterioration in the environment.

Various studies have not detected any convincing selective advantage of individual specialization. Northern gannets that associated consistently with fishing vessels were not in better body condition than those which avoided vessels (Patrick et al. 2015); short- and long-term consistency in trophic level or carbon source was not related to body mass index in wandering albatrosses (Ceia et al. 2012); there were no effects of foraging area or site fidelity on chick feeding frequency or meal mass in Adélie penguins *Pygoscelis adeliae* (Watanuki et al. 2003) nor on breeding success in European shags (Daunt et al. 2014); although Brünnich's guillemots that were generalists tended to deliver slightly more energy per day, specialists and generalists did not differ in any other aspect of fitness (Woo et al. 2008); great skuas that were bird specialists consistently laid earlier, had larger clutch volumes and improved chick condition but did not have higher breeding success or survival than specialist fish predators (Votier et al. 2004); lastly, consistency within or among years in trip or dive characteristics did not influence body condition in northern gannets (Wakefield et al. 2015). The lack of a clear fitness benefit in many cases may be related to changes over time in the predictability of resources, which could fluctuate within and between breeding seasons. Specialists may be at an advantage when predictability is high in certain areas, whereas generalists likely benefit when resource availability is less predictable and more heterogeneous.

Links to population dynamics and conservation

An understanding of variation both among and within individuals allows the characterization of populations and has implications for their resilience in the face of environmental change (Nussey et al. 2007). Unless there is time for selection to act, populations that lack variability and individuals that lack plasticity in movements and foraging behaviour are

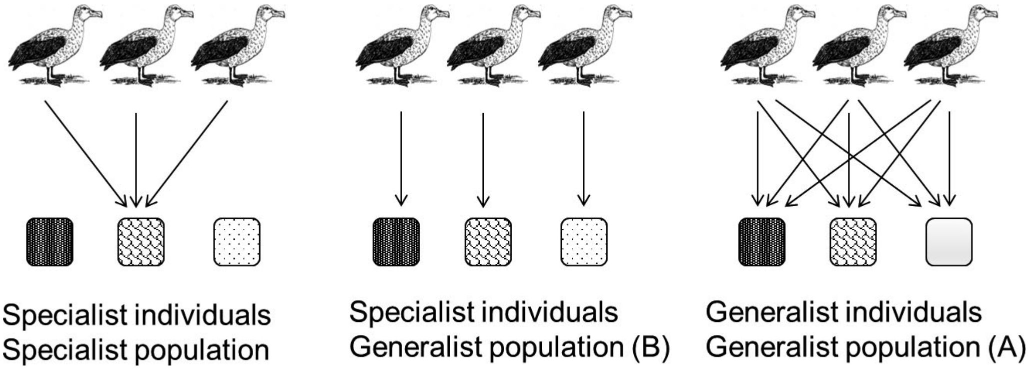

Fig. 1. Use of different resources or habitats (represented by different shading) for more or less generalist or specialist populations

likely to be at a considerable disadvantage. This is illustrated by the schematic based on Bolnick et al. (2003), which illustrates different hypothetical situations of resource (or habitat) use in Fig. 1: (1) generalist individuals from a generalist population all target multiple alternative resources (type A); (2) specialist individuals from a generalist population consistently target one of multiple alternative resources (type B); and (3) specialist individuals from a specialist population all consistently target the same resource. The implications are that in the absence of a change in behaviour, the loss or deterioration of one resource or habitat would be catastrophic for the specialist population (and for the specialists in the generalist population that targeted that resource) but of less consequence for the generalists, depending on density-dependent competition for the resources that remain. This can have implications in the design of marine protected areas, since population-based approaches may not identify important areas used by a relatively low proportion of specialized individuals, or these areas may not be prioritized for management. However, those areas, and the specialists that use them, may buffer population-level impacts of a deterioration in habitats used by the majority of birds. The same principle applies to a localized increase in pollutants, competition with fisheries or fisheries bycatch, etc. Indeed, many threats show extensive spatial heterogeneity, such as fisheries bycatch risk (Phillips et al. 2009a, Thiers et al. 2014) and exposure to pollutants, including plastics, mercury, persistent organic pollutants and hydrocarbons (Young et al. 2009, Montevecchi et al. 2012, Leat et al. 2013, Tartu et al. 2013).

The importance of assessing the extent and duration of specialization can be illustrated by considering exposure to fisheries. In the Falklands, there were significant differences between 2 study colonies of black-browed albatrosses in the degree of bird association with vessels, despite equal distances to fishing areas (Granadeiro et al. 2011, 2014). Those studies showed that a minority of individuals repeatedly followed vessels, suggesting they specialized in the short-term on fisheries waste, but tracking in a subsequent year and stable isotope analyses suggested that any fisheries specialism did not persist. In contrast, individual northern gannets did show specialization in following vessels or feeding on fisheries waste (Patrick et al. 2015). Hence, in the absence of any mitigation, fisheries bycatch represents a constant risk to black-browed albatrosses that would be maintained indefinitely if a proportion of the generalist population is attracted to vessels at random, but a particular risk for a specific group of specialist northern gannets that might be removed and not replaced. The demographic implications of these and other threats depends on the diversity of strategies (from specialist to generalist) in the population, the probability of individuals encountering adverse conditions, the degree of individual plasticity and the heterogeneity in vital rates associated with among-individual specialization. Seabirds are clearly highly adaptable in response to environmental pertubation, and some specializations can be relatively short-lived (Wakefield et al. 2015). Movement of individuals during the breeding and nonbreeding seasons are clearly flexible, but other aspects of behaviour (such as departure bearings of fledglings) or timing of some events may be innate, possibly responding to magnetic cues or stimuli that are highly predictable, such as photoperiod; however, even then, there may be some capacity for fine-tuning in response to environmental factors (Helm et al. 2013).

CONCLUSIONS

As this review has shown, many intrinsic factors (including stage of the annual cycle, breeding status, age and sex) drive individual differences in movement patterns and behaviour of seabirds. Understanding the nature, drivers and consequences of this variation is revealing in terms of ecology and life-histories and determines the response of individuals, populations and species to environmental changes, including anthropogenic threats. In addition, the effects of intrinsic factors and their interactions with each other and with the environment need to be considered in sampling design and analyses, and before drawing conclusions about underlying processes and mechanisms. They also need to be taken into account when evaluating evidence for individual specialization and its causes and consequences. Effects of factors such as sex, stage, age, as well as individual specializations are common in terms of distribution, habitat use, diving, diet and other components of foraging strategies at sea, but their roles and extents are highly variable. Site fidelity is scale-dependent for migrants, greater at the regional level than in the use of staging areas and routes, and can be low during the breeding season (Table 4). Timing of movements during the nonbreeding period is often consistent, but with some flexibility in response to local conditions. As might be expected, seabirds retain the flexibility to respond to local environmental conditions or cues and intrinsic factors (body condition, physiological constraints, etc.).

There is much scope for more studies on the timescale or periods in which effects of sex, age and specialization are apparent (from days to years) and the drivers underpinning these factors (resource availability and predictability, density-dependent competition, intrinsic characteristics, learning). Adults clearly use memory (Regular et al. 2013) to guide subsequent decisions; under what conditions (i.e. changes in resource availability or habitat suitability) they might re-enter an exploratory phase as adults and refine their movement and foraging strategies is unknown. Although the papers in this Theme Section have increased our understanding of the implications of individual variation and specialization, there are still many gaps in our knowledge. With regard to individual specialization in particular, we would recommend research on the circumstances in which it offers a selective advantage, the degree of genetic or cultural transmission, the level of plasticity in response to the environment, the energetic and other physiological consequences and effects (immediate or carry-over) on survival and reproduction. This is particularly important in a rapidly changing world, as the degree of plasticity of individuals affects the capacity of populations to respond to changes in conditions.

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REVIEW

Methods for detecting and quantifying individual specialisation in movement and foraging strategies of marine predators

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ABSTRACT: There is increasing realisation that individuals in many animal populations differ substantially in resource, space or habitat use. Differences that cannot be attributed to any *a priori* way of classifying individuals (i.e. age, sex and other group effects) are often termed 'individual specialisation'. The aim of this paper is to assess the most common approaches for detecting and quantifying individual specialisation and consistencies in foraging behaviour, movement patterns and diet of marine predators using 3 types of data: conventional diet data, stable isotope ratios and tracking data. Methods using conventional diet data rely on a comparison between the proportions of each dietary source in the total diet and in the diet of individuals, or analyses of the statistical distribution of a prey metric (e.g. size); the latter often involves comparing ratios of individual and population variance. Approaches frequently used to analyse stable isotope or tracking data reduced to 1 dimension (trip characteristics, e.g. maximum trip distance or latitude/longitude at certain landmarks) include correlation tests and repeatability analysis. Finally, various spatial analyses are applied to other types of tracking data (e.g. distances between centroids of distributions or migratory routes, or overlap between distributions), and methods exist to compare habitat use. We discuss the advantages and disadvantages of these approaches, issues arising from other effects unrelated to individual specialisation per se (in particular those related to temporal scale) and potential solutions.

KEY WORDS: Behavioural consistency · Foraging site fidelity · Foraging specialisation · Marine mammals · Niche variation · Repeatability · Seabirds · Site fidelity

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INTRODUCTION

Ecologists have often treated conspecific individuals as broadly equivalent, after accounting for age, sex and other group effects (Bolnick et al. 2003, Yamamoto et al. 2014, Wakefield et al. 2015). However, there is increasing realisation that individuals in many animal populations differ substantially in resource use ('niche variation'), and the term 'individual specialisation' has been used to describe heterogeneity in resource use (Araújo et al. 2011, Patrick et al. 2014, Ceia & Ramos 2015). The extent of niche variation has important implications, including the potential not only to reduce the degree of intra-specific competition, but also to increase individual efficiency in finding and handling food (Estes et al. 2003,

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Cook et al. 2006, Kotzerka et al. 2011, Ceia & Ramos 2015). Moreover, if a wide range of habitats and resources are used, a particular species or population may be better buffered against anthropogenic impacts, as individuals are likely to respond in different ways to changes in the environment (Tinker et al. 2008, Phillips et al. 2009, Dias et al. 2011, Masello et al. 2013). Hence, the characterisation of divergent behaviour or strategies may provide important insights into the ecology, evolution, conservation and management of the species (Thiemann et al. 2011, Wakefield et al. 2015, Ramírez et al. 2016).

The interest in individual variation, however, extends far beyond the marine ecology literature, and has evolved independently in several fields, resulting in a fragmented literature with different terminology (Dall et al. 2012). While some researchers have focused on individual niche specialisation (particularly in terms of behavioural traits associated with foraging behaviour and diet choice), others have focused on documenting behavioural syndromes or animal personalities (boldness, aggressiveness, activity, exploration and neophobia), and the division of labour within insect societies or hunting groups (Gazda et al. 2005, Dall et al. 2012). Although these similar concepts (individual niche specialisation, behavioural syndromes or animal personalities, and the division of labour) are applied in different contexts, they are largely concerned with the same behavioural properties, and each field uses similar statistical methodology for describing individual variation (Cleasby et al. 2015).

Individual specialisation occurs when individuals use a narrow subset of the ecological niche of the population, for reasons not attributed to any *a priori* ways of classifying individuals (Bolnick et al. 2003, Woo et al. 2008, Votier et al. 2010, Dall et al. 2012, Patrick et al. 2014). Indeed, there are multiple biological reasons to distinguish between phenotypic variation that is sex- or age-related and individual-level specialisation (Bolnick et al. 2002). In marine predators, sex differences may arise from the influence of size dimorphism on sex-specific parental roles, intersexual competition, foraging and locomotory efficiency (including diving capability), or habitat specialisation (González-Solís et al. 2000, Shaffer et al. 2001, Phillips et al. 2004a, Breed et al. 2006, Staniland & Robinson 2008, Quillfeldt et al. 2011, Stauss et al. 2012); these mechanisms are potentially, but not necessarily, different from those generating individual specialisation. Similarly, differences in behaviour are often associated with variation in foraging abilities (i.e. competitive ability) or performance of adults of different ages or experience (Navarro et al. 2010). After accounting for effects of sex and age, other sources of variation among individuals may still exist; this residual variation is what describes individual specialisation. The unexplained within-individual variation is generally assumed to be distributed normally and uniformly between individuals when using this approach (Westneat et al. 2015).

Although a variety of approaches have been used to detect individual specialisation in traits (e.g. diet and foraging behaviour), most approaches rely on contrasting the amount of variation within individuals with the variation between individuals, using repeatability analysis. A repeatable behaviour will show relatively low within-individual variance compared to between-individual variance (Bell et al. 2009, Nakagawa & Schielzeth 2010, Dingemanse & Dochtermann 2013). Consistently divergent behaviours have also been termed specialisations. The definition of behavioural consistency, however, is not trivial when looking at the statistical methodology, and there is still no universal agreement (but see Cleasby et al. 2015). In the context of specialisation, consistency relates to the within-individual variation. The within-individual variation needs to be compared to the between-individual variation in order to test for specialisation (to determine a 'high' vs. a 'low' within-individual variance). Although behavioural consistency can reflect specialisation, it does not necessarily indicate individual specialisation as defined here. For example, if groups of individuals (e.g. males vs. females, adults vs. juveniles) differ in their preferences, but these group differences are not taken into account, then researchers might wrongly conclude that there is individual specialisation.

Individual specialisation and behavioural consistency are known to be widespread across a range of taxa and behaviours; they have been demonstrated for a number of species of marine predators in foraging behaviour, migratory routes, dive characteristics, diet, timing of events, activity patterns and habitat choice, and foraging site fidelity during breeding and non-breeding periods (Hoelzel et al. 1989, Staniland et al. 2004, Croxall et al. 2005, Phillips et al. 2005, 2006, Sargeant et al. 2005, Guilford et al. 2011, Thiebot et al. 2011, Patrick et al. 2014, Yamamoto et al. 2014, Wakefield et al. 2015). Because marine predators forage on highly patchy and more or less predictable food resources at the coarse- to meso-scale (tens to hundreds of kilometres) and over days and weeks, the incidence of specialisation is unsurprising (Weimerskirch 2007, Ceia & Ramos 2015, Wakefield et al. 2015). The recurrent use of similar areas may increase familiarity with feeding conditions, including fine-scale resource availability and distribution (Hamer et al. 2007, Ramírez et al. 2016). Marine predators will often target regions characterised by local physical features or processes, including eddies, frontal systems, upwelling zones and shelf breaks, that increase primary production or serve to aggregate various types of prey (Kappes et al. 2010, Louzao et al. 2011, Pinet et al. 2011, Baylis et al. 2012, Arthur et al. 2015, Wakefield et al. 2015). Foraging behaviour and diet specialisations may therefore emerge as a result of the spatial and temporal availability and predictability of prey (Woo et al. 2008, Navarro & González-Solís 2009, Patrick et al. 2015, Sommerfeld et al. 2015). Moreover, because marine predators frequently target such productive areas in the breeding and non-breeding seasons, and are central-place foragers during breeding, competition may be high and lead to the use of divergent foraging strategies (Estes et al. 2003, Villegas-Amtmann et al. 2008, Patrick et al. 2014, Ceia & Ramos 2015).

Several conventional approaches, such as visual observations and the analysis of pellet, midden, regurgitate or stomach contents, have been used to test for, or to quantify, consistency in diet in marine predators (Votier et al. 2004a,b, Hamer et al. 2007, Maldini et al. 2010, Scheel & Anderson 2012). More recently, these approaches have been replaced or supplemented by the use of biologging technology and stable isotope analysis of carbon and nitrogen (Phillips et al. 2005, Furness et al. 2006, Anderson et al. 2009, Newsome et al. 2009, Matich et al. 2011, Kernaléguen et al. 2015). The aim of this review is to scrutinise the most common methods used to detect and quantify individual specialisation and behavioural consistencies in foraging, movement patterns and diet of marine predators, particularly seabirds and marine mammals (Table 1). A series of fixed factors unrelated to individual specialisation per se are also discussed briefly, as these need to be taken into account when applying several of the approaches presented here. The review focuses on 3 types of data: those derived from (1) diet assessed using conventional approaches, (2) diet assessed using stable isotopes, and (3) tracking. In each case, we present the various statistical analyses used to date, providing an overview of the specific advantages and disadvantages.

DIET USING CONVENTIONAL APPROACHES

Many methods are used to study marine predator diet. Traditionally, these involve the collection and analysis of regurgitated prey items and pellets, stomach contents, faeces, direct observations of prey caught or carried by returning adults, or dropped items collected at breeding colonies (Pierce & Boyle 1991, Barrett et al. 2007, Moreno et al. 2016). The analysis of diet specialisation depends not only on the number of individuals sampled but also, and most importantly, on the number of independent feeding events recorded per individual in order to calculate an index of diet variation (Araújo et al. 2011). Monte Carlo simulations are the only way to do a power analysis, but some prior knowledge of the expected level of variability in a given population is necessary. Although repeated observations over time are required to quantify specialisation correctly, the first studies testing (and rejecting) the null hypothesis that conspecifics share an identical resource distribution were derived from cross-sectional data collected from a population at one specific point in time (e.g. Baltz & Morejohn 1977, Lønne & Gabrielsen 1992). Unlike this snapshot approach, longitudinal studies, where sampling at intervals reflects multiple feeding events of the same individual, allow specialisation to be properly quantified at a particular temporal scale.

The simplest approach to detect specialisation is to identify groups of specialists and generalists based on the proportion of each dietary source in the total diet, and assign individuals to these groups (e.g. Pierotti & Annett 1991, Annett & Pierotti 1999, Oro et al. 2005, Hamer et al. 2007). For example, by observing prey items being delivered to pigeon guillemot *Cepphus columba* chicks for an average of 4 full days over multiple years, Golet et al. (2000) defined specialists as individuals whose diet contained more than 50 % of a particular item or class of items. Using a higher threshold for the definition of specialist predators, Votier et al. (2004a) categorised great skuas *Stercorarius skua* as specialist fish or bird predators when the contents of regurgitated pellets collected over multiple periods between egg-laying and chick-fledging comprised 70 % or more of the respective prey, or as generalists when none of the prey items comprised 70 % or more of the diet. When data on diet are not available, behavioural information (such as dive depths and the proportion of trips associated with fishing boats) or the use of areas where particular prey occur (proportion of time at each feeding site) have been used to assign individuals to different diet groups (e.g. Ropert-Coudert et al. 2003, Montevecchi et al. 2009, Masello et al. 2013, Granadeiro et al. 2014, Patrick et al. 2015, Tyson et al. 2015). The threshold used for separating specialists and generalists is often arbitrary. Ideally, researchers could

Table 1. Summary of the most common methods used to detect and quantify individual specialisation and behavioural consistencies in foraging, movement patterns and diet of marine predators. WIC: within-individual component, GLMM: generalised linear mixed-effects model, TNW: total niche width, UDOI: utilisation distribution overlap index

Method	Data type	Example	Reference	Notes
Comparing categories based on percentage of use	Categorical	Prey items	Votier et al. (2004a)	Does not allow statistical testing of the degree of individual consistency
		Habitat types or areas where particular prey occur	Ropert-Coudert et al. (2003)	
Ratios of variance (repeatability)	Continuous variable	Prey trait (e.g. size)	Woo et al. (2008)	Using GLMMs allows the inclusion of fixed effects (not when using Bolnick's WIC/TNW ratio)
		Stable isotope ratios	García-Tarrasón et al. (2015)	
		Trip summary statistics	Wakefield et al. (2015)	
GLMM with random slopes	Response variable and continuous environmental variables	Use/availability locations	–	Resource selection function (habitat selection)
		Foraging trip characteristics, e.g. path straightness	Patrick et al. (2014)	Random slope model
Distances	Spatial data	Between distribution centroids	Navarro & González-Solís (2009)	
		Between migratory routes	Dias et al. (2011)	
	Ranges		Orben et al. (2015)	
Overlaps	Utilisation distributions	In geographical space	Wakefield et al. (2015)	Bhattacharyya's affinity, UDOI, etc.
		In environmental space (each variable at a time)	Wakefield et al. (2015)	Bhattacharyya's affinity, UDOI, etc.

deal with this issue by testing the sensitivity of their results to different cut-offs. Furthermore, although this approach can be used to infer differences in diet between individuals, which can be interpreted as a form of individual specialisation, it does not allow estimation of its statistical significance.

To solve these issues, Bolnick et al. (2002) introduced a framework to quantify and test statistically for individual specialisation in diet that has since been used in a wide range of taxa. By using ratios of variance in a continuous trait measured for each prey item (e.g. prey size), it is possible to estimate how much of the total population variance is explained by differences within vs. between individuals. In practice, the average intra-individual variance ('within-individual component' of the niche, WIC) is calculated, and divided by the sum of the inter-individual variance ('between-individual component', BIC) and the intra-individual variance (WIC + BIC = TNW, the 'total niche width'). This index (WIC/TNW) varies from 0 (complete individual specialisation) to 1 (no individual specialisation). Empirical values can be compared with a null model (randomisation of prey items between individuals). This approach can be implemented in the R package RInSp (Zaccarelli et al. 2013). The method can also be extended to discrete data such as the frequency of alternate prey in the diet by using diversity indices as a proxy for variance (Bolnick et al. 2002). Instead of the raw number (or mass) of diet items, values are transformed into a proportion matrix. Examples of diversity indices applied for this purpose are the Shannon-Weaver index and a modified version of Hill's ratio (Golet et al. 2000, Tinker et al. 2008, Woo et al. 2008). Alternative indices for quantifying individual specialisation are based on diet overlap measures between the individual and population (Bolnick et al. 2002).

DIET (TROPHIC POSITION/CARBON SOURCE) USING STABLE ISOTOPES

Stable isotope analysis of carbon ($^{13}C/^{12}C$, $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) are used increasingly to test for consistency in trophic level and foraging habitat over multiple timescales. In marine ecosystems, the ratios of stable carbon and nitrogen isotopes in consumer tissues reflect those of their prey during tissue formation in a predictable manner (Phillips et al. 2009). Carbon stable isotope ratios mainly reflect the foraging habitat or carbon source of the consumer, whereas nitrogen stable isotope ratios indicate trophic position (Bearhop et al. 2000, Cherel et al. 2006, Ceia et al. 2012). Since different tissues turn over at different rates, each integrates diet information over various temporal scales (Bearhop et al. 2006, Matich et al. 2011, Ceia & Ramos 2015). For instance, plasma retains information from a few days prior to sample collection, and red blood cells from the previous 3 to 4 wk, whereas feathers and fur represent diet during moult, since keratin is metabolically inert after synthesis (Bearhop et al. 2006, Ceia et al. 2012, Barquete et al. 2013). Pinniped (otariid) and sea otter *Enhydra lutris* vibrissae, chelonian shells, baleen plates and mammalian teeth sampled sequentially can be used to represent several years of diet information (Hobson & Sease 1998, Walker & Macko 1999, Cherel et al. 2009, Vander Zanden et al. 2010, Eisenmann et al. 2016). Consequently, the similarity between stable isotope ratios measured in different tissues with different turnover rates or during different periods can be used as a proxy for individual diet and habitat specialisations (Wakefield et al. 2015).

$\delta^{13}C$ or $\delta^{15}N$ are often analysed separately; however, because $\delta^{13}C$ has a trophic component, the studentised residuals of the relationship between $\delta^{13}C$ and $\delta^{15}N$ can be included in models testing for short- and long-term consistency to control for the variability in $\delta^{13}C$ that could be due to $\delta^{15}N$ (Votier et al. 2010, Ceia et al. 2012). Alternatively, a multivariate model which allows direct modelling of the covariance/correlation between these traits can be used to control for the variability in $\delta^{13}C$ due to that in $\delta^{15}N$; however, this approach, to our knowledge, has not been used in the marine predator literature to date.

The most common approach, applicable to different types of data (stable isotope ratios, trip metrics, habitat use), includes the use of repeatability (*R*) analysis (i.e. intraclass correlation coefficient, ICC), where the level of individual specialisation in a population can be estimated as the proportion of the total variance accounted for by differences among individuals, according to the following formula:

$$R = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2} \quad (1)$$

with σ_α^2 being the between-individual variance and σ_ε^2 the within-individual variance. The way to estimate the variance components will depend on the distribution of the data (Nakagawa & Schielzeth 2010). For Gaussian data, such as ratios of carbon and nitrogen, repeatabilities can be calculated either with the *F* table of an ANOVA with individual identities as fixed factors (e.g. Hamer et al. 2001, Gray et al. 2005, Vander Zanden et al. 2013, Oppel et al. 2015) or with linear mixed-effects models with individual identities treated as a random effect (e.g. Dias et al. 2011, Matich et al. 2011, Grist et al. 2014, McFarlane Tranquilla et al. 2014, Kernaléguen et al. 2015, Wakefield et al. 2015). Note that the framework proposed by Bolnick et al. (2002), examining the within-individual component and between-individual component of a niche, is essentially the same as the residual variance (within-individual variance) and between-individual variance when using mixed-effects models. Indeed, the ratio WIC/TNW is very similar to the equation for repeatability, except that the numerator represents the within- rather than between-individual variation. Linear mixed-effect models have the advantage of directly estimating the variance necessary for the calculation of repeatability; the quantities σ_α^2 and σ_ε^2 can be extracted from the output of a mixed model. For non-Gaussian data (e.g. binary, proportion and count data), generalised linear mixed-effects models (GLMMs) with the appropriate link function are required (e.g. García-Tarrasón et al. 2015, Potier et al. 2015). The advantage of using mixed-effect models to calculate repeatability is that additional covariates can be included as fixed effects to account for known sources of variation. However, controlling for fixed effects will affect variance component, and hence repeatability, estimates (Wilson 2008; adjusted repeatabilities, Nakagawa & Schielzeth 2010). The inclusion of predictors associated with individual observations (season, year, etc.) will tend to increase the repeatability, while predictors associated with the individual-level component (sex, age, etc.) will tend to decrease repeatability (Wilson 2008, Nakagawa & Schielzeth 2010). ANOVA tables use the ratio of the sums of squares to estimate repeatabilities (Lessells & Boag 1987). The statistical significance of the repeatability can be tested with a randomisation test: measurements (e.g. isotope ratios) are reshuffled many times between individuals and repeatability is calculated for each randomisation. The corresponding p-value is the proportion of randomisations that produce a repeatability index greater or equal to the observed repeatability. This can be implemented in the R package rptR (Nakagawa & Schielzeth 2010). The importance of modelling differences in within-individual variation — e.g. using (double) hierarchical generalised linear models, or (D)HGLMs as presented in Cleasby et al. (2015) — has been recognised in a variety of fields and, recently, by ecologists, but is not discussed in detail in the present review because, as far as we are aware, it has featured only in a few studies of marine ecology (but see Cleasby et al. 2015 for a review of indices).

In theory, when data are normally distributed and the design of the study is balanced (equal number of measurements for each individual), an even simpler approach is to test for a correlation (Spearman's or Pearson's correlation) between pairs of measurements taken at different points in time for each individual (correlation-based repeatability; Nakagawa & Schielzeth 2010). If there are more than 2 measurements per individual, correlations can be calculated between each pair of measurements, and averaged for each individual. The main issue with correlations is that they ignore other factors, and so this might lead to within-individual consistency being high because the measurements were taken under the same conditions, rather than because the individual is consistent (Dingemanse et al. 2012).

A general question when calculating repeatability, or any other index of individual specialisation, is what are the appropriate sample sizes. Wolak et al. (2012) calculated confidence intervals for a number of repeatability estimates presented in the literature and found that for most of these studies, the associated precision was low because of inappropriate sample sizes. They provide guidelines for estimating how many individuals, and how many measurements per individual, are necessary to get a certain level of precision. In general, the higher the value of the repeatability index, the fewer the number of measurements and individuals needed for reasonable precision. Wolak et al. (2012) also emphasise that the same precision can be achieved with different combinations of number of individuals or number of measurements. In the particular case of stable isotopes, when there are often only 2 measurements per individual, the number of individuals sampled will need to be high. The formula provided by Wolak et al. (2012) for this estimation can only be applied for repeatabilities calculated using the variance components of a 1-way ANOVA table, hence for Gaussian data. For more complex model structures or non-Gaussian data, no such formula exists. However, power analyses can still be carried out at the level of each variance component in a mixed-model framework (potentially with both random intercepts and random slopes), using the R package pamm (Martin et al. 2011).

BIOLOGGING STUDIES

A variety of devices have been used to examine animal movements, including platform terminal transmitter (PTT), GPS, and geolocator or global location sensing (GLS) loggers. These devices have different performances, and the general trade-off is between temporal resolution, deployment duration, device mass and cost (Wakefield et al. 2009). PTTs can provide multiple locations per day with accuracy typically <15 km (Burger & Shaffer 2008, Phillips et al. 2007, Costa et al. 2010). Due to their high cost, these devices have, to an extent, been replaced in the last decade by GPS loggers. The latter have a much better spatial accuracy (within 10 m) and temporal resolution (up to 1 Hz) (Guilford et al. 2008, Phillips et al. 2007, Kotzerka et al. 2010). In diving predators that only surface for short periods, very rapid (<100 ms) acquisition Fastloc GPS is required, and is slightly less accurate than conventional GPS (50% of locations within 36 m; Dujon et al. 2014). Because of the very high temporal resolution, fine-scale behavioural information can be inferred from movement (Guilford et al. 2008, Freeman et al. 2010). The use of miniaturised GPS loggers, however, is still limited by the short lifespan (weeks) of devices without solar panels. The use of GLS loggers avoids some of these problems as they have low power requirements, and are small enough to be attached long-term to a ring on the tarsus or a flipper tag (Wilson et al. 2002, Phillips et al. 2004b, Shaffer et al. 2005, Staniland et al. 2012). This technology is unsuitable for fine-scale spatial analysis, but is ideal for monitoring large-scale movements during the non-breeding season or over extended periods. Amongst the disadvantages, GLS loggers will provide only 2 locations per day with an average accuracy of 186 ± 114 km, and latitude is difficult to estimate from light for 3 to 4 wk around the equinoxes (Phillips et al. 2004b, Shaffer et al. 2005). Other devices can be deployed that collect immersion, acceleration, temperature, images or other data allowing more detailed investigations into at-sea activity (Phalan et al. 2007, Mackley et al. 2010, 2011, Gutowsky et al. 2014, Kernaléguen et al. 2015).

Biologging studies can be used to assess the potential specialisation or flexibility of individuals from within a population because individuals can be tracked across multiple trips or over the course of a year or longer (Pinaud & Weimerskirch 2005, Soanes et al. 2013, Muller et al. 2014). As such, the data can be used to examine repeatability in foraging destinations (i.e. site fidelity), migration schedules (timing and duration of events), fidelity to wintering areas and routes, and consistency in habitat use or preference (Croxall et al. 2005, Phillips et al. 2005, 2006, Guilford et al. 2011, Thiebot et al. 2011, Baylis et al. 2015a, Yamamoto et al. 2014, Arthur et al. 2015).

Analyses of trip summary statistics

Spatial information collected by tracking devices will typically be in 2 dimensions (latitude and longitude). Therefore, in order to apply the methods listed above (correlations and repeatability analysis), spatial data are typically reduced via summary statistics to a single dimension, or are analysed separately (e.g. Phillips et al. 2005, Dias et al. 2013, Ceia et al. 2014, Yamamoto et al. 2014, Potier et al. 2015). The most common summary data derived from each trip that have been used in this way include the total duration, total distance travelled (summed great circle distances between fixes), maximum range (great circle distance to the furthest location), and bearing at departure or to the furthest point (Hamer et al. 2001, 2007, Soanes et al. 2013, Ceia et al. 2014, Patrick et al. 2014, Baylis et al. 2015b, Oppel et al. 2015, Potier et al. 2015). For the non-breeding season, the analyses are often of migration schedules (timing and duration of events; Croxall et al. 2005, Phillips et al. 2005, Dias et al. 2011, Yamamoto et al. 2014), or the total distance travelled during the migration (Muller et al. 2014). Other 1-dimensional data used in studies of individual specialisation include dive characteristics and activity metrics (Laidre et al. 2002, Staniland et al. 2004, Cook et al. 2006, Ratcliffe et al. 2013, Patrick et al. 2014, Potier et al. 2015, Wakefield et al. 2015).

Correlation tests can be performed to compare the above measures collected at different points in time (e.g. Phillips et al. 2005, Soanes et al. 2013). However, these tests do not allow individual specialisation per se to be quantified. The alternative is to carry out repeatability analyses, as presented in the 'Diet (trophic position/carbon source) using stable isotopes' section, e.g. of proportions of V-shaped dives (Patrick et al. 2014, Wakefield et al. 2015), wintering destinations (Perez et al. 2014) or number of dives per foraging trip (Potier et al. 2015).

Spatial analyses: distance between centroids of distributions or migratory routes

It is possible to study individual specialisation in space, and not only in trip characteristics, based on distances between the centroid of the locations at 2 different times for the same individuals tracked during the breeding season (Navarro & González-Solís 2009, Ceia et al. 2014), or between centroids in different winters (Dias et al. 2011, Fifield et al. 2014, McFarlane Tranquilla et al. 2014, Yamamoto et al. 2014, Lea et al. 2015). Distances can also be calculated between pairs of migratory routes (e.g. for the same individual during consecutive years), either between positions at certain landmarks (Yamamoto et al. 2014), or as the mean distance between each position on one route and the nearest position on the other (Guilford et al. 2011, Dias et al. 2013). The smaller that distance, the more consistent the individual. To compare the within- and between-individual distances (i.e. evaluate the statistical significance of individual consistency), one approach is to use distances calculated for pairs of centroids or routes as the response variable in a (G)LMM with individual (same vs. different) as a random effect, and check for the significance of the random effect (Dias et al. 2013). The second, and more widely used approach, is to compare the calculated within-individual distances with a null distribution of distances generated by reshuffling either locations or migratory tracks between individuals (Navarro & González-Solís 2009, Dias et al. 2011, Fifield et al. 2014, McFarlane Tranquilla et al. 2014). This method based on distances does not take into account the spread of the locations around the centroids: hence, although useful to detect a shift in the general distribution, it would not detect a change only in range size. It also has the disadvantage of only allowing individual specialisation to be detected, but not quantified.

Spatial analyses: overlap between distributions

Specialisation can also be estimated as the overlap between distributions of the same individual over time. One approach is to overlay the locations (dives, landings or feeding events etc.) on a grid, and count the number of shared grid cells between different trips made by the same individual (Hedd et al. 2001, Baylis et al. 2015b, Orben et al. 2015, Sommerfeld et al. 2015). These values are usually compared with null models based on randomisation of individual identities. Problems include the sensitivities to grid cell size and to the resolution of the tracking data. Indeed, if the data are too coarse, there is a risk that genuine differences between individuals will be missed. Ideally, data should be analysed on a scale that is as fine as possible, although not smaller than the accuracy of the tracking device; however, if the grid cells are too small, potentially no 2 points from the same bird will ever fall in the same cell even if these points are relatively close.

Probabilistic measures offer an alternative approach; a utilisation distribution (UD) is generated from tracking data, and the polygons representing core and general use areas (typically 50% and 90/95%, respectively) are then compared in an analysis of overlap to determine the probability of individuals being located repeatedly in the same area. This method has been used to compare foraging areas in consecutive trips during the breeding season (Phillips et al. 2006, Pettex et al. 2012, Soanes et al. 2013), and areas used from one year to the next (Chilvers 2008, McFarlane Tranquilla et al. 2014, Muller et al. 2014). The problem is that it does not exploit the information on the complete UDs (cf. Ceia et al. 2014, 2015, Fifield et al. 2014, Wakefield et al. 2015). In contrast, the indices described by Fieberg & Kochanny (2005) provide a more elegant means of representing the overlap between pairs of UDs, mainly based on the product of 2 UDs. They suggested the use of Bhattacharyya's affinity when the aim is to quantify the degree of similarity among UD estimates (see Wakefield et al. 2015), and the utilisation distribution overlap index (UDOI) when a measure of space-use sharing is desired. Isopleths can, of course, still be informative when using these indices. The observed distribution of the indices can be compared to randomised distributions. In general for methods using UDs, care needs to be taken in the definition of the smoothing factor (*h* value) required for kernel analysis, since it can influence the resulting UD. A constant value of *h* for all individuals should be preferred (Fifield et al. 2014); otherwise, variation in behaviour can be indistinguishable from that due to the choice of smoothing parameter.

Environmental (habitat) analyses

Tracking data provide information not only on the geographical space, but also on how individuals use their environment (habitat). Indeed, remotely-sensed environmental data can be extracted for each animal location and, as with other types of movement information, traditionally each environmental dimension is analysed separately, typically calculating the overlap (Bhattacharyya's affinity) between the usage distributions represented by pairs of trips for each individual (Wakefield et al. 2015). Alternatively, it is possible to include all variables in the same model, using random slope models (allowing for the response to environmental conditions to vary between individuals). This has been used to investigate how environmental conditions influence the track characteristics, e.g. speed or straightness of the path of different individuals (Patrick et al. 2014). The same approach using random slopes can be used in a resource selection function framework in which habitat selection is estimated by contrasting environmental conditions at 'used' locations (i.e. the recorded locations) and 'available' locations (randomly simulated locations in the accessible area around the recorded locations), in general using a generalised linear model (GLM) with a logistic link. This can be extended to GLMMs, using random slopes (individuals as a random effect) to detect differences between individuals in selection for each variable.

CONTROLLING FOR PSEUDO-REPEATABILITY

Some effects can create bias in the estimation or interpretation of levels of individual variation, which can inflate repeatability estimates, leading to pseudo-repeatability (Dingemanse & Dochtermann 2013). This inflation occurs when predictor variables (i.e. fixed effects) that influence within-individual variation vary between individuals because of a sampling or measurement error; or when biologically relevant parameters (i.e. fixed effects) that explain between-individual differences are not taken into account in models (Dingemanse & Dochtermann 2013, Westneat et al. 2015). Other explanations proposed for heterogeneity in residual within-individual variance are the 'organismal error' (when the variance in phenotype is due to errors made by individuals when assessing their environment, e.g. individuals misidentify an environmental cue and produce a response which would be better suited to another environment) and the 'random residual within-individual variance' (when variation is due to a random process; e.g. stochastic variation in density and location of prey), which are discussed in detail in Westneat et al. (2015).

Several issues related to temporal scale exist. Indeed, consistency detected at different timescales has different ecological interpretations (see Réale & Dingemanse 2001 for a related discussion on the study of animal personality). If individuals are consistent over a short but not over a long timescale, the 'specialisation' detected is likely to be due to variation in the state of the individuals (e.g. hunger level or reproductive state), or other short-term uncontrolled effects (e.g. immediate environmental conditions). If individuals are consistent over a long timescale, the cause is likely to be due to genetic, parental, individual quality or possibly permanent environmental effects. If specialisation increases over long timescales, the causes are likely to be related to some learning process (over the lifespan of an individual) or selective disappearance (over several generations, i.e. if specialists are fitter, generalists will selectively disappear from the population). This emphasises the importance of carrying out studies that, ideally, cover multiple time intervals (Kernaléguen et al. 2015).

Conversely, incorrect combination of time periods can lead to erroneous interpretations. Indeed, if individuals specialise on different resources or environments over different seasons, studying specialisation over the whole year, for example, might prevent the detection of individual specialisation (although this issue can be dealt with by including the correct fixed effects). In the case of seabirds, although several studies have revealed that dietary and behavioural specialisations are widespread, it is unclear for how long these specialisations are maintained (Masello et al. 2013, Patrick et al. 2014; but see Wakefield et al. 2015). It is likely, however, that repeatability in foraging behaviour declines at longer temporal scales because of temporal changes in the availability and predictability of resources (Woo et al. 2008, Bell et al. 2009, Ceia et al. 2014). Weimerskirch (2007) also suggested that site fidelity not only depends on the timescale, but also on the habitat visited. Almost all published studies to date were limited to data from relatively few individuals tracked or observed over short periods of time (Žydelis et al. 2011). Novak & Tinker (2015) also raise this point for time-aggregated observations related to diet, noting that increasing sampling time increases knowledge of an individual's diet but comes with the risk that the ability to detect meaningful temporal patterns in prey selection is reduced.

The timing of the study can also bias the results for reasons that are not necessarily linked to individual preferences. For example, if individuals are tracked only during consecutive trips or for a few consecutive years, when conditions may be more similar than after longer intervals, the lack of within-individual flexibility in behaviour may reflect either that there was no environmental change influencing prey availability, or site fidelity (Chilvers 2008, Pettex et al. 2012, Carneiro et al. 2016). However, if tracked for multiple years with contrasting environmental conditions and prey availability, the repeated use of an area would indicate site fidelity. Such consistency in space use could also reflect behavioural plasticity, and the two mechanisms are hard to tease apart.

Timing and spatial accessibility are also important when studying between-individual differences. If all individuals in the study do not have access to the same environment or prey (either because the conditions change or because individuals live in distant areas with different characteristics), then the population might exhibit apparent specialisation, even though individuals are not specialised. Thus, to be sure that it is indeed specialisation that is observed, studies should minimise the risk of differences in habitat or resource availability between individuals, which in practice is a major challenge. Note that this can to some extent be resolved by combining trophic markers such as stable isotope ratios with tracking in multiple years (Baylis et al. 2015b).

Finally, populations can exhibit different foraging behaviours depending on the season (e.g. for seabirds, even within the breeding season, energy requirements and the constraint of the colony usually differ between pre-laying, incubation, brood-guard and later chick-rearing). It is important to take these changes into account, otherwise apparent individual differences might arise as an artefact of mismatches in the temporal scale of the measurements.

EFFECTS SPECIFIC TO STABLE ISOTOPE DATA

Studies using stable isotopes as a measure of individual specialisation/consistency in resource use should ideally use methods that allow the partitioning of isotope variation between different factors, and individual effects, such as calculating the adjusted repeatability from mixed-effects models. It is also possible to control for some of this variation during sample collection and preparation. Factors that should be taken into account when estimating short- and long-term spatial consistency or dietary specialisation (δ^{13}C and δ^{15}N values) relate to (1) the comparison of tissue types with different enrichment factors for carbon and nitrogen isotopes (Cherel & Hobson 2007, Quillfeldt et al. 2008), (2) the use of tissues with different turnover rates (e.g. plasma and red blood cells), but with some overlap in terms of diet integration period (Votier et al. 2010, Ceia et al. 2015), (3) the differences in baseline isotope ratios in foraging areas used by individuals (in the marine environment, different oceanic processes and sources of organic matter can result in spatial changes in baseline stable isotope ratios; Moreno et al. 2011), and (4) the variation in baseline isotope ratios between different periods and years (Araújo et al. 2011, Wakefield et al. 2015). In addition, intrinsic factors, which are linked to physiological and life history traits (sex, breeding stage, experience, reproductive status etc.) can also be taken into account, although this will tend to decrease repeatability estimates (see Wilson 2008 for a discussion).

Tissue type

Keratinous tissues such as feathers, fur, vibrissae and chelonian shells are enriched in δ^{13}C and δ^{15}N when compared with blood, even when synthesised over the same time periods, due to different protein sources, use of endogenous reserves during feather synthesis, or when plasma contains δ^{15}N-depleted uric acid (Hobson et al. 1996, Cherel et al. 2005, Cherel & Hobson 2007, Quillfeldt et al. 2008). Lipid concentrations can also lead to particularly depleted δ^{13}C values (Bearhop et al. 2000, Votier et al. 2010). Lipid extraction from fatty tissues is therefore recommended prior to δ^{13}C analysis (Cherel & Hobson 2007, Wakefield et al. 2015). However, extraction techniques can affect δ^{15}N in an unpredictable manner (Cherel et al. 2005, Bond & Jones 2009, Wakefield et al. 2015). Ideally, 2 samples, one to measure δ^{13}C (delipidated) and one to measure δ^{15}N (non-delipidated), should be analysed (Paiva et al. 2010, Wakefield et al. 2015). The low lipid level of keratinous tissues, blood cells and of whole blood does not affect their δ^{13}C, and so lipid extraction is not required (Cherel et al. 2005, Bond & Jones 2009, Matich et al. 2011, Ceia et al. 2012, 2015). High and varying concentrations of lipid in blood plasma, however, can result in depleted δ^{13}C values (Votier et al. 2010, Ceia et al. 2012, 2015). Lipid extraction can often be impracticable because of the small quantities of blood plasma (Votier et al. 2010, García-Tarrasón et al. 2015, Wakefield et al. 2015). In order to account for the remaining potential differences in enrichment factors, correction factors can be used (Cherel et al. 2005, Quillfeldt et al. 2008, Votier et al. 2010, García-Tarrasón et al. 2015) or tissue type included as a fixed effect in adjusted repeatability analysis (Wakefield et al. 2015).

Overlap in diet integration periods

Several studies have modelled short-term consistency in isotope ratios by comparing values between plasma and red blood cells collected in a single event (e.g. Ceia et al. 2012, 2014, 2015, Wakefield et al. 2015). Although each tissue has a different turnover rate, the integration of prey isotopes into body tissues is a continuous process, and the analysis of short-term consistency using the same blood sample inevitably leads to some overlap in the periods which the samples represent (Votier et al. 2010, Ceia et al. 2015). To overcome this issue, when combined with tracking analysis, some studies have collected blood in 2 sampling events associated with the capture (deployment) and recapture (retrieval) of tracking devices, using the red blood cell fraction from initial capture and the plasma fraction from the recapture for subsequent analysis (Votier et al. 2010, Ceia et al. 2015), or only the plasma collected during both events (García-Tarrasón et al. 2015).

Spatial and temporal variation in isotopic baselines

Marine isoscapes can change depending on nutrient source, primary productivity, depth, latitude and oceanic frontal region, which can confound direct comparisons of trophic levels between animals from different regions (Stowasser et al. 2012, Moreno et al. 2016). Information on isotopic ratios of potential prey from different foraging areas (which can be determined from tracking devices) are essential to distinguish the relative importance of prey vs. habitat specialisation (Moreno et al. 2016). Otherwise, it is not possible to tell whether a change in isotopic value from t_1 to t_2 (or tissue type x and y) represents a wider diet or spatial niche, or the same diet consumed in areas or periods with different isotope baselines (Ceia et al. 2014, Moreno et al. 2016). The latter applies in particular to species that forage across environmental boundaries and change their foraging areas on a seasonal basis (Stowasser et al. 2012). However, because most marine organisms are associated with specific water masses, even when apparent differences in trophic position are most likely related to the use of areas with different baselines, dietary differences may still be informative about the use of particular prey (Jaeger et al. 2014). To date, there has been only one study including estimates of baselines as fixed effects in adjusted repeatability analysis of $\delta^{13}C$ and $\delta^{15}N$ in the blood of northern gannets *Morus bassanus* from the Bass Rock, within and across years (Wakefield et al. 2015).

EFFECTS SPECIFIC TO TRACKING DATA

Studies of behavioural consistency and individual specialisation based on tracking data should, where possible, apply a variety of complementary approaches. It is straightforward to include fixed factors in analyses of summary statistics, but more difficult to control for these effects in spatial analysis. For the latter, the analyses have to be carried out separately for each level of those factors (e.g. males and females treated separately), but this implies the need for bigger sample sizes. In addition to sex and age effects, life-history stage and breeding status (failed or successful) can potentially influence foraging strategies and therefore should also be considered when testing for individual specialisation. Breeding status, for example, may not only affect timing of events (e.g. Croxall et al. 2005, Phillips et al. 2005, Bogdanova et al. 2011, Dias et al. 2011, Yamamoto et al. 2014), but also the use of migratory destinations and routes. When this information is not known, such effects can be reduced by restricting comparisons to particular time windows, for example to minimise the risk that apparent differences between individuals might relate to differences in migration schedules that ultimately took similar routes (Guilford et al. 2011). Behaviour may also differ between different types or phases of foraging trips (outward and return journeys, and hunting and searching for food), or migration (outward and return migration, and residence at the main staging and wintering areas). For birds, during chick-rearing, different types of trips can be performed by adults while provisioning their chicks; short trips to maximise delivery rate per unit of time and long trips that enable adults to restore their own reserves (Weimerskirch et al. 1994, Weimerskirch 1998; but see Phillips et al. 2009). All these potential differences need to be taken into consideration when analysing individual specialisation, as the constraint to return sooner to the colony can prevent individuals from visiting areas that would otherwise be optimal.

CONCLUSIONS

Individual specialisation can be calculated by using repeated measurements for each individual, then calculating the within- and between-individual variation. Although there are several alternatives (see Table 1), the most common and flexible approach is to calculate repeatability, using the variances extracted from GLMMs with individual as a random effect (either random intercepts or random slopes). To obtain estimates of individual specialisation, care needs to be taken to exclude effects that can lead to pseudo-repeatability. In addition, analysing a variety of data types simultaneously can provide better insights. Analysis and interpretation can be improved if the study involves a representative number of individuals having access to the same habitat and resources (preferably over the same periods), and over short and long timescales. Statistical analyses of individual differences should be rigorous and follow advice mentioned in this review. Studies that conformed to these recommendations have found convincing evidence of behavioural consistency and individual specialisation in marine predators, albeit typically over relatively short timescales, as well as in a wide range of other taxa (e.g. Woo et al. 2008, Matich et al. 2011, Ceia et al. 2014, Patrick et al. 2014, Wakefield et al. 2015). In contrast, the ecological implications of consistent differences in resource or habitat selection at the individual or population level remain unclear (Ceia & Ramos 2015). However, such differences are likely to affect the conclusions of population dynamics models (as does individual consumer behaviour or trait variation; Okuyama 2008, Schreiber et al. 2011). Indeed, individual specialisation can affect interactions between individuals (e.g. by reducing intraspecific competition; Bolnick et al. 2011, Matich et al. 2011). Such differences may also reduce the predictive power of existing ecological models, for example species distributions models that are used increasingly to predict the response of a species to climate change or following an introduction (Pearman et al. 2008), wherein projections are made from average values for the population. Indeed, if individuals differ in their environmental tolerance (or preferences), species−environment relationships inferred from only a sample of individuals might not be representative of the ability of the species to cope with change.

Although in this review we have presented the most common methods used by the marine ecology research community to study individual specialisation and behavioural consistency, it is important to note that there have been a number of interesting methodological developments in the animal personality field which build on repeatability analysis to ask targeted research questions, especially related to within- vs. between-individual variation, and partitioning of variance components (van de Pol & Wright 2009, Twiss & Franklin 2010, Dingemanse & Dochtermann 2013). Several of these methods have the potential to be applied to marine predators. Furthermore, the analysis of movement data has become increasingly sophisticated, with the development of state-space models and approaches based on hidden Markov models that can be applied to the detailed information from whole tracks. These relatively new approaches are statistically complex and have yet to be used in the context of individual specialisation, but offer the possibility of capturing fine-grained behavioural responses and preferences that are likely overlooked when summarising movements with a few simple statistics. Combined with the decreasing costs and increasing accuracy of biologging devices, we expect these new methods to greatly increase our ability to study specialisation in marine predators.

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Contribution to the Theme Section 'Individual variability in seabird foraging and migration'

Multi-colony tracking reveals spatio-temporal variation in carry-over effects between breeding success and winter movements in a pelagic seabird

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ABSTRACT: Carry-over effects, whereby events in one season have consequences in subsequent seasons, have important demographic implications. Although most studies examine carry-over effects across 2 seasons in single populations, the effects may persist beyond the following season and vary across a species' range. To assess potential carry-over effects across the annual cycle and among populations, we deployed geolocation loggers on black-legged kittiwakes *Rissa tridactyla* at 10 colonies in the north-east Atlantic and examined relationships between the timing and destination of migratory movements and breeding success in the year of deployment and subsequent season. Both successful and unsuccessful breeders wintered primarily in the north-west Atlantic. Breeding success affected the timing of migration, whereby unsuccessful breeders departed the colony earlier, arrived at the post-breeding and main wintering areas sooner, and departed later the following spring. However, these patterns were only apparent in colonies in the south-west of the study region. Furthermore, the effect of breeding success was stronger on migration timing in the first part of the winter than later. Timing of migratory movements was weakly linked to subsequent breeding success, and there was no detectable association between breeding success in the 2 seasons. Our results indicate temporal structure and spatial heterogeneity in the strength of seasonal interactions among kittiwakes breeding in the north-east Atlantic. Variable fitness consequences for individuals from different colonies could have important implications for population processes across the species' range and suggest that the spatio-temporal dynamics of carry-over effects warrant further study.

KEY WORDS: Seasonal interactions · Migration · Reproduction · Life-history strategies · Geolocation · Black-legged kittiwake · *Rissa tridactyla* · North Atlantic

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INTRODUCTION

Understanding the fitness consequences of life-history decisions is fundamental to the study of population ecology (Stearns 1992). These decisions may impact on fitness immediately or affect subsequent life-history stages (Lindström 1999, Metcalfe & Monaghan 2001). Among potentially important downstream fitness consequences are seasonal carry-over effects, whereby processes in one season have consequences in subsequent seasons (Norris & Marra 2007, Harrison et al. 2011). Carry-over effects have been demonstrated in a wide array of taxa, including insects, amphibians, fish and mammals (reviewed by Harrison et al. 2011). Much of the research on carry-over effects has been undertaken on birds, where studies initially focussed on the effect of winter ecology on subsequent breeding performance, based primarily on stable isotope signatures in feathers grown in winter. Widespread evidence now indicates that diet and habitat quality in winter are linked to key breeding parameters such as timing of arrival at breeding grounds and reproductive success, mediated by body condition during migration (Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004, Sorensen et al. 2009). More recently, studies have investigated links between breeding performance and migration in the subsequent winter using a range of methods, including field readable rings and miniaturised data loggers (Inger et al. 2010, Bogdanova et al. 2011, Latta et al. 2016). These studies demonstrated strong seasonal interactions in line with theoretical models of the costs of reproduction (Ylönen et al. 1998), such that reproductive success is linked to timing of departure on migration and non-breeding location and habitat quality. Overall, these studies suggest that carry-over effects may have profound repercussions for future fitness and population dynamics (Norris & Marra 2007, Harrison et al. 2011).

The majority of studies of carry-over effects have considered associations between 2 seasons. However, decisions or conditions experienced during the winter may affect performance not just in the subsequent summer but also in the following winter and beyond; similarly, the costs of reproduction in summer may extend beyond the following winter into subsequent seasons (Senner et al. 2014; Fig. 1). Accordingly, a growing number of studies have tested seasonal interactions at longer temporal scales than the traditional 2-season comparison (Inger et al. 2010, Hoye et al. 2012, Senner et al. 2014, Latta et al. 2016). A second limitation of existing research is that studies have typically focussed on single populations, yet seasonal interactions may vary across a species' range (Fig. 1). For example, differences in local environmental conditions during the summer may lead to variable downstream effects on characteristics such as timing of migration, with carry-over effects potentially weaker when conditions are more favourable (Legagneux et al. 2012, Harrison et al. 2013). Alternatively, if differ-

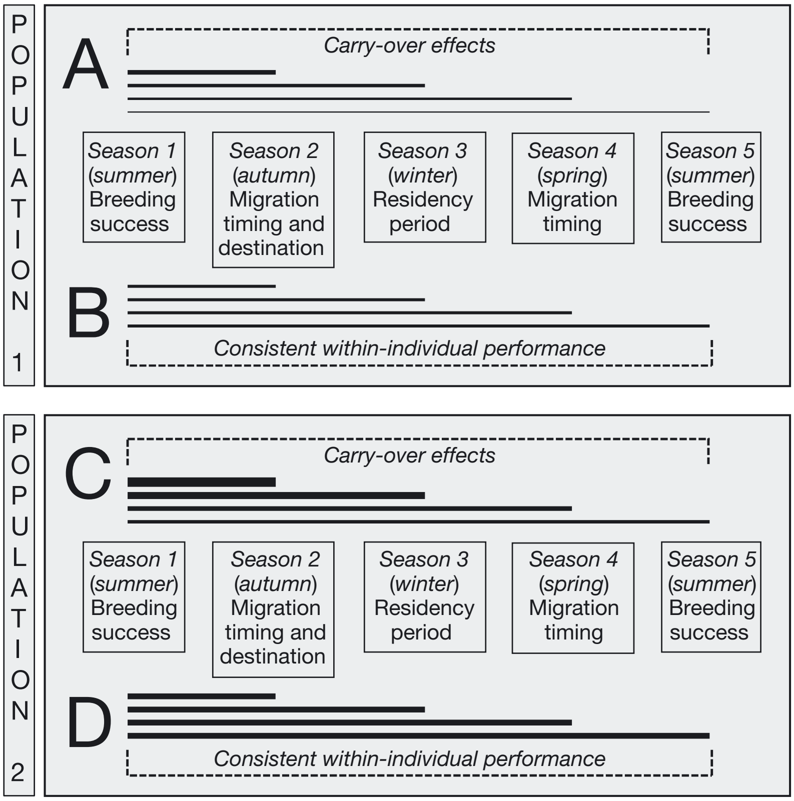

Fig. 1. Temporal structure and spatial variation in seasonal interactions. Temporal structure (illustrated as links between summer breeding success and subsequent seasons from autumn to the following summer) in Population 1 may exist, whereby seasonal interactions (A) weaken over time, evidence for 'true' carry-over effects (width of line denoting strength of link) or (B) are stable over time as a result of consistent within-individual performance. Spatial variation may exist whereby strength of seasonal interactions varies between populations: (C) carry-over effects are stronger in Population 2 (vs. A); similarly, (D) seasonal interactions resulting from consistent within-individual performance are more pronounced in Population 2 (vs. B)

ent populations have common wintering grounds, individuals may adjust their migration schedules to reach the wintering grounds at the same time in order to maximise survival probability. Such variation in timing could shape the strength of carry-over effects across a species' range, with potentially major consequences for meta-population dynamics (Norris & Marra 2007, Harrison et al. 2011).

Studies that quantify seasonal interactions over longer periods than the traditional 2-season time scale in multiple populations can also contribute to the challenging question of whether such interactions arise because of genuine carry-over effects (Norris & Marra 2007, Harrison et al. 2011) or because of cross-seasonal correlations due to stable within-individual performance in breeding and overwinter life-history decisions (Daunt et al. 2006, 2014, Harrison et al. 2011; Fig. 1). Quantifying the relative importance of extrinsic and intrinsic effects has proved challenging in correlative studies, since they are confounded (individuals may vary both in performance and environments experienced). Two approaches have been used to date to tease apart these effects: experimental manipulation in one season as a causal test of carry-over effects (Studds & Marra 2005, Legagneux et al. 2012, Catry et al. 2013, Schultner et al. 2014) and longitudinal measurements in individuals across a range of environmental conditions whereby they act as their own controls (Daunt et al. 2014). Studies that investigate the temporal structure in the strength of seasonal interactions in multiple populations provide a third option. Specifically, effects that are found consistently across populations to be stronger on events in the adjacent season than in subsequent seasons would provide evidence for genuine carry-over effects, whereas a sustained relationship over time would suggest that intrinsic effects predominate (Fig. 1).

In this study, we used data spanning 1 full annual cycle (breeding season to subsequent breeding season) from 10 colonies of black-legged kittiwake *Rissa tridactyla* (hereafter 'kittiwake') across a 23° latitudinal range and 45° longitudinal range in the northeast Atlantic to test for spatio-temporal variation in carry-over effects between reproductive performance and migratory movements. Previous work has demonstrated significant links between reproductive performance, timing of autumn migration and winter destination at 1 colony in the region (Bogdanova et al. 2011). In addition, a multi-colony study of winter distribution reported marked variation in timing of migration yet strong winter admixing among individuals from different breeding populations (Frederiksen et al. 2012), which could form the requisite conditions whereby strength of carry-over effects vary across a species' range.

Our study tested 3 specific hypotheses. First, we hypothesised that, across colonies, there would be an overall relationship between breeding success and scheduling and location of migration, such that unsuccessful individuals depart the colony earlier, migrate farther, reach their winter destinations sooner and spend longer at those destinations, in line with previous findings in this and other species (Summers et al. 1996, Phillips et al. 2005, 2007, Bogdanova et al. 2011). Second, we hypothesised that there would be spatial variation in the strength of carry-over effects among colonies, since variation in environmental conditions among colonies is likely, and more favourable conditions are predicted to dampen carry-over effects (Legagneux et al. 2012, Harrison et al. 2013). Third, we tested alternative hypotheses on the temporal structure of seasonal interactions: (1) relationships are stronger with the adjacent season than with subsequent seasons, representing evidence for true carry-over effects (Harrison et al. 2011); (2) relationships are sustained across time, representing evidence that intrinsic performance underpins seasonal interactions (Daunt et al. 2006).

MATERIALS AND METHODS

Study sites and field data collection

The study was undertaken on adult kittiwakes breeding at 10 colonies across the north-east Atlantic (Table 1, Fig. 2; and see Frederiksen et al. 2012). In the 2009 breeding season, individuals were captured at the nest site using noose poles and fitted with geolocation loggers (Mk13 British Antarctic Survey; 20 × 9 × 6.5 mm; mass: 1.8 g) attached to a plastic leg ring. Deployment methods and protocols were the same at all colonies, and handling time was typically less than 5 min. Breeding success was subsequently recorded for the tracked adults as the number of chicks fledged per nest or, at some colonies, the number of chicks alive at mid to late chick-rearing, a reliable indicator of number of chicks fledged (Lewis et al. 2001). Breeding success was unavailable for 1 of the colonies (Hafnarhólmi, Iceland). In 2010, the study individuals were recaptured, the loggers retrieved and breeding success recorded at all 10 colonies. Deployment and retrieval took place between mid-incubation and mid-chick-rearing, with the majority of captures occurring during early

Table 1. Study colonies of black-legged kittiwakes *Rissa tridactyla*, number of geolocation loggers deployed (Depl.), number of individuals tracked successfully (Retr.: loggers retrieved), and those with known breeding success in both years, in 2009 only and in 2010 only

Colony	Lat.	Lon.	Depl.	Retr.	—Breeding success— 2009 & 2010	 2009	 2010
Norway							
Grumant	78° 10′ N	15° 09′ E	20	16	13	0	2
Bjørnøya	74° 23′ N	19° 08′ E	20	15	5	8	0
Hornøya	70° 23′ N	31° 09′ E	20	15	13	1	0
Anda	69° 04′ N	15° 10′ E	20	12	10	2	0
Røst	67° 30′ N	12° 05′ E	39	22	13	0	5
Iceland							
Hafnarhólmi	65° 32′ N	13° 45′ W	20	12	0	0	9
Faroe Islands							
Stóra Dímun	61° 41′ N	06° 45′ W	20	10	9	0	0
UK							
Fair Isle	59° 32′ N	01° 38′ W	18	15	15	0	0
Isle of May	56° 11′ N	02° 33′ W	25	16	14	0	0
Rathlin	55° 29′ N	06° 19′ W	18	5	5	0	0
Total			220	138	97	11	16

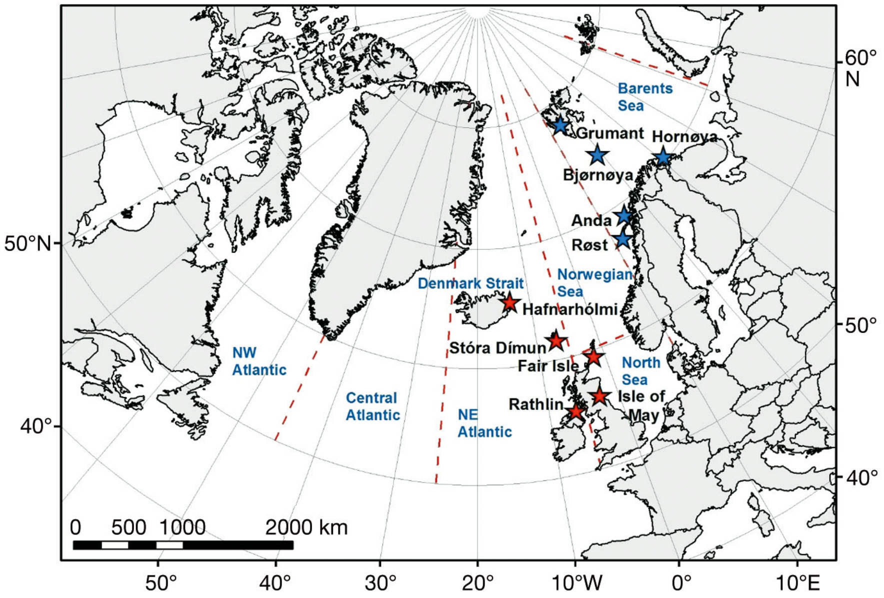

Fig. 2. Location of study colonies of black-legged kittiwakes *Rissa tridactyla* (blue stars: NE colonies, red stars: SW colonies); dashed red lines indicate the boundaries of wintering areas

chick-rearing. In total, 220 loggers were deployed in 2009, 138 of these were retrieved in 2010, of which 124 (89.9%) had breeding success data for 2009, 2010 or both years, 5 (3.6%) were excluded because of logger malfunction, and 9 (6.5%) were excluded because breeding success data were not available. Sample size of individuals that were tracked successfully and for which breeding success was known is shown in Table 1. The sex of a subset of the individuals was determined using molecular techniques (Griffiths et al. 1996) or morphometric measurements (head-bill and wing length; Gasparini et al. 2002).

A previous study at 1 of these colonies (Isle of May National Nature Reserve, Scotland) found no negative impact of the loggers on breeding success or probability of returning to the colony in the following year (Bogdanova et al. 2011). We did not test for logger effects in the current study, but since field protocols at all colonies were the same as in the previous study, we have no reason to expect negative impacts of the devices.

Data processing

Light intensity data recorded by the geolocation loggers were processed to obtain the timing of sunrise and sunset. Best results were obtained with a threshold light intensity of 10 and a sun elevation angle of -3°. For each day at local noon and midnight, latitude was estimated from day length and longitude from the timing of local noon/midnight in relation to UTC. Locations were excluded during the breeding season when there are frequent light interference events, and around the equinoxes (8 September to 20 October and 20 February to 3 April; Frederiksen et al. 2012), when latitude cannot be calculated reliably. In Arctic areas, it was not possible to obtain locations during the period of constant daylight in the summer. For example, at 66, 70, 74 and 78° N, the sun elevation angle is constantly above −3° for the periods 26 May to 18 July, 9 May to 5 August, 25 April to 19 August and 14 April to 30 August, respectively. The retained locations were smoothed to reduce the influence of outliers when calculating migration metrics. Full details of the data processing and calibration are provided by Frederiksen et al. (2012).

Migratory movements were identified based on visual examination of the location data in ArcGIS (v.10.1, ESRI) and were indicated by series of fixes in a consistent direction (average [±SE] distance between adjacent fixes: 254 ± 37 km). In contrast, clusters of fixes lacking directional movement represented residency time within wintering areas (average distance between adjacent fixes: 99 ± 5 km). Outside the breeding season, individuals from the study colonies range widely across the North Atlantic and adjacent seas (North Sea, Norwegian Sea, Barents Sea and Labrador Sea; Bogdanova et al. 2011, Frederiksen et al. 2012). Wintering areas were defined as follows: the North Atlantic was split into 3 parts of approximately equal size (NW: >45° W; Central: 25–45° W; NE: 5–25° W; following Bogdanova et al. 2011); the remaining areas were geographically defined seas (North Sea, Norwegian Sea and Barents Sea; Fig. 2). For each individual, all areas visited outside the breeding season were identified using an automated procedure whereby each location in the dataset was assigned an identity based on the wintering area within which it was positioned. The identity and number of areas visited varied among individuals both among and within colonies. Individuals were considered to visit an area if they spent more than 3 d therein; if visits lasted 3 d or less, the individual was considered to be in transit.

The following metrics of timing of migration were extracted from the location data: for autumn migration: (1) date of departure from the vicinity of the colony (defined as the area within the average location error of 180 km from the colony, Phillips et al. 2004), (2) date of arrival at the post-breeding area (defined as the area visited immediately after breeding) and (3) date of arrival at the main wintering area (defined as the area where the individual spent the most time in winter); for spring migration: (1) date of departure from the main wintering area and (2) date of arrival in the vicinity of the colony. There was no evidence that individuals used a pre-breeding area after the spring migration equivalent to the post-breeding area visited prior to the autumn migration (see 'Results: Effects of breeding success and colony location on subsequent migratory movements'). In contrast to a previous year at the Isle of May, where 42 % of individuals undertook a pre-breeding excursion to the central Atlantic (Bogdanova et al. 2011), 11 individuals from 3 colonies in this study (Rathlin, Northern Ireland; Fair Isle, Scotland; Stóra Dímun, Faroe Islands) undertook an excursion at this time, representing just 9 % of tracked individuals. Moreover, the destinations of these movements were closer and more variable than those recorded for Isle of May individuals in the previous study, so we did not consider them further here. As movements from the study colonies typically involved an east–west component, the timing of migratory movements occurring during the autumn or spring equinox could generally be extracted using longitude only. In the 3 colonies with the highest latitudes (>70° N; Hornøya, mainland Norway; Grumant and Bjørnøya, Svalbard Archipelago, Norway), dates of departure from the colony at the end of the breeding season and arrival at the post-breeding area could not be determined as they coincided with the summer period of constant daylight. Furthermore, some individuals migrated directly to the main wintering area. In addition, 1 individual from Anda (mainland Norway) and 2 individuals from Rathlin stayed in the vicinity of the colony throughout the winter. Thus, migration metrics were not available for all individuals at all colonies (sample sizes in each analysis are shown in Table 2). For each individual, winter residency period was the total amount of time (number of days) spent within the main wintering area. Presence in this area during the equinox periods could be established from longitude.

Effects of breeding success and colony location on subsequent migratory movements

Effects of breeding success and colony location on the timing of subsequent migratory movements and winter residency period were investigated using linear mixed models (n = 108 individuals from 9 colonies). Response variables were (1) date of departure from the vicinity of the colony, (2) date of arrival at the post-breeding area, (3) date of arrival at the main wintering area, (4) winter residency period, (5) date of departure from the main wintering area and (6) date of arrival in the vicinity of the colony. Fixed effects were breeding success in 2009, colony latitude and longitude, and the random effect was colony identity. We adopted the same approach as Bogdanova et al. (2011) in modelling breeding success as a binary variable (successful, i.e. raised at least 1 chick, vs. unsuccessful, i.e. raised no chicks), since the majority of successful kittiwakes raised 1 chick (63 % in 2009 and 76 % in 2010). Previous work has shown differences between the sexes in carry-over effects (Bogdanova et al. 2011, Schultner et al. 2014). However, we could not include sex in the models, as the sample size of sexed individuals was not sufficient to simultaneously test for potential effects of this variable and of breeding success and colony location. However, there was no evidence that breeding success and sex were confounded, as the distribution of males and females among successful and unsuccessful breeders was well-balanced (successful: 47 % males, 53 % females; unsuccessful: 43 % males, 57 % females). The simplest ('null') model contained only a random effect for 'colony' but no fixed effects. The most complex ('full') model contained 'colony' as a random effect, the 3 fixed effects and all interactions. Since the study colonies are distributed in a south-west to north-east direction, evidence for a colony latitude by longitude interaction can be interpreted as an effect of colony location (Fig. 2). In contrast, main effects of latitude and longitude represent north–south and east–west patterns among colonies, respectively. We considered all possible subsets of the variables in the full model, which led to a candidate set containing 19 models.

For the purposes of model comparison, models were fitted using maximum likelihood as they had different fixed effects but the same random structure (Zuur et al. 2009). Support for different candidate models was assessed using Akaike's information criterion adjusted for small sample size (AICc). The model with the lowest AICc value was considered best supported. Models were deemed strongly supported if they differed from the best model by less than 2 AICc units (Burnham & Anderson 2002), unless they were otherwise identical to the best model but contained 1 more parameter, in which case this rule of thumb is not appropriate (Burnham & Anderson 2002) and the more complex models were disregarded on the grounds of parsimony. The final model was re-fitted using restricted maximum likelihood to obtain more unbiased parameter estimates and their standard errors (Zuur et al. 2009). Marginal coefficient of determination (R^2_m representing the variance explained by the fixed effects) and conditional coefficient of determination (R^2_c representing the variance explained by both fixed and random effects; Nakagawa & Schielzeth 2013) were calculated for the best model in each candidate set. Analyses were performed in R (R Core Team 2015; packages nlme, Pinheiro et al. 2016; and MuMIn, Bartoń 2015).

Effects of previous breeding success, timing of migration and winter residency period on subsequent breeding success

Effects of previous breeding success (in 2009), timing of migratory movements and winter residency period on subsequent breeding success (in 2010) were investigated using generalised linear mixed models with binomial error structure (n = 113 individuals from 10 colonies). The response variable was breeding success in 2010, the random effect was colony identity, and potential explanatory variables were (1) breeding success in the previous year (2009), (2) date of departure from the vicinity of the colony, (3) date of arrival at the post-breeding area, (4) date of arrival at the main wintering area, (5) winter residency period, (6) date of departure from the main wintering area and (7) date of arrival in the vicinity of the colony. Due to varying sample sizes for the different explanatory variables (see 'Data processing') and collinearity between some of the timing variables, it was not feasible to consider all of these simultaneously within model selection. Therefore, initial exploratory analyses were carried out, testing separately for relationships between each of the explanatory variables and breeding success in 2010 by comparing the model containing the respective explanatory variable with the intercept-only model. Only variables that were potentially associated with subsequent breeding success based on the initial analysis (whose inclusion resulted in a lower AICc value compared to the intercept-only model) were considered for inclusion in the full model. The 'null' model contained colony identity as a random effect but no covariates. A 'full model' was then constructed, based upon the explanatory variables that were found to be important in the initial exploratory analyses. All subsets of the variables in this full model were then considered, with model selection and assessment of model goodness-of-fit carried out as described in the analysis of effects of breeding success on subsequent winter movements (see previous section). Analyses were performed in R (packages lme4, Bates et al. 2015; and MuMIn, Bartoń 2015).

Winter distribution in relation to previous and subsequent breeding success

For each colony, we examined the relationships between breeding success in 2009 and 2010 and at-sea distribution in the intervening non-breeding season. This involved calculating the kernel density of locations of successful and unsuccessful breeders in each month from the time of departure from the vicinity of the colony in late summer, to return in the following spring. Kernel density was calculated in the R package adehabitatHR (Calenge 2006), with a smoothing parameter h of 180 km, corresponding to the average error of the location data (Phillips et al. 2004). Core areas (50 % kernel contour) were plotted in a Lambert azimuthal equal-area projection. To quantify variation in monthly non-breeding distribution linked to breeding success in 2009 and in 2010, we estimated the similarity between the utilisation distributions of successful and unsuccessful breeders within the core areas using Bhattacharyya's affinity measure (Fieberg & Kochanny 2005). This measure ranges from 0 (no overlap) to 1 (identical distributions). To test whether the observed similarity in distributions between the 2 groups of breeders deviated from that expected by chance, we used a permutation test, where for each colony, we fixed the number of successful and unsuccessful individuals to be the same as in the observed data but randomised the allocation of breeding success to individuals. The permutation test was run for 1000 iterations and the median, 2.5 and 97.5 percentile values for Bhattacharyya's affinity measure over these iterations were extracted: observed values outside these boundaries would indicate a significant difference from random at a 5% significance level. Here, we were particularly interested in detecting levels of similarity that were lower than expected by chance (which would be shown by an observed value below the 2.5 percentile). In both 2009 and 2010, at some colonies, all study individuals bred successfully or unsuccessfully, precluding a comparison of the utilisation distributions in these cases.

The study colonies formed 2 well-defined geographic clusters: UK, Faroese and Icelandic (Rathlin, Isle of May, Fair Isle, Stóra Dimun, Hafnarhólmi) in the south-west of the region, hereafter referred to as SW colonies, and Norwegian (Røst, Anda, Hornøya, Bjørnøya, Grumant) in the north-east of the region, hereafter referred to as NE colonies (Fig. 2). The results are presented by colony cluster to aid descriptions of geographic patterns, but clusters were not used in the analyses.

RESULTS

Effects of breeding success and colony location on subsequent migratory movements

Breeding success was moderately high in 2009, with 72% of tracked individuals raising at least 1 chick. After leaving the vicinity of the colony, 33% of kittiwakes from the SW colonies moved to a post-breeding area in the Denmark Strait, 25% moved to other areas (North Sea, Irish Sea, central Atlantic), and 37% travelled directly to the main wintering area in the north-west Atlantic (Fig. 3); the remaining 5% of individuals remained in the vicinity of the colony. In contrast, most individuals (72%) from the NE colonies initially moved to a post-breeding area in the Barents Sea (Fig. 3), 12% moved to the post-breeding area in the Denmark Strait, 9% migrated to other areas (Norwegian Sea, North Sea, central Atlantic), 5% moved directly to the north-west Atlantic and 2% remained close to the colony.

Date of departure from the vicinity of the colony was related to colony location (as indicated by the interaction of colony latitude by longitude) and breeding success (Table 2). Kittiwakes in SW colonies left earlier than those in NE colonies and, across colonies, unsuccessful breeders departed earlier than their successful counterparts (Fig. 4a). There was 1 model within 2 AICc units of the best model (excluding those with 1 extra parameter, see 'Materials and methods'), containing the 3 main effects (breeding success, latitude and longitude) but no interaction term (see Table S1a in the Supplement at www.int-res.com/articles/suppl/m578p167_supp.pdf). Date of

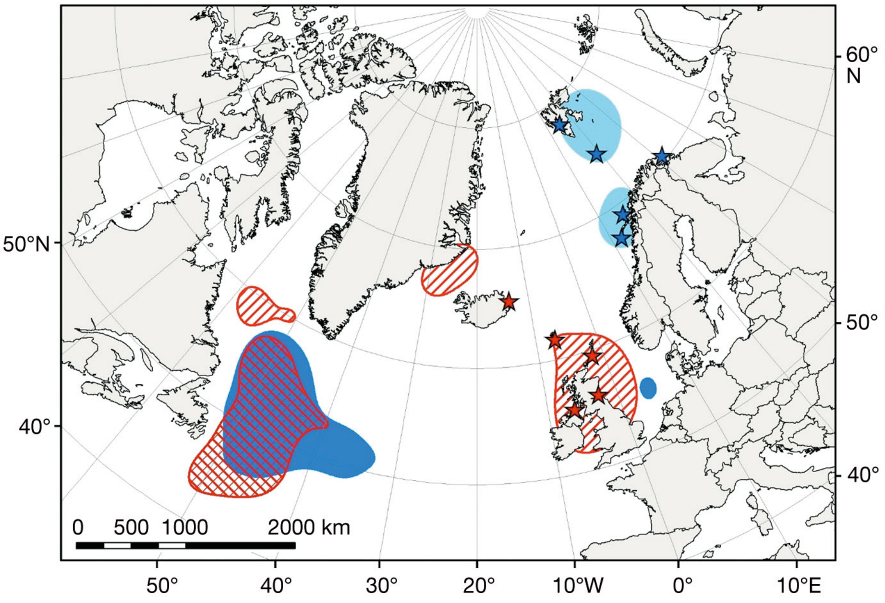

Fig. 3. Core areas (50% density kernel contours) within the post-breeding area (August to September; light blue: NE colonies, single red hatching: SW colonies), and within the main wintering area of black-legged kittiwakes *Rissa tridactyla* (December; dark blue: NE colonies, red cross hatching: SW colonies). NE colonies shown with blue stars; SW colonies shown with red stars

Table 2. Linear mixed models testing for relationships between breeding success of black-legged kittiwakes *Rissa tridactyla* in 2009 (BS), colony latitude and longitude, and timing of subsequent migratory movements or winter residency period. Only the best model for each migration metric is presented. For the full set of candidate models, their AICc values and Akaike weights see Table S1 in the Supplement at www.int-res.com/articles/suppl/m578p167_supp.pdf. R^2_m: marginal coefficient of determination (representing the variance explained by the fixed effects); R^2_c: conditional coefficient of determination (representing the variance explained by both fixed and random effects, see 'Materials and methods' for details)

Migration metric	N individuals	N parameters	Parameter estimate (standard error)							R^2_m	R^2_c
			BS	Lat	Lon	BS:Lat	BS:Lon	Lat:Lon	BS:Lat:Lon		
Departure from colony area	54	6	18.11 (12.63)	−6.98 (1.88)	−41.00 (27.54)			0.67 (0.41)		0.40	0.44
Arrival at post-breeding area	47	7	−4895.64 (1440.47)	−88.74 (23.76)	52.68 (14.78)	81.52 (23.85)	−49.47 (14.84)			0.45	0.45
Arrival at main wintering area	84	9	−299.00 (193.20)	−7.11 (4.05)	−68.17 (25.46)	5.22 (3.11)	37.00 (19.42)	1.03 (0.38)	−0.55 (0.29)	0.23	0.60
Winter residency period	108	9	0.06 (196.58)	4.03 (4.35)	52.46 (28.03)	−0.74 (3.26)	−31.73 (21.93)	−0.82 (0.42)	0.49 (0.33)	0.20	0.51
Departure from main wintering area	84	7	−224.71 (60.59)	−3.59 (1.13)	−30.26 (5.88)	3.45 (0.92)		0.44 (0.09)		0.32	0.32
Arrival in colony area	98	5		−2.36 (0.98)	−40.16 (6.08)			0.59 (0.09)		0.66	0.77

arrival at the post-breeding area was related to an interaction between colony location and breeding success (Table 2). Among individuals from SW colonies, unsuccessful breeders arrived earlier than successful ones, whereas among individuals from NE colonies, date of arrival was unaffected by breeding status (Fig. 4b). Date of arrival at the main wintering area was also affected by a similar interaction between colony location and breeding success (Table 2): unsuccessful breeders from SW colonies arrived earlier than successful indi-

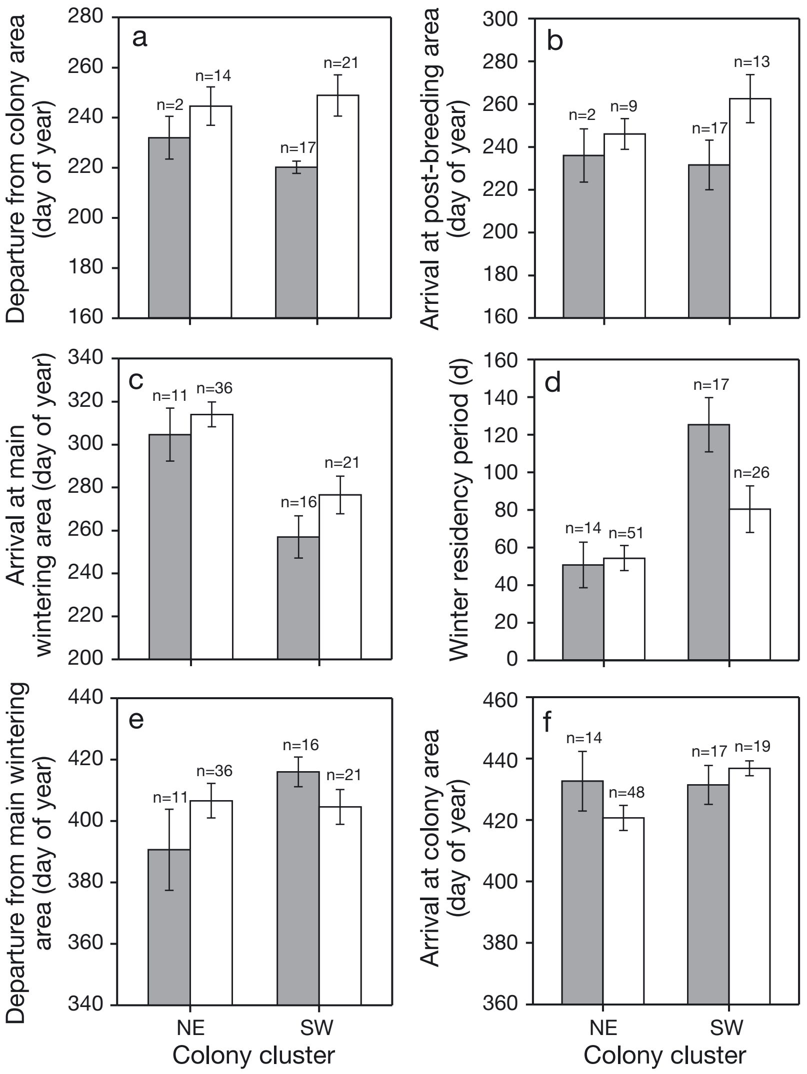

Fig. 4. Timing of migratory movements of black-legged kittiwakes *Rissa tridactyla* and winter residency period in 2009/2010 winter in relation to breeding success in 2009 and colony location: (a) date of departure from the colony area; (b) date of arrival at the post-breeding area; (c) date of arrival at the main wintering area; (d) winter residency period; (e) date of departure from the main wintering area; and (f) date of arrival in the colony area for unsuccessful (grey bars) and successful (white bars) individuals from NE and SW colonies. Days of the year run from 1 January 2009; values are mean ± SE; sample sizes of individuals are shown above the bars

viduals, whereas arrival dates of successful and unsuccessful individuals from NE colonies were similar (Fig. 4c). There were 4 models within 2 AICc units of the best model, all of which contained colony latitude, longitude and their interaction, suggesting a strong effect of colony location (Table S1c).

Winter residency period in the north-west Atlantic was also influenced by interactive effects of breeding success and colony location (Table 2). Unsuccessful kittiwakes from SW colonies spent longer in the main wintering area than successful breeders, whereas among individuals from NE colonies, the time spent in this area was similar in the 2 groups (Fig. 4d). There were 2 models within 2 AICc units of the best model, both containing colony latitude, longitude and the interaction between them (Table S1d).

Date of departure from the north-west Atlantic was also related to an interaction between breeding success and colony location (Table 2). Unsuccessful breeders from SW colonies departed later than successful individuals, whereas they tended to depart earlier among tracked individuals from NE colonies (Fig. 4e). Date of arrival in the vicinity of the colony at the end of the winter was related to colony location only (Table 2); individuals from SW colonies returned later than individuals from NE colonies (Fig. 4f).

Overall, the effects of breeding success and colony location on subsequent migration strategy were strong, but gradually weakened over the course of the winter (evident in the R^2_m values in Table 2), to the point that prior breeding success was not included in the final model explaining date of arrival in the vicinity of the colony in the subsequent season (Table 2).

Effects of previous breeding success, timing of migration and winter residency period on subsequent breeding success

Breeding success in 2010 was lower than in 2009, with 55 % of tracked individuals successfully raising at least 1 chick. Breeding success was most related to colony identity (as evident from the R^2_m and R^2_c values in Table 3). In addition, there was weak evidence that unsuccessful breeders in 2010 had arrived at the main wintering area in the NW Atlantic earlier, and had departed later in the previous winter (Tables 3 & 4). Breeding success in 2010 was not related to date of departure from the vicinity of the colony, date of arrival in the post-breeding area in 2009 or date of arrival in the vicinity of the colony in the spring 2010, and we found no effect of breeding success in 2009 on breeding success in 2010 (Table S2).

Table 3. Generalised linear mixed models testing for relationships between timing of key migratory movements of black-legged kittiwakes *Rissa tridactyla* during the previous non-breeding season and breeding success in 2010 (n = 92 birds; TA: timing of arrival in the main wintering area; TD: timing of departure from the main wintering area). The best model is shown in **bold**; R^2_m: marginal coefficient of determination (representing the variance explained by the fixed effects); R^2_c: conditional coefficient of determination (representing the variance explained by both fixed and random effects, the latter being colony identity)

Model	No. of parameters	AICc	AICc weight	R^2_m	R^2_c	Parameter	Estimate ± SE
TA + TD + TA × TD	5	83.2	0.25	0.07	0.76		
						TA × TD	−0.019 ± 0.021
						TA	0.094 ± 0.086
						TD	−0.074 ± 0.066
						Intercept	−0.325 ± 0.271
TA + TD	**4**	**82.9**	**0.28**	**0.07**	**0.73**		
						TA	**0.014 ± 0.009**
						TD	**−0.013 ± 0.010**
						Intercept	**−0.079 ± 0.052**
TA	3	83.2	0.24	0.05	0.70		
						TA	0.015 ± 0.009
						Intercept	−0.028 ± 0.028
TD	3	84.3	0.14	0.02	0.71		
						TD	−0.014 ± 0.011
						Intercept	−0.041 ± 0.044
Intercept only	2	85.1	0.09	0.00	0.67		
						Intercept	0.016 ± 0.010

Winter distribution in relation to previous and subsequent breeding success

Comparison of the winter distribution of individuals in relation to their success in the previous breeding season (2009) was possible for 4 colonies (Grumant, Hornøya, Røst and Rathlin). At the remaining 5 colonies, all individuals were either successful or unsuccessful. Overlap in utilisation distributions (based on Bhattacharyya's affinity index; Fig. 5) of successful and unsuccessful individuals within the core areas was high in the late summer (August) when individuals were still

Table 4. Percentage of unsuccessful and successful black-legged kittiwake *Rissa tridactyla* breeders in 2010 in relation to date of arrival at the main wintering area and to date of departure from the main wintering area. For illustrative purposes, the timing of movements was split into 2 categories, early and late, based on median values. However, the statistical analysis was carried out with timing fitted as a continuous variable (see 'Materials and methods')

	Unsuccessful in 2010 (%)	Successful in 2010 (%)
Arrival at main wintering area		
Early	68	32
Late	41	59
Departure from main wintering area		
Early	48	52
Late	54	46

in the vicinity of the colony (Fig. 5). Thereafter, overlap was moderate to low throughout the winter, with lower overlap generally observed during the main migration periods (Fig. 5). Overlap was again high in the following spring (April; Fig. 5) when kittiwakes had returned to the vicinity of their breeding colonies. However, in none of the colonies did monthly overlap in distribution of successful and unsuccessful breeders deviate significantly from that expected by chance (Fig. 5; observed values inside the 2.5 and 97.5 percentile values).

Comparison of the winter distributions of individuals that were successful and unsuccessful in the subsequent breeding season (2010) was possible for 7 colonies (Anda, Grumant, Hornøya, Røst, Hafnarhólmi, Isle of May and Rathlin). At the remaining 3 colonies, breeding success was the same for all study individuals, precluding comparison between these 2 groups. Overlap in utilisation distributions of successful and unsuccessful individuals from the NE colonies within core areas was high in summer (August) and the following spring (April) when the individuals had returned to the vicinity of the colony. Overlap was moderate in September, falling to low or 0 in the rest of the winter (October to February), with the exception of Røst where overlap was high between November and February (Fig. 6d). A similar pattern to that in the NE colonies was observed in 1

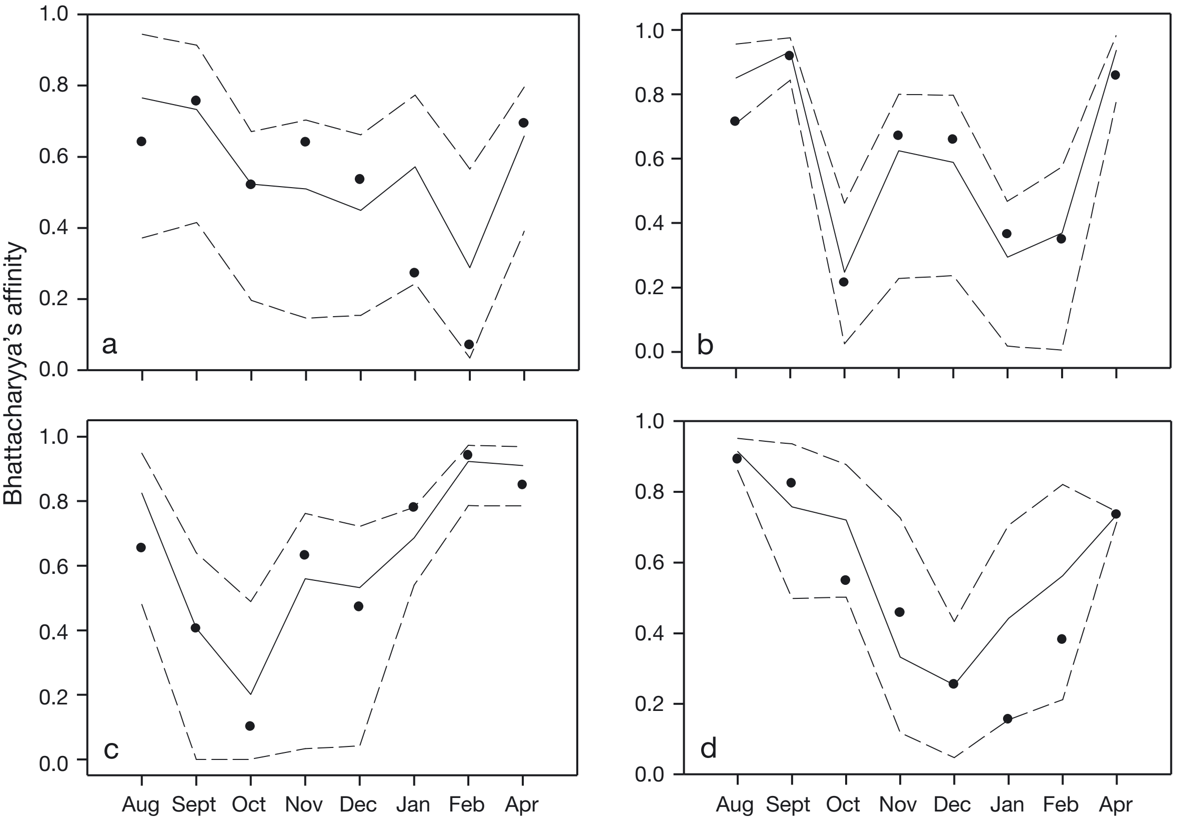

Fig. 5. Similarity in distribution of successful and unsuccessful black-legged kittiwake *Rissa tridactyla* breeders in 2009 from (a) Grumant, (b) Hornøya, (c) Røst and (d) Rathlin within the core areas used (50% kernel contours) in the subsequent winter. Similarity was assessed using Bhattacharyya's affinity measure (Fieberg & Kochanny 2005): shown are observed values (filled circles) and median (solid line), 2.5 and 97.5 percentiles (dashed lines) from randomised permutation (see 'Materials and methods' for details)

of the SW colonies (Rathlin, Fig. 6g). In the remaining 2 SW colonies (Hafnarhólmi, Fig. 6e; Isle of May, Fig. 6f), overlap in utilisation distributions of successful and unsuccessful individuals was high in the summer and following spring, moderate in mid-winter and low to moderate during migration (September to October and February; Fig. 6). Monthly overlap in distribution of the 2 groups of breeders did not deviate significantly from that expected by chance for any of the colonies, although the observed values

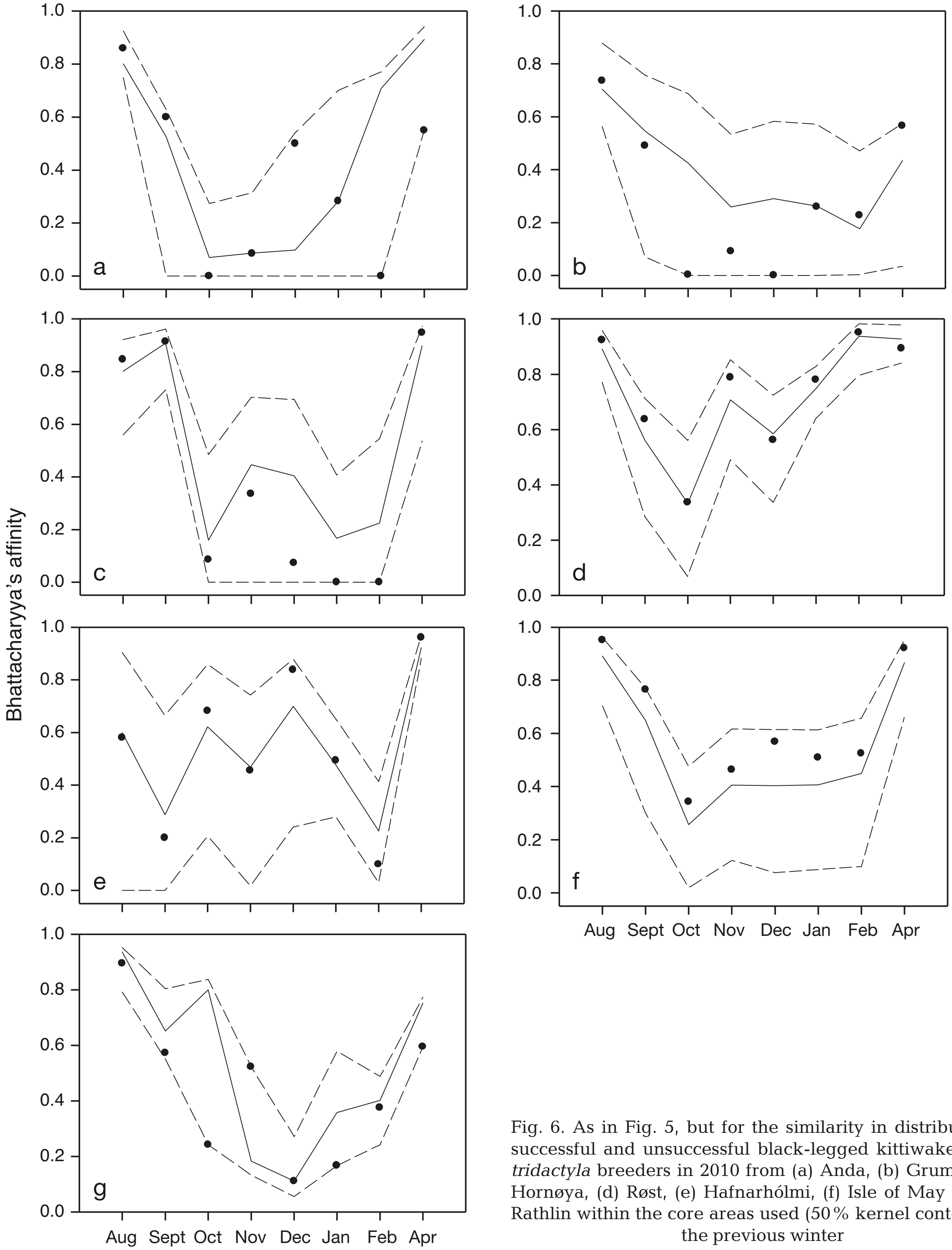

Fig. 6. As in Fig. 5, but for the similarity in distribution of successful and unsuccessful black-legged kittiwakes *Rissa tridactyla* breeders in 2010 from (a) Anda, (b) Grumant, (c) Hornøya, (d) Røst, (e) Hafnarhólmi, (f) Isle of May and (g) Rathlin within the core areas used (50% kernel contours) in the previous winter

(particularly for NE colonies) fell close to or at the 2.5 percentile of the permutation distribution during much of the winter (Fig. 6).

DISCUSSION

To our knowledge, this study is the first to test for individual carry-over effects across more than 2 seasons in multiple populations. We found strong evidence of spatio-temporal variation in the strength of carry-over effects between breeding success and winter migration. Effects of breeding success on migratory movements weakened over the course of the winter, and by the time individuals arrived back at the colony the following year, differences between previously successful and unsuccessful individuals had disappeared. Furthermore, these links between breeding success and subsequent winter migration patterns were only apparent at colonies in the southwest of the study region; no effect was discernible in kittiwakes at Norwegian colonies. In contrast, effects of winter migration on subsequent breeding success were much weaker, and there was no evidence of any association with breeding success in the previous year; instead, breeding success was predominantly associated with colony identity. Winter distribution was not associated with breeding success in the previous or following summer, suggesting that seasonal interactions were most strongly linked to timing of migration, rather than winter destination. Our results suggest that the strength of carry-over effects shows considerable structure across space and time, with potentially important consequences for meta-population dynamics.

We found partial support for our first hypothesis, that there would be an overall relationship between breeding success and scheduling and location of migration. Thus, unsuccessful individuals departed the colony earlier and, for some colonies, reached their winter destination sooner and spent longer at those destinations, in line with previous findings (Summers et al. 1996, Phillips et al. 2005, 2007, Bogdanova et al. 2011). However, our study contrasted with previous work on 1 study population (on the Isle of May), which found a relationship between breeding success and subsequent winter destination, with unsuccessful individuals typically migrating to the NW Atlantic and successful individuals to the northeast Atlantic or North Sea (Bogdanova et al. 2011). However, in the present study, which was based on data collected 2 yr later, there was no evidence of spatial segregation, and the majority of successful and unsuccessful individuals wintered in the northwest Atlantic. Such contrasting downstream consequences of breeding outcome among years at the same colony may be linked to differences in prevailing conditions, such that carry-over effects are stronger when conditions are less favourable (Legagneux et al. 2012, Harrison et al. 2013). Thus, conditions may have been poorer in the season preceding the winter when there were effects on destination. In support of this, breeding success was significantly lower on the Isle of May than in the season before effects were apparent on migration schedules (0.24 vs. 1.36 chicks fledged per pair).

We found support for our second hypothesis, that there would be spatial variation in the strength of carry-over effects among colonies. We found marked spatial variation in the links between breeding success and winter migration, such that, with the exception of timing of colony departure, positive associations were only found in individuals from SW colonies. Most individuals from both colony clusters spent time in a post-breeding area before migrating to their main wintering area. Individuals from the NE colonies moved to the Barents Sea, a highly productive area close to their colonies (Jakobsen & Ozhigin 2011). They remained there until late autumn when constant darkness and ice cover may have made conditions unfavourable for foraging. In contrast, many individuals from SW colonies moved to the North Sea or Denmark Strait, which are also known to be highly productive in late summer (Paramor et al. 2009, Pálsson et al. 2012), departing for their main wintering area before kittiwakes from NE colonies. Breeding success may have a differing effect on migration schedules in different regions because of variation in prevailing environmental conditions. Oceanographic features such as sea temperature anomalies and primary productivity are important drivers of prey distribution and abundance and are therefore key characteristics of the foraging habitats of marine top predators, including seabirds (e.g. Block et al. 2011). If foraging conditions in the Barents Sea are more favourable than in other regions, any difference between successful and unsuccessful individuals may disappear. Conditions at SW colonies may be less favourable since they lie closer to the edge of the species' range. These regional differences could operate via a similar mechanism whereby environmental conditions determine interannual variation in strength of carry-over effects in single populations (Legagneux et al. 2012, Harrison et al. 2013). This assertion is supported by the substantially later migration from the post-breeding area of individuals from NE colonies, and the lower proportion of the population that migrated directly to the main wintering area compared with SW colonies.

The effect of breeding success on migration in SW colonies weakened over the course of the winter in this study, and this pattern was also apparent in previous results from the Isle of May (Bogdanova et al. 2011). Furthermore, there was only limited evidence of an effect of timing of migration on subsequent breeding success, and no evidence that these effects varied across the region. Moreover, there was no evidence that breeding success in the second year was related to success in the previous year. Instead, there was a strong effect of colony identity on breeding success, suggesting that productivity was sensitive to prevailing, local conditions, in line with many previous studies (Clutton-Brock 1988, Newton 1989), and these may potentially have overridden any carry-over effects from the previous winter.

Establishing whether seasonal interactions result from genuine carry-over effects, whereby events or processes in one season have causal effects on subsequent seasons, or cross-seasonal correlations due to stable within-individual performance, is challenging. Powerful approaches exist, in particular manipulative experiments (Studds & Marra 2005, Legagneux et al. 2012, Catry et al. 2013, Schultner et al. 2014) or long-term longitudinal measurements whereby individuals act as their own controls (Daunt et al. 2014). Our approach to investigating the temporal structure in the strength of carry-over effects at multiple colonies provides an additional method of distinguishing between genuine carry-over effects and cross-seasonal correlations (our third hypothesis). The weakening of seasonal interactions over time found consistently across multiple colonies indicates that genuine carry-over effects were likely operating between summer and winter in kittiwakes in the North Atlantic (Hypothesis 3a). Had we found a sustained strength of seasonal interaction across the full annual cycle, a more likely explanation would have been consistent performance within individuals associated with intrinsic ability (Hypothesis 3b). Within-individual consistency coupled with among-individual variation could result from effects of age and experience on breeding success and winter migration. Although our data provide support for true carry-over effects, we cannot discount the possibility that intrinsic effects also partially underpinned the links between breeding success and subsequent migratory movements (Daunt et al. 2006, 2014).

Our analysis only included individuals that made a breeding attempt in 2010 and thus excluded any individuals skipping breeding in that year. This restriction could be important since skipped breeding may not be evenly distributed across groups (Cam et al. 1998) and not including this effect could therefore lead to a bias in the results. However, there was no clear indication of significant non-breeding, i.e. individuals holding sites but not breeding, which is what generally happens in this species (as opposed to individuals being completely absent from the colony for the breeding season; Harris & Wanless 1997). Other potential sampling issues that could have biased our results include cases where individuals were not recaptured in 2010 because they had re-located to inaccessible parts of the study colonies, since breeding dispersal is known to occur in this species, typically associated with breeding failure (Boulinier et al. 2008, Ponchon et al. 2015). However, at the colonies, researchers carried out searches for individuals carrying loggers well outside the location where deployments took place. In addition, site fidelity was high at all colonies and thus few breeding attempts resulting from re-location are likely to have been missed. The study was also unable to quantify rates of partner change between 2009 and 2010, a potentially important determinant of change in breeding success (Black 1996). Incorporating partner change might have helped explain some of the variation in breeding success in 2010 and therefore improved our ability to detect carry-over effects.

Quantifying the strength of downstream fitness effects arising from seasonal interactions is a crucial goal in population ecology. There is now strong evidence that carry-over effects are widespread in nature, but what is less clear is the extent to which they vary temporally and spatially. Our study provides evidence for a decay in strength over time and marked spatial variation in seasonal interactions, and also indicates that the effects of breeding success on subsequent winter migration are much stronger than the effects of migration on subsequent breeding. These complex dynamics are likely to have important consequences for range-wide population dynamics, since carry-over effects have the potential to explain a considerable amount of variation in individual fitness (Norris & Marra 2007, Harrison et al. 2011). The precise spatio-temporal structure of these links will determine which seasonal conditions are most important and which demographic rates and regions are most affected. If the patterns recorded here are consistent across years, the population dynamic consequences of carry-over effects are likely to occur primarily in the south-western part of the range, mediated by conditions during the breeding season affecting over-winter survival probability. Associated geographic variation in population trajectories could, ultimately, lead to species range shifts. To achieve a comprehensive understanding of these fitness consequences, an important future priority is therefore to investigate to what extent the spatial variation in seasonal interactions recorded in this study is consistent across years. An additional priority for future research is to quantify spatio-temporal variation in carry-over effects on demographic rates that we could not consider here, notably survival, breeding propensity and dispersal (Boulinier et al. 2008, Reiertsen et al. 2014). Furthermore, given their potential to drive both temporal and spatial variation in the strength of carry-over effects, investigating the role of environmental conditions should be a key consideration for future studies.

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Contribution to the Theme Section 'Individual variability in seabird foraging and migration'

Mate similarity in foraging Kerguelen shags: a combined bio-logging and stable isotope investigation

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ABSTRACT: Similarity or dissimilarity between 2 individuals that have formed a pair to breed can occur in morphology, behaviour and diet. Such patterns influence partners' cooperation when rearing their offspring, consequently influencing reproductive success. They may confer different benefits, depending on species and contexts. However, the extent to which breeding partners are more similar in morphology, behaviour, and diet is poorly documented. Furthermore, the relationship between behavioural consistency and mate choice is particularly poorly understood. To investigate these issues, Kerguelen shags *Phalacrocorax verrucosus*, which are monogamous with high mate fidelity across years, were studied. Partners were equipped with GPS and diving behaviour loggers. Feather and blood samples were analysed for stable isotopes (δ^{13}C, a proxy of foraging habitat, and δ^{15}N, a proxy of diet/trophic position). Generalized linear mixed effects models and permutation tests were used to investigate pair similarity in morphology, foraging behaviour, behavioural consistency, overlap in foraging areas, and diets/foraging habitats. Mates were found not to exhibit size-assortative mating, but were more similar in foraging behaviour. They did not show assortative or disassortative mating based on foraging behavioural consistency. Furthermore, they followed more similar bearings and overlapped more in foraging areas. In accordance with this, partners were more similar in δ^{15}N. Given the lack of assortative mating by morphology, the similarity in behaviour could be due to individuals selecting mates with similar foraging abilities, linked with individual quality, and/or subsequently using information gained from their partners' foraging strategies (e.g. local enhancement). This could help breeding pairs increase their foraging efficiency and reproductive success.

KEY WORDS: Pair similarity · Mate choice · Kerguelen shags · Spatial use · Diving behaviour · Diet · Stable isotopes

INTRODUCTION

Similarity in behavioural traits within breeding pairs can have important, long-lasting effects on reproductive success and fitness in species with biparental care, probably because of reduced sexual conflict over the provision of parental investment associated with choosing a partner with compatible provisioning rules (Schuett et al. 2011). This allows mates to enhance their cooperation and coordination in the provision of care, essential in species with biparental care and associated with improved reproductive per-

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formance, including offspring growth and survival (Spoon et al. 2006, Schuett et al. 2010, 2011, Rangassamy et al. 2015). Disassortative mating with respect to the partners' recognition cues may, however, lead to reduced inbreeding (Holman et al. 2013). In terms of personality, disassortative mating can lead to the production of offspring of intermediate personality, associated with lower variance in survival in the long-term and higher life expectancy (Dingemanse et al. 2004, Schuett et al. 2010). Risk partitioning may increase the fitness of both partners; while one parent could adopt a risk-averse strategy to provide enough food to ensure that the chicks reach fledging, the other partner might provide the extra bulk for improved post-fledging survival through a risk-prone strategy (Elliott et al. 2010). In contrast, combinations of dissimilar behavioural traits within pairs could result in unstable and disharmonious conditions, generating high stress levels that have the potential to negatively influence reproduction (Von Holst 1998, Rangassamy et al. 2015). In general, the extent of mate similarity in behaviour is poorly investigated (Schuett et al. 2010).

Empirical evidence suggests that mate similarity or dissimilarity confer different advantages and are selected for in different species or environmental conditions in a non-mutually exclusive way (Dingemanse et al. 2004, Schuett et al. 2010). In the dumpling squid *Euprymna tasmanica*, mates showing similar levels of boldness had higher probabilities of reproducing successfully, which might result from either behavioural mate preference or genetic compatibility between partners (Sinn et al. 2006). Similarly, in some bird species, highly behaviourally compatible pair members had higher reproductive success potentially as a result of better cooperation of individuals of similar behavioural traits (Both et al. 2005, Spoon et al. 2006). In contrast, thick-billed murre *Uria lomvia* pairs exhibited a higher reproductive success when they were constituted of one risk-averse and one risk-prone partner (Elliott et al. 2010). Similarly, in animals with distinct foraging territories such as raptors, overall feeding rates become higher when mates adopt different foraging strategies (Andersson & Norberg 1981).

Behavioural consistency could also be used to assess the quality of potential mates, and, therefore, influence mate choice (Byers 2007, Botero et al. 2009, de Kort et al. 2009). Consistency in behaviour can signal predictability and, as such, can provide benefits to partners in many aspects of their social life (Schuett et al. 2010). Consistency could also be an indicator of quality and it has been suggested that consistency could be generated by sexual selection if individuals tend to preferentially choose mates that are consistent or individuals outperform competitors when they are consistent (Dall et al. 2004). Assortative mating in terms of behavioural consistency could be important to enhance behavioural coordination within breeding pairs, leading to increased reproductive success (Spoon et al. 2006). In contrast, in cases in which pairs constituted of a risk-prone and a risk-averse mate have a better reproductive success, disassortative mating by behavioural consistency might be preferable; risk-prone individuals might indeed be more inclined to explore new environments (Dingemanse et al. 2003, Bremner-Harrison et al. 2004), and therefore exhibit lower behavioural consistency, compared to their risk-averse mates. Data on assortment in terms of behavioural consistency is lacking, but studies in zebra finches *Taeniopygia guttata* suggest that pairs comprised of partners that differ in behavioural consistency raise offspring in poorer condition (Schuett et al. 2010, 2011).

Mate similarity or dissimilarity can also be influenced by sexual dimorphism and size-assortative mating. Sexual size dimorphism is widespread in animal taxa, and species exhibiting dimorphism are known to exhibit differences in behaviour and diet (Andersson & Norberg 1981, Camilleri & Shine 1990, Magurran & Garcia 2000, Marcelli et al. 2003, Isaac 2005, Weimerskirch et al. 2006). For example, male and female European polecats *Mustela putorius* forage at different times of the day (Marcelli et al. 2003) and some snake species exhibit dimorphism leading to dietary divergence between males and females (Camilleri & Shine 1990). Hence, sexual dimorphism would be expected to influence mate similarity and lead to a higher mate dissimilarity in behaviour and/or diet within dimorphic species (Andersson & Norberg 1981, Elliott et al. 2010) in comparison to monomorphic species. However, when size-assortative mating occurs, such dissimilarity is likely to be reduced as mates are then more similar in morphology and, therefore, expected to be more similar in behaviour as well in comparison to non-mated individuals. The interplay between dimorphism, size-assortative mating, and mate similarity in behaviour and diet has rarely been investigated.

Seabirds are generally socially monogamous, exhibit biparental care, and show high mate fidelity (Bried & Jouventin 2002). As such, seabird partners establish specific foraging strategies in order to enhance their reproductive success through, for example, better coordination of provisioning behaviour (Davis 1988, Shoji et al. 2011, Thiebot et al. 2015). Despite the potentially long-lasting and important consequences of pair similarity on reproductive success, only 2 studies, to the best of our knowledge, have focused on identifying pair similarity in the diet and behaviour of seabirds. They showed that partners do not necessarily display similar food preferences (Harris et al. 2016), and that similarity in partners' diets can lead to a decline in chick growth rates and fledglings produced (Watanuki 1992). To fill these knowledge gaps, testing the pair similarity in key traits affecting offspring provisioning and condition, such as in foraging metrics and behavioural consistency during the breeding season, is needed, particularly in dimorphic species in which males and females are expected to differ in behaviour and diet.

Kerguelen shags *Phalacrocorax verrucosus* are suitable for investigations of relationships in the behaviour, consistency in foraging and diet of partners within a breeding pair. Individuals exhibit strong specialisation in such traits that can be maintained over the long-term, regardless of their sex, and therefore could be used by individuals to evaluate the quality of potential mates (Bearhop et al. 2006, Cook et al. 2006, Camprasse et al. 2017a). They are long-lived, resident, and benthic foraging seabirds, and individuals repetitively exploit the same foraging areas (Camprasse et al. 2017a). In addition, both parents often exhibit high nest fidelity, mate retention, and share incubation and chick-rearing duties (Aebischer et al. 1995, Sapoznikow & Quintana 2008, C. A. Bost pers. obs.). Kerguelen shags exhibit sexual dimorphism, with males being larger and heavier than females, as well as specialisations in feeding times, with females foraging in the morning and males foraging in the afternoon (Cook et al. 2013); these patterns might be expected to lead to mates exhibiting differences in behaviour, which makes Kerguelen shags interesting models to investigate the interplay between sexual dimorphism, size-assortative mating, and pair similarity.

In the present study, the similarity in foraging behaviour and morphology within pairs of Kerguelen shags was examined through the use of morphometric measurements and the combination of stable isotope dietary analysis and bio-logging techniques. Our aim was to determine whether (1) individuals exhibit size-assortative or -disassortative mating; (2) the foraging behaviour of partners was more or less similar compared to non-mated birds; (3) the consistency in foraging behaviour of partners was more or less similar compared to non-mated birds; (4) partners overlapped more or less than non-mated birds in foraging locations; and (5) partners exhibited more similar or dissimilar diets/foraging habitats compared to non-mated birds.

MATERIALS AND METHODS

Instrumentation

Field work was conducted at Pointe Suzanne (49°26′S, 70°26′E), Kerguelen Island, southern Indian Ocean, during the 2014/2015 breeding season. Sampling occurred during 2 sessions. First, a total of 20 Kerguelen shag *Phalacrocorax verrucosus* individuals (both partners from 10 nests) were equipped with GPS data loggers (I-gotU GT120, Mobile Action; 44.5 × 28.5 × 13 mm, 12 g in air corresponding to ca. 0.5% of mean body mass) for 3 to 6 d at the end of the incubation/early chick-rearing period (26 November to 10 December, hereafter 'incubation/early chick-rearing'), when chicks were no older than 1 wk. During this session, nest checks every 2 or 3 d allowed us to determine the age of the chicks. Second, a total of 22 birds (both partners from 11 nests, including 6 new nests and 5 nests used during the first deployment session) were equipped for 3 to 12 d during the late chick-rearing period (6 to 18 January, hereafter 'late chick-rearing'), of which the 10 previously sampled birds were deployed with GPS data loggers while the remaining 12 individuals were equipped both with GPS data loggers and time-depth recorders (TDRs, LAT1800S, Lotek Wireless; 36 × 11 × 7.2 mm, 4.8 g in air corresponding to ca. 0.2% of mean body mass). During this second session, chicks were ca. 30 to 40 d old, except for one pair that had a chick ca. 10 to 15 d old. Monitoring of the nests could not be conducted at all times but a high proportion of observed change-overs (75.8%) occurred after females came back from their morning trips, after which they tended to stay at the colony for the day (E. C. M. Camprasse pers. obs.), and therefore chicks were still in the presence of a parent most of the time. All but one brood had a single chick at deployment. This unique brood, however, lost their second chick immediately after deployment. While no quantitative data was collected on the rest of the population, this low number of chicks per brood was a general pattern within the colony compared to the maximum of 3 chicks that Kerguelen shag pairs can raise during a single breeding season. In conjunction with poor breeding success in sympatrically breeding Gentoo penguins at the time of the study, such a pattern seems indicative of unfavourable environmental conditions (Camprasse et al. 2017b, this Theme Section).

Individuals were captured at the colony using a noose attached to a fishing pole, weighed in a cloth bag using a suspension scale (±25 g, Pesola), and banded with an individually numbered coloured plastic ring on one leg and an individually numbered metal ring on the other leg for identification. The data loggers, encased in heat-shrink plastic for waterproofing, were attached to the back feathers using waterproof tape (Tesa 4651) and cyanoacrylate glue (Loctite 401). Handling times ranged from 15 to 20 min during which the bird's head was covered with a hood to reduce stress. Females tended to forage in the morning while males foraged mostly during the afternoon (Cook et al. 2013). Whenever possible, we took advantage of this difference in schedule to deploy data loggers before the birds left the colony.

Individuals were gently recaptured 3 to 18 d later as previously described. The data loggers were removed, individuals were weighed again, and morphometric measurements (bill length, bill width, head length, wing length, and tarsus length) were taken using a vernier caliper (±0.05 mm), or ruler (±1 mm) (except for one bird for which we obtained mass but not morphometric measurements). In addition, 3 to 6 dorsal dark contour feathers were plucked and a blood sample (0.5 to 1.5 ml) was collected by venipuncture of a tarsal vein.

GPS loggers were programmed to sample position at 1 min intervals during incubation/early chick-rearing and at 2 min intervals during the chick-rearing period. The TDR units were set to record depth at 1 s intervals.

GPS data were obtained for only 17 of the 20 individuals equipped during the first round of deployments due to logger failure, resulting in 7 pairs with spatial data for both partners at this stage. During the second deployment session, spatial data were obtained for 21 out of 22 individuals, and thus 10 pairs had complete data for both members. Of these 10 pairs, 6 pairs were from new nests and 4 pairs were from those that were deployed with loggers during incubation; of these 4, 2 had complete data from the first deployment session. This resulted in a total number of 15 different pairs with data on both members. For 13 of those pairs, both members had data on more than one trip and could be used to evaluate consistency in spatial use.

Isotopic analyses

The measurement of ratios of stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) is a powerful tool to investigate the food and feeding ecology of consumers (Cherel et al. 2005a). More specifically, $\delta^{13}C$ and $\delta^{15}N$ values of seabirds are considered to be proxies of their foraging habitats and diets/trophic position, respectively (Cherel & Hobson 2007). Overall, $\delta^{13}C$ values decrease along a latitudinal gradient (Cherel & Hobson 2007, Jaeger et al. 2010) and $\delta^{15}N$ values increase with trophic level (Cherel et al. 2010). $\delta^{13}C$ enrichment also occurs for inshore or benthic species as opposed to offshore or pelagic ones (Hobson et al. 1994). Isotopic values (details in Cherel et al. 2008) were measured on whole blood (hereafter 'blood') and contour feathers (hereafter 'feathers') of the studied shags. The rationale is that the 2 complementary tissues integrate different periods of information. Blood is a metabolically active tissue that covers a period of weeks before sampling, whereas feathers, a metabolically inert tissue, reflect the foraging ecology at the time they were grown. In other species from the blue-eyed shag complex, such as the Antarctic shag *P. bransfieldensis*, contour feathers are replaced in March, immediately after breeding (Bernstein & Maxson 1981). Here, blood and feathers collected during the breeding period reflect the breeding period itself and the previous post-breeding moulting period that took place almost 1 yr before the study, respectively.

In the laboratory, blood samples were freeze-dried and powdered. Lipid extraction was not necessary as the C:N mass ratio was <3.5 for all blood samples (Cherel et al. 2005b). A single contour feather per bird was cleaned of surface lipids and contaminants using a 2:1 chloroform:methanol bath, air-dried, and cut into small pieces. Nitrogen and carbon isotopic ratios were measured with a continuous flow-isotope ratio mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite for carbon and atmospheric N_2 for nitrogen. Replicate measurements of internal laboratory standards (acetanilide and peptone) indicated measurement errors <0.15 ‰ for both $\delta^{13}C$ and $\delta^{15}N$. Isotopic values were obtained for both members of 15 pairs.

Data processing

All data processing and analyses were conducted in the R Statistical Environment, version 3.2 (R Core Team 2015). GPS records were visually inspected and individual trips were determined. The *diveMove* package (Luque 2007) was used to apply a speed filter on the GPS data to remove erroneous locations and obtain summaries of diving metrics from TDR records (only dives >1 m were considered in analyses). As dive depths (i.e. depths at the deepest part of a dive) were not normally distributed within individuals, the mode of dive depths instead of the mean was recorded for each trip. The means of dive durations and the sum of vertical distance travelled per trip were also calculated. These values were used to calculate a mean of means (or mean of modes) and coefficients of variation (CVs) across foraging trips for each individual. The packages *trip* (Sumner 2013) and *sp* (Pebesma & Bivand 2015) were used to obtain foraging metrics for each trip (bearings, total distances travelled, maximum distances and trip durations). Bearing for each trip was calculated as the angle between the colony and the most distal point of the tracks and standard deviation in bearing was calculated for each individual using the *circular* package (Lund & Agostinelli 2011). Means and CVs for all metrics were obtained per individual and per stage, except bearings, for which SD was calculated.

Kernel home ranges for each trip of each individual were determined in the *adehabitatHR* package (Calenge 2006). Because Kerguelen shags tend to fly to their foraging grounds and dive predominantly at the most distal part of their trip (Camprasse et al. 2017a), and because we wanted to know whether sexes or partners forage in the same locations, only core foraging area (50% home range) was calculated. Each trip for each male within each breeding stage was compared to each trip for each female sampled within the same stage by calculating the overlap in core foraging area between these 2 trips with the 'kerneloverlap' function in the *adehabitatHR* package using the Bhattacharyya's affinity (Fieberg & Kochanny 2005).

An index of spatial use consistency was calculated for each individual within each stage. For each pair of trips within a deployment, a kernel overlap was calculated (e.g. for a bird with 3 trips, 3 overlap values were obtained, between Trip 1 and Trip 2, Trip 2 and Trip 3 and Trip 1 and Trip 3), as described above for the overlap between males and females. The average of these numbers was obtained and used as an index of consistency for each individual within each stage.

Data analyses

Linear mixed effects models were used to confirm sexual dimorphism in mass in study birds, as mass data was obtained both at incubation/early chick-rearing and in late chick-rearing for some birds, and always both at deployment and retrieval. Dimorphism in size was checked using only 1 of the morphometrics obtained (tarsus length, as the other ones were correlated using a linear regression) as single measurements were obtained. When looking at pair similarity, 2 kinds of analyses were run depending on the structure of the data: when a single observation per individual was available, permutation tests were run, and when multiple observations were available (i.e. one observation per trip on multiple consecutive trips), generalized linear mixed models (GLMMs) with crossed random effects were used. p-values <0.05 were considered significant for all tests. Specifically, a significant p-value for the permutation tests or binomial GLMM meant that partners were more similar or dissimilar than expected by chance and summarizing the data for 'true pairs' and 'false pairs' gave the direction of the effect.

To investigate any potential correlations in morphology in partners, a principal component analysis (PCA) was run on masses at deployment and retrieval and on the 5 body measurements. The Euclidean distances for all possible combinations of males and females were calculated from the scores obtained thanks to the PCA for each individual. Euclidean distances were used as a way to examine the pattern of similarities in the body size and mass of individuals in the sample (Wojczulanis-Jakubas et al. 2011). Permutation tests were carried out in the *permute* package (Simpson 2014) on the matrix containing the Euclidean distances and whether they came from actual paired individuals (value of 1) or not (value of 0) with the null hypothesis being that partners were not more similar than expected by chance. Permutation tests (10 000 iterations) randomly assigned each Euclidean distance to a type of pairing. Permutational p-values were used and they are defined as the proportion of randomized values as extreme or more extreme than the observed value (Manly 1991).

The 3 dive-level variables that we extracted from the TDR data (dive duration, maximum depth, and vertical distance) were correlated, so we only considered maximum depth in the analysis (maximum depths and trip duration: Spearman's rho = 0.93, $p < 0.0001$, maximum depths and sums of vertical distances: Spearman's rho = 0.36, $p = 0.05$). Maximum depths were used in modelling as representative of habitat selection in the vertical dimension. The absolute values of the differences in maximum depth between males and females were used to investigate the similarity or dissimilarity between paired females and males within the chick-rearing stage, because we were not specifically interested in which sex had the higher value, but just in the distance between them. We estimated the probability of pairs constituting true pairs using logistic regression in a generalized linear mixed-effects modelling framework ('glmer' in the *lme4* package (Bates et al. 2011), with a binomial distribution and logit link). Best models were selected based on their Akaike information criteria. For the diving behaviour model, differences between males and females in maximum dive depths were used as explanatory variables, while the individual bird ID was used as a crossed random effect with males crossed with females of each possible pair (with 1 being the 'true pair' and 0 being a 'false pair'). Total distance travelled, maximum distance and trip duration were highly correlated (total distance and trip duration: Spearman's rho = 0.60, $p < 0.0001$, total distance and maximum distance: Spearman's rho = 0.96, $p < 0.0001$). Therefore, only total distance travelled was included in the analysis of pair similarity or dissimilarity in spatial use. As such, to investigate whether partners exhibited a similar spatial use, a model similar to the one described above included the absolute values of the differences in total distances between males and females for each possible pair and for each stage. In the final model, these differences, stage and their interaction were used as explanatory variables.

To determine if partners were more similar or dissimilar than non-mated birds in consistency, classical multidimensional scaling was applied and the Euclidean distances for all possible combinations of males and females were calculated separately for each stage. Pairing was indicated (with 1 being 'true pair' and 0 being 'false pair'). Permutation tests were performed and permutational p-values were obtained, as described above, for dive behaviour consistency and spatial use consistency, respectively. For the former, Euclidean distances were calculated from the coefficients of variation in maximum depth, dive duration and sum of vertical distance travelled; in this case, all 3 variables were used as their coefficients of variation were not correlated. For the latter, the variables included in the calculation of the Euclidean distances were the following, uncorrelated measures of consistency: index of spatial use consistency, standard deviations in bearing, and coefficients of variation in trip duration, total and maximum distances.

To examine whether partners of the same nest overlapped more or less than birds from different nests, 2 tests were run: one with bearings and one with the kernel overlap values. In both cases, the probability of pairs constituting true pairs was analysed by logistic regression using a generalized linear mixed-effects model (GLMM with a binomial distribution and logit link). The absolute values of the differences between bearings in true and randomised pairs, and the overlap values between males' and females' trips, stage, and their interaction were used as explanatory variables in 2 different models, while individual bird ID was used as a crossed random effect with males crossed with females of each possible pairing.

To investigate whether partners had a more similar or dissimilar diet/trophic level compared to non-mated birds, the Euclidean distances for all possible combinations of males and females were calculated, separately for each stage, either for $\delta^{13}C$ and $\delta^{15}N$ values combined, for $\delta^{13}C$ values only, or for $\delta^{15}N$ values only, in blood and feathers. Permutation tests were carried out on the matrices containing the Euclidean distances and whether they came from actual paired individuals.

RESULTS

Equipped Kerguelen shags *Phalacrocorax verrucosus* were sexually dimorphic (Table 1). Overall, males were (mean ± SD) 0.29 ± 0.06 kg heavier ($t_{30} = 4.60$, $p < 0.001$) and had tarsus lengths 2.60 ± 0.65 mm ($t_{29} = 3.97$, $p < 0.001$) greater than females. Partners were not more similar or dissimilar to each other in morphological traits and body mass than expected by chance. Indeed, permutation tests indicated no significant differences between paired individuals and the rest of the individuals sampled (permutational p = 0.18).

Diving data were obtained for all 12 birds equipped with TDR during late chick-rearing. Males tended to dive deeper and be more variable in dive depths than females (Fig. 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m578p183_supp.pdf) as shown in Camprasse et al. (2017a). The difference

Table 1. Morphometric measurements (mean ± SD; min.–max.) of all Kerguelen shags equipped at the Pointe Suzanne colony, Kerguelen Islands

Measurement	Females (n = 14)	Males (n = 15)
Body mass (kg)	2.1 ± 0.2 (1.9–2.6)	2.4 ± 0.2 (2.0–2.8)
Head length (mm)	132.1 ± 6.9 (124.5–149.0)	133.6 ± 4.4 (125.5–142.0)
Tarsus length (mm)	63.6 ± 1.5 (60.9–66.2)	66.1 ± 2.9 (61.4–69.2)
Beak width (mm)	13.2 ± 1.4 (11.9–16.9)	14.0 ± 1.0 (12.7–15.7)
Culmen length (mm)	50.3 ± 1.7 (47.3–52.6)	52.4 ± 3.8 (40.9–56.6)
Wing length (mm)	272.0 ± 7.4 (252.0–282.0)	278.9 ± 27.9 (183.0–295.0)

in maximum depth between mates was lower than for non-mated birds (binomial GLMM: $\chi^2 = 68.34$, df = 1, $p < 0.0001$); on average mates differed in depths by 17.1 ± 0.9 m, as opposed to 27.6 ± 0.5 m in non-mated birds. Males and females did not differ in trip metrics, including trip durations, maximum distances, total distances, and bearings (Tables 2 & S2). Partners were more similar in spatial use than expected by chance. Indeed, the differences in total distances travelled were smaller in true pairs compared to randomised pairs (binomial GLMM: $\chi^2 = 26.14$, df = 1, $p < 0.0001$). Further, there was a significant effect of stage on the differences in total distances (binomial GLMM: $\chi^2 = 7.74$, df = 1, $p = 0.005$), and a significant interaction between pairing and stage (binomial GLMM: $\chi^2 = 24.90$, df = 1, $p < 0.0001$). Specifically, mates differed in total distances travelled by 14.95 ± 0.80 km at incubation/early chick-rearing, and 16.38 ± 0.71 km in late chick-rearing; in contrast, the differences in total distances for non-paired birds did not significantly change between incubation/early chick-rearing (19.80 ± 0.36 km) and in late chick-rearing (19.61 ± 0.25 km).

Table 2. Summary of trip metrics for Kerguelen shags instrumented at the Pointe Suzanne colony, Kerguelen Islands, separated by sex and breeding stage. Data are mean ± SD

Parameter	Females		Males	
	Incubation (n = 8, 35 trips)	Chick-rearing (n = 10, 61 trips)	Incubation (n = 7, 48 trips)	Chick-rearing (n = 11, 90 trips)
Trip duration (h)	5.9 ± 1.8	6.1 ± 3.1	5.4 ± 2.9	5.1 ± 2.6
Maximum distance (km)	10.2 ± 6.5	9.0 ± 6.7	9.5 ± 8.0	11.1 ± 5.5
Total distance (km)	26.6 ± 14.0	22.7 ± 15.2	25.0 ± 19.5	29.6 ± 20.3
Bearing (°)	47.6 ± 0.15	60.8 ± 0.36	75.4 ± 0.44	55.9 ± 0.26
Index of consistency	0.6 ± 0.13	0.5 ± 0.18	0.4 ± 0.20	0.5 ± 0.16

Within pairs, no specific pattern was observed in terms of the consistency of males and females, both in terms of diving behaviour (Fig. 1) and spatial use. Paired birds were not more similar or dissimilar in consistency in maximum depth, dive duration, and sum of vertical distance (permutational $p = 0.14$). Lastly, paired birds were not more similar or dissimilar in spatial use consistency (consistency index, SD in bearing, CV in maximum distance, total distance, and trip duration) compared to non-paired birds (permutational $p = 0.51$).

Males always departed after their mates came back from their morning foraging trips during incubation/early chick-rearing, and did so 75.8% of the time during late chick-rearing. Within pairs, males and

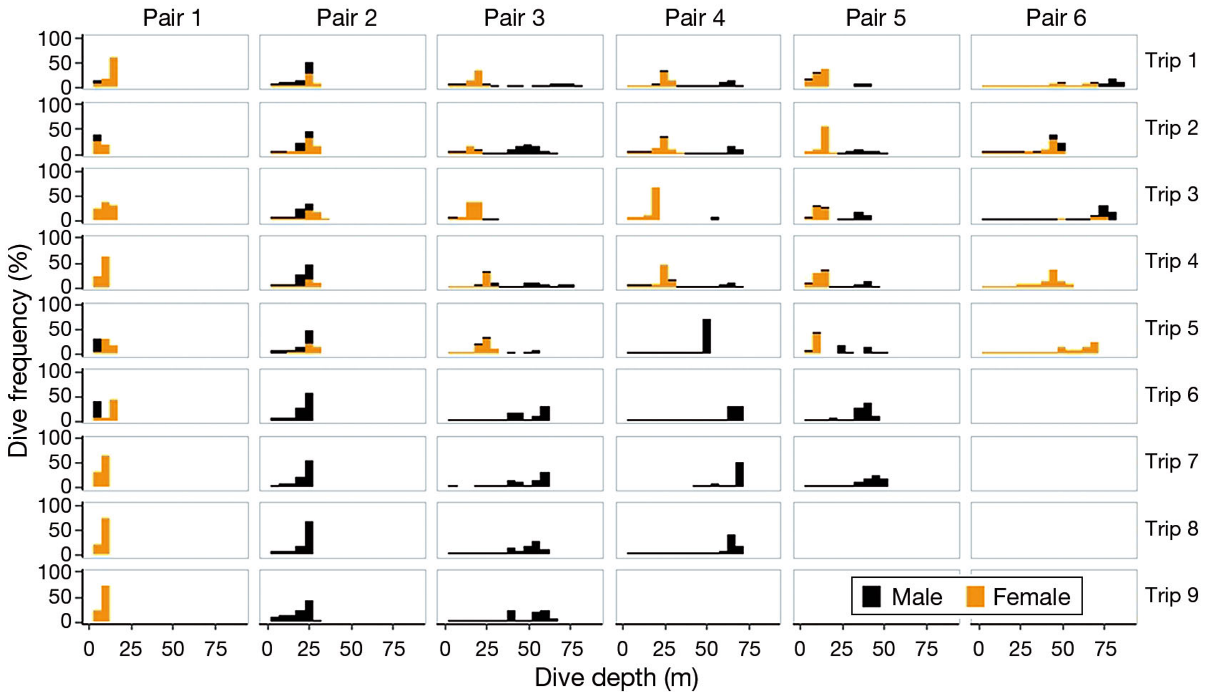

Fig. 1. Dive distributions in relation to dive depth for pairs of Kerguelen shags *Phalacrocorax verrucosus* equipped at the Pointe Suzanne colony, Kerguelen Islands

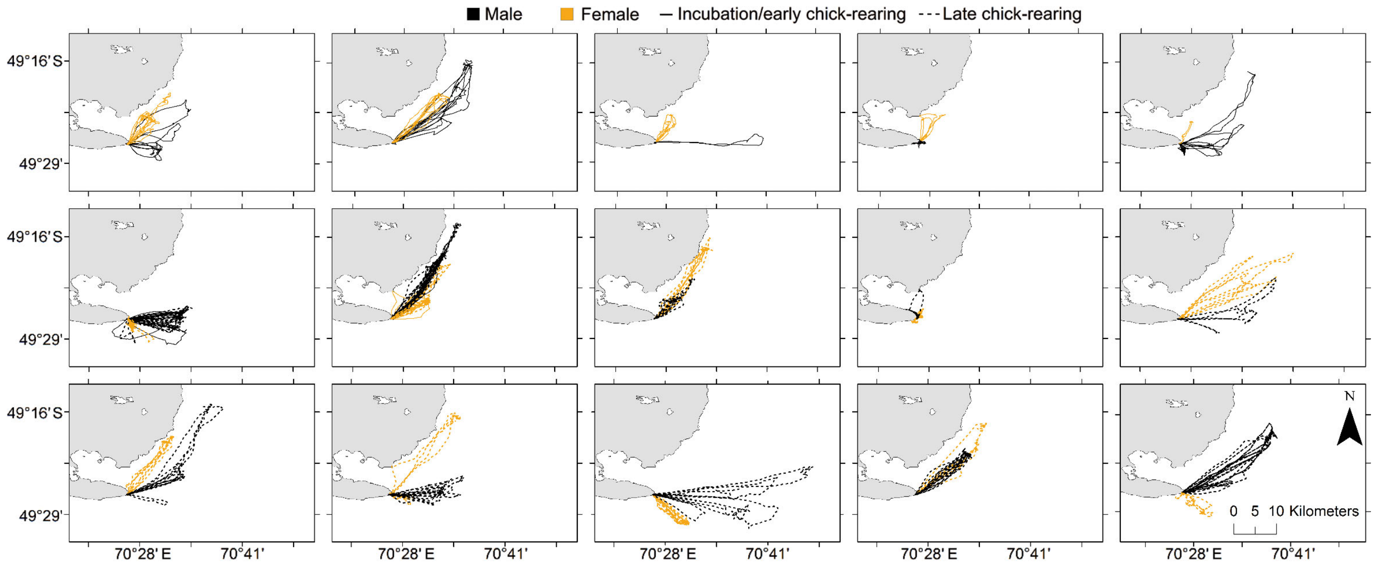

Fig. 2. Consecutive GPS tracks for all pairs of Kerguelen shags *Phalacrocorax verrucosus* equipped at the Pointe Suzanne colony, Kerguelen Islands

females followed similar bearings to their foraging areas (binomial GLMM: $\chi^2 = 187.14$, df = 1, $p < 0.0001$) (Fig. 2) and there was a significant effect of stage on differences in bearings (binomial GLMM: $\chi^2 = 32.36$, df = 1, $p < 0.0001$), but no interaction between stage and the differences in bearings (binomial GLMM: $\chi^2 = 2.60$, df = 1, $p = 0.11$). Mates differed in bearings by 41.8 ± 2.9° at incubation/early chick-rearing and 51.98 ± 2.2° in late chick-rearing; in contrast, the differences in bearings for non-paired birds were 55.7 ± 1.0° at incubation/early chick-rearing and 70.68 ± 0.8° in late chick-rearing. Overall, paired birds overlapped significantly more than non-paired birds (binomial GLMM: $\chi^2 = 159.05$, df = 1, $p < 0.0001$) and overlap was not affected by stage (binomial GLMM: $\chi^2 = 1.60$, df = 1, $p = 0.21$). The mean overlap was 14.5 ± 0.6% for paired birds and 9.8 ± 0.2% for non-paired birds.

There were large inter-individual differences in both δ^{13}C and δ^{15}N values in blood of the sampled Kerguelen shags (difference: 5.5 and 3.6 ‰, respectively) (Table S3, Fig. S1). Blood δ^{13}C values ranged from −19.97 to −14.44 and δ^{15}N values ranged from 12.88 to 16.68. There were no differences in blood isotopic values between sexes, thus confirming that males and females had similar foraging habitats (δ^{13}C) and diet/trophic levels (δ^{15}N) during breeding. When taking into account both blood δ^{13}C and δ^{15}N values, partners were not more similar or dissimilar than expected by chance for both stages (permutational $p = 0.43$ and $p = 0.31$, at incubation/early chick-rearing and late chick-rearing, respectively). Blood δ^{13}C values of paired birds were not more similar or dissimilar than expected by chance (permutational $p = 0.86$ and $p = 0.74$, at incubation/early chick-rearing and late chick-rearing, respectively). However, blood δ^{15}N values of paired birds were closer than expected by chance (permutational $p = 0.04$ and $p = 0.01$, at incubation/early chick-rearing and late chick-rearing, respectively). Indeed, in contrast to blood δ^{13}C values, male blood δ^{15}N values were positively linearly correlated to female δ^{15}N values (Fig. 3). As with blood, there were large inter-individual differences in feathers in both δ^{13}C and δ^{15}N values of the sampled Kerguelen shags (difference: 6.7 and 3.9 ‰, respectively), with δ^{13}C values ranging from −20.06 to −13.32 and δ^{15}N values ranging from 13.47 to 17.41. Partners did not have more

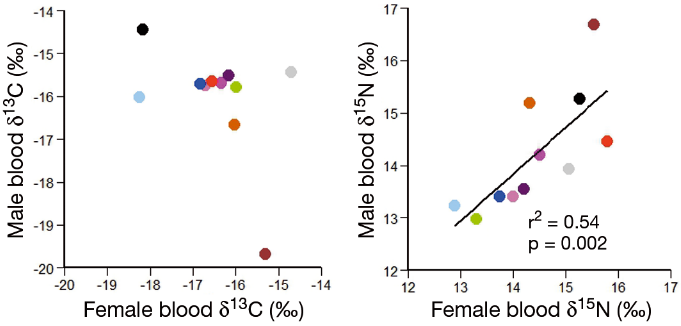

Fig. 3. Correlations in blood δ^{13}C and δ^{15}N values of partners of Kerguelen shags *Phalacrocorax verrucosus* (partners are indicated by shared colours, n = 11 pairs) sampled at the Pointe Suzanne colony, Kerguelen Islands; δ^{15}N ♂ = 0.89 · δ^{15}N ♀ + 1.42

similar feather isotopic values, whether taking into account both $\delta^{13}C$ and $\delta^{15}N$ values, $\delta^{13}C$ values only, or $\delta^{15}N$ values only (permutational p = 0.59, 0.68, and p = 0.10, respectively).

DISCUSSION AND CONCLUSIONS

In the present study, we investigated the similarity or dissimilarity in the foraging strategies of Kerguelen shag *Phalacrocorax verrucosus* partners using the complementary approaches of bio-logging and stable isotope analysis. The salient results can be summarized as follows: (1) mates did not show assortative or disassortative mating by either morphometrics or behavioural consistency; (2) they were, however, more similar than expected by chance in foraging behaviour, followed more similar bearings, and overlapped more in foraging areas, and (3) they had more similar diets/similar trophic levels than expected by chance.

Our results confirm previous findings that Kerguelen shags are dimorphic in body size and mass (Cook et al. 2013). Within breeding pairs, males were always heavier and generally structurally larger than their female partners. Such strong sexual dimorphism suggests a differential niche utilization for males and females in the population (Selander 1966, Cook et al. 2013) with the potential to affect pair similarity/dissimilarity in foraging behaviour. Indeed, it is expected that dimorphic mates exhibit a higher dissimilarity compared to monomorphic species, as dimorphic birds can display divergent foraging behaviours based on their morphology (Weimerskirch et al. 2006, Elliott et al. 2010). While Kerguelen shags are dimorphic and exhibit temporal segregation with females foraging mostly in the morning and males mostly in the afternoon, differences in their foraging behaviour and its consistency during the time of this study were shown to be limited (Camprasse et al. 2017a). If sexual dimorphism led males and females to display different foraging strategies, then pair dissimilarity in foraging behaviour would be expected. However, in the present study, differences in foraging behaviour between males and females were limited, so if any pair dissimilarity in foraging behaviour were found, it would be due to different factors.

In the present study, we found no evidence of size-assortative or -disassortative mating. Although seabirds are known to mate assortatively by size (Wagner 1999, Forero et al. 2001, Helfenstein et al. 2004), structural size is not necessarily enough to explain mate choice (Bried & Jouventin 2002, Berzins et al. 2009). Indeed, in some cases, assortative mating is based on ornamental traits such as plumage or foot/beak colour, rather than structural size (Berzins et al. 2009, Nolan et al. 2010). For example, in other *Phalacrocorax* species, assortative mating with respect to crest size has been shown to occur, with crest size being an indicator of individual condition (Daunt et al. 2003). Alternatively, lack of size-assortative mating has been shown in birds and might happen when a specific trait is sexually selected in one sex only (Murphy 2008), which seems less likely in our study species as it has not been shown in shags. Instead of preferring mates that are similar to themselves, all individuals could also show the same preferences for a trait, especially when it is an honest signal indicative of individual quality (Jones et al. 2008, Schuett et al. 2010).

Despite the sexual dimorphism and the lack of size-assortative mating that was expected to reduce the degree of behavioural similarity in dimorphic mates, our findings suggest that partners are still more similar than non-mated birds in foraging behaviour. Indeed, mates exhibited smaller differences in dive depths and total distances travelled compared to non-paired birds. This pairing in terms of foraging behaviour might result from an active choice if individuals are able to evaluate potential mates and their quality, as individual quality and foraging parameters have been shown to be linked (Lewis et al. 2006, Lescroël et al. 2010). For example, in common murres *Uria aalgae*, females of higher quality had increased chick feeding rates and lower trip durations (Lewis et al. 2006). Similar patterns were found in Adélie penguins *Pygoscelis adeliae*, especially at the end of the breeding season, with poorer breeders diving deeper and making longer trips (Lescroël et al. 2010). Alternatively, this pair similarity could be a consequence of developing similar behaviours after pairing, as a result of communication between mates. Studies investigating the similarity or dissimilarity in behaviour in partners are lacking. Contrasting with our results, imperial shag *Phalacrocorax atriceps* pairs were shown to be constituted of either both benthic members, both pelagic members, or a mixture of both (Harris et al. 2016). Positive assortment by behaviour has been shown in a few studies in groups such as birds (Both et al. 2005, Schuett et al. 2011), fishes (Budaev et al. 1999), and cephalopods (Sinn et al. 2006). In other contexts, better reproductive outcomes might be associated with the fact that more similar individuals exhibit improved cooperation and coordination, leading, for example, to better provisioning of offspring (Spoon et al. 2006, Schuett et al. 2010, Sánchez-Macouzet et al. 2014). This might explain the fact that mates were more similar to each other at incubation/early chick-rearing compared to late chick-rearing, as increased cooperation and coordination is more crucial when mates are incubating or guarding small chicks, as this is the period where parents are most at risk of losing their eggs or chicks through accidental dislodgement, predation, and/or hypothermy (Tveraa et al. 1998, Kober & Gaston 2003, Catry et al. 2006).

There is some evidence that certain combinations of levels of consistency within pairs can influence their reproductive success, and behavioural consistency might be important for mate choice (Schuett et al. 2010, 2011). An individual might benefit from choosing a partner exhibiting consistent behaviour; for example, it might profit from having a mate showing a consistent level of paternal care or territory defence by avoiding having to constantly re-assess its mate's quality and accordingly adjust its own behaviour (Schuett et al. 2010). Assortative mating by behavioural consistency might be expected when consistency is an indicator of quality and/or predictability in provisioning behaviour and parental care; consistent individuals would then be expected to mate preferentially with consistent individuals, resulting in inconsistent individuals having to mate with each other (Schuett et al. 2010). Furthermore, it might be beneficial to choose a mate with high consistency, associated with the benefits mentioned above, but dissimilar behaviour, linked with the acquisition of more diversified prey items, for example (Watanuki 1992). Risk partitioning can increase fitness in paired individuals, with one partner adopting a risk-averse strategy to provide enough food for chicks to be able to fledge and the other exhibiting a risk-prone strategy to provide the extra bulk for enhanced post-fledgling survival (Elliott et al. 2010). As risk-prone individuals can be more inclined to explore new environments and, therefore, be less consistent in their foraging behaviour (Dingemanse et al. 2003, Bremner-Harrison et al. 2004), disassortative mating by behavioural consistency has the potential to be beneficial in pairs, resulting in improved fitness. Despite these apparent advantages of assortative or disassortative mating by behavioural consistency, no such pattern was observed in Kerguelen shags at our study site. Hence, individuals in the present study might predict their mates' provisioning behaviour based on their similarity in foraging behaviour rather than whether they are similarly consistent or not.

We propose that breeding success is related more to foraging behaviour than consistency in foraging behaviour. For example, poorer breeders might have longer trip durations, associated with longer distances travelled and better breeders might dive deeper (Lewis et al. 2006, Lescroël et al. 2010). The breeding success of pairs (number of fledglings, fledgling mass) in our study could not be determined, however, and we could not determine whether more similar or dissimilar partners in terms of behaviour or behavioural consistency had a higher breeding success. Future studies should aim at incorporating such parameters, as well as investigate the influence of differences in environmental conditions and thus prey availability, on pair similarity. In order to better understand the interplay between pair similarity and environmental conditions, it would be necessary to quantify pair similarity and breeding success in moderate environmental conditions, when among-pair variation is likely to be greatest.

In the present study, partners were found to follow more similar bearings, especially at incubation/early chick-rearing, as well as to overlap significantly more in foraging areas compared to non-mated birds. To the best of our knowledge, such a pattern differs from the only study reporting on mate overlap in spatial use in central-place foragers: imperial shag partners in Argentina did not seem to overlap, although whether partners overlapped more or less than non-paired birds was not tested (Harris et al. 2016). The results shown in our study suggest that such patterns could result from mate choice and/or could allow birds to reduce time spent searching for food if individuals use information gained regarding their partners' foraging strategies to adopt more efficient tactics (e.g. local enhancement). Indeed, seabirds, including cormorants, are known to be able to use visual, tactile, and olfactive cues from their congeners for more efficient foraging (Ward & Zahavi 1973, Silverman et al. 2004, Weimerskirch et al. 2010) as are other groups of animals (Galef & Wigmore 1983, Drapier et al. 2002, White et al. 2008). Furthermore, seabirds are able to use information transfer and depart the colony following the direction from which conspecifics are returning to the colony (Tremblay et al. 2014). A transfer of information between paired birds would be facilitated by the temporal segregation in foraging between males and females, with males cueing on their partners' flight directions as they return from morning foraging trips and follow more similar bearings to their partners compared to other conspecifics (Tremblay et al. 2014). Such similarity not only in bearings but also in foraging areas might also explain why mates tended to dive at more similar depths, as Kerguelen shags are benthic divers.

The spatial overlap in foraging range shown here could explain why partners tended to consume prey at similar trophic levels. This pattern did not occur outside of the breeding season, when birds are not constrained to come back to the nest and therefore are less likely to gather information from their partners, as judged by the δ^{15}N values of feathers. Assortative mating by diet has been shown to occur in fishes and may reflect either the ability of individuals to evaluate potential mates or a consequence of another preference (e.g. habitat choice, morphology) (Snowberg & Bolnick 2008, Martin 2013). Therefore, assortative mating by diet could either reflect a preference for partners that have similar diets or be a consequence of other factors after pairing based on other criteria has occurred. As it is unclear how individuals are able to assess prospective mates' diet, it seems more likely that individuals choose mates based on their individual quality, for example via the selection of mates with similar crest sizes (Daunt et al. 2003), and then feed at similar trophic levels as a consequence of exhibiting similar foraging behaviour and prospecting for food in similar areas. In contrast, no correlation was observed within breeding pairs in the plasma δ^{15}N values of imperial shags and all potential combinations of foraging behaviour were found within pairs (both partners were benthic feeders, or pelagic feeders, or the pairs were mixed, Harris et al. 2016). Similarity in food preferences within breeding pairs has also been reported in great skuas *Stercorarius skua* and slaty-backed gulls *Larus schistisagus*, in which, in contrast to Kerguelen shags, mates frequently hunt together (Watanuki 1992, Votier et al. 2004). In slaty-backed gulls, the increase in diet overlap between mates corresponded with a decrease in chick growth rates and number of fledglings produced (Watanuki 1992). Therefore, the benefits for partners of foraging on similar prey remain unclear, unless it derives from mates communicating on where to find food for reduced searching time and improved chick provisioning as suggested above.

Other factors could lead to mates being more similar foragers than expected by chance which also affect their ability to rear offspring (Bradley et al. 1995, Jouventin et al. 1999, Ludwig & Becker 2008); some species exhibit age-specific dietary and spatial segregation, primarily determined by a 'cohort effect' that would lead individuals sharing a common life history to forage preferentially together or to share similar foraging limitations (Pelletier et al. 2014). Lastly, subcolony variation, known to occur even in small colonies, could indirectly influence the overlap in foraging areas and the similarity in diet within pairs (Masello et al. 2010, Bogdanova et al. 2014). In those studies, individuals at similar locations within the colony tended to forage in the same direction. In our study, however, birds were equipped within a few meters of each other yet still foraged repeatedly in different directions (Camprasse et al. 2017a).

In conclusion, Kerguelen shags were paired with partners that displayed more similar foraging behaviour, foraging bearings, and overlap in foraging areas and diet trophic level than expected by chance. We suggest that shags may pair with individuals of similar quality (e.g. via selection for individual of similar crest size or other traits signalling quality), resulting in mates having similar foraging abilities. They thus have the potential to forage in areas of similar characteristics. Further exchange of information between mates at change-overs could then lead mates to follow similar bearings and overlap more in foraging areas compared to non-paired birds; in turn, this may lead mates to feed at more similar trophic levels. Investigating the ways in which birds assess mate quality (e.g. in terms of foraging efficiency, ornamentation, condition or experience) is crucial to build on the conclusions of the present study. Collecting data during years of different environmental conditions will also help understand if the patterns highlighted in our study are maintained in years of better food availability. Lastly, more studies are necessary to understand the reproductive consequences of mate similarity and should incorporate, for example, long-term measures of reproductive success (Fraser et al. 2002). Such a step is crucial to understand the repercussions of mate choice in seabirds.

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Contribution to the Theme Section 'Individual variability in seabird foraging and migration'

Flexibility in otherwise consistent non-breeding movements of a long-distance migratory seabird, the long-tailed skua

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ABSTRACT: Quantifying within- and between-individual variation in animal migration strategies is a first step towards our understanding of the ability of migrants to adjust to changes in the environment. We studied consistency (or, conversely, flexibility) in movement patterns at large (>1000 km) to meso-scales (100–1000 km) during the non-breeding season of the long-tailed skua *Stercorarius longicaudus*, a long-distance migratory Arctic seabird, using light-based geolocation. We obtained 97 annual tracks of 38 individuals and quantified similarity between routes. Overall, tracks of the same individual were generally within about 200 to 300 km of their previous year's route, and more similar than tracks of different individuals. Some flexibility was observed during migration, but individuals were faithful to their staging areas in the North Atlantic and in the Benguela Current off Namibia and South Africa. Over the course of the winter, an increasing number of individuals started to deviate — up to 5200 km — from the previous year's route. Intriguingly, individuals could be highly consistent between 2 consecutive years and flexible between other years. Site-shifts in late winter seem to reflect responses to local conditions, but what promotes this larger flexibility remains unclear and requires further study. Our results show that individual long-tailed skuas are generally consistent in their itineraries, but can show considerable flexibility in some years. The flexibility in itineraries suggests that long-tailed skuas are able to adjust to environmental change, but the mechanisms leading to the observed within- and between-individual variation in movement patterns are still poorly understood.

KEY WORDS: Individual consistency · Repeatability · *Stercorarius longicaudus* · Seabirds · Tracking · Non-breeding movements · Flexibility

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INTRODUCTION

The ability to track the movements of individual birds throughout multiple annual cycles has fuelled interest in individual variation in migration and wintering patterns (e.g. Phillips et al. 2005, Dias et al. 2011, Guilford et al. 2011, Vardanis et al. 2011). Quantifying variation in movement patterns within and between individuals is a first step to ultimately understand the ability of populations to adjust their movement patterns to changes in the environment, as selection acts on phenotypic variation (Alerstam 2006, van Noordwijk et al. 2006).

Intriguingly, species vary in the degree of individual consistency (or, conversely, their flexibility) in movement patterns, i.e., the degree to which individuals use the same migration routes or staging areas between years (Dias et al. 2011, Guilford et al. 2011, McFarlane Tranquilla et al. 2014, Vardanis et al. 2016). We are only starting to understand what drives consistency in individual use of staging areas, but it is generally assumed that the spatio-temporal predictability of resources is important (Newton 2010, Trierweiler et al. 2013). Seabirds are an interesting species group in this respect, as oceanic areas show large spatio-temporal differences in both availability and predictability of resources (Longhurst 2006, Weimerskirch 2007). While seabirds likely target areas with high productivity for foraging (which can vary in predictability; Weimerskirch 2007), migration routes connecting staging areas are often strongly linked to wind patterns that allow efficient travelling (Felicísimo et al. 2008), and they often traverse large areas with low availability and/or predictability of resources. Thus, movement patterns of seabirds during the non-breeding season might consist of a combination of consistent itineraries in periods or areas with high resource availability and more flexible, nomadic movement patterns in periods or areas with low resource availability, such as areas crossed during migration. A synthesis on how consistency in staging site and migration routes use might vary throughout the non-breeding season is still lacking.

Using light-based geolocation to track individuals, we studied the consistency of movement patterns of the long-tailed skua *Stercorarius longicaudus* during the non-breeding season at large (>1000 km) to meso (100–1000 km) scales. This long-distance migratory seabird breeds in the sub- to high Arctic. Details of migration routes, stopovers and movements during winter in the southern Atlantic have only recently been revealed (Sittler et al. 2011, Gilg et al. 2013). Gilg et al. (2013) showed that long-tailed skuas have a strategy of itinerancy, i.e. visiting multiple places throughout the winter (Moreau 1972). This behaviour is not uncommon among seabirds (e.g. Phillips et al. 2005, Hedd et al. 2012, Fijn et al. 2013, van der Winden et al. 2014, Orben et al. 2015) but notably different from a strategy of residency where only a single wintering site is used (McFarlane Tranquilla et al. 2014, Yamamoto et al. 2014). Itinerancy is an interesting strategy in the context of consistency versus flexibility in site use, as it, at least intuitively, leaves more possibility for flexibility, even during the winter period.

We quantified variation in individual movement patterns throughout the entire non-breeding season, thus including migration and winter periods. In particular, we investigated if, where and when movement patterns differ between and within individuals. As long-tailed skuas seem to exploit areas with predictable high productivity, e.g. the Benguela Current and the central North Atlantic (Gilg et al. 2013), we expected individuals to revisit the same staging areas and thus to exhibit high levels of consistency in their itineraries.

Most earlier studies on the consistency of bird migration were based on individuals tracked over 2 consecutive years (e.g. Dias et al. 2011, Guilford et al. 2011, McFarlane Tranquilla et al. 2014). Although this allows partitioning of within- and between-individual variation in behaviour, 3 or more years of tracking data are needed to study whether individuals vary in their behavioural flexibility (i.e. not the level, but the 'width' of their behavioural response; Dingemanse & Wolf 2013). This idea has, to our best knowledge, not been explored to date, but is needed to understand if and how migrants may cope with environmental change. We tracked individual long-tailed skuas for 3 or more years and investigated whether individual birds display the same level of consistency or flexibility across years, or can be consistent between some years but flexible between other years.

MATERIALS AND METHODS

Study species, study areas, capture techniques and geolocator deployment

Two subspecies are recognized in the long-tailed skua: the nominate subspecies *Stercorarius longicaudus longicaudus* breeds from Scandinavia eastwards and is replaced by the white-bellied subspecies *S. l. pallescens* from eastern Siberia to Svalbard (Manning 1964). Only the migration of *S. l. pallescens* has been revealed before, by Gilg et al. (2013), showing that skuas breeding in Greenland and Svalbard depart from the breeding areas in late August, migrate via a stopover in the central North Atlantic towards West Africa and arrive at the main wintering grounds off southern Africa between late September and late November. Spring migration commences in March or April, and birds arrive on the breeding grounds in late May/early June.

Adult long-tailed skuas of the nominate subspecies *S. l. longicaudus* were captured between 2011 and 2015 in the Vindelfjällen Nature Reserve near Ammarnäs, Sweden (65° 59′ N, 16° 01′ E). Adults of the Nearctic subspecies *S. l. pallescens* were captured between 2010 and 2015 at Kongsfjorden, Svalbard (79° 57′ N, 12° 6′ E) and 3 sites in Greenland: Zackenberg (74° 28′ N, 20° 34′ W), Karupelv (72° 50′ N, 24° 00′ W) and Hochstetter Forland (75° 09′ N, 19° 40′ W). Birds were captured on the nest using bow nets or remote-triggered nooses and away from the nest using hand-held net guns or noose carpets (in a few cases, birds were lured by a decoy and playback of the 'long call' — a call used in courtship and territorial disputes). Geolocators of 3 types (Mk-18L and Mk-18H, produced by the British Antarctic Survey, and C65, produced by Migrate Technology) were leg-mounted using a Darvic ring. The total added weight (geolocator, Darvic ring, cable tie, self-amalgamating tape and super glue) amounted to ca. 2.2, 2.6 and 1.8 g for the Mk-18L, Mk-18H and C65 types, respectively, which is 0.5 to 1.2 % of the mean body mass of adult long-tailed skuas (n = 129). In addition, biometry and a blood sample for DNA sexing were taken. Individuals were sexed using molecular techniques (Fridolfsson & Ellegren 1999). Single tracks from 8 individuals from Greenland and Svalbard have been published earlier (Gilg et al. 2013). The period between 2 subsequent breeding seasons is referred to as a year; the data obtained in this period are referred to as a track. References to seasons are from a northern hemisphere perspective.

Geolocator data analyses

After recapture of the tagged birds, geolocators were removed and data were downloaded from the geolocators and decompressed using BASTrak (British Antarctic Survey) or IntigeoIF software (Migrate Technology). The subsequent analysis was carried out entirely using R 3.1.2 (R Core Team 2015) and a set of packages, in particular the R package 'GeoLight' (Lisovski & Hahn 2012). Geolocators recorded ambient light level in arbitrary units (Mk-18L, Mk-18H) or lux (C65) in 1 min intervals and saved the maximum of these values every 5 min. Sun events were calculated unsupervised from light measurements using the function 'twilightCalc' and a light threshold value of 10 (Mk-18H) or 2 (C65). Spending the non-breeding season entirely at open sea, light measurement data from the long-tailed skuas was generally 'clean', i.e. most sun events could automatically be assigned with a relatively low amount of misclassification (due to e.g. shading events). This was checked by visual inspection of plots of date against time of sunrise or sunset, from which unlikely twilight events were identified and removed. For a sequence of potential sun angles, locations were calculated for each noon and midnight. We selected the sun angle resulting in a good fit of location estimates to the shape of the continents and a close match in latitude estimates before and after the equinoxes. Final sun angles for individual loggers ranged from −1° to −3° for the Mk-18H model and −4.5° to −6.0° for the C65 model. Position estimates from light-based geolocation typically have a mean error of ±185 km for flying seabirds (Phillips et al. 2004) and these errors are especially large in close proximity to the equinoxes. Therefore, positions within 14 d from either side of the equinoxes (20 March and 22 September) were removed. Remaining positions were smoothed by calculating the 3 d running mean, using equations from Gilg et al. (2013). All further analyses were based on smoothed positions, with no data around the equinoxes.

Staging areas

We followed Gilg et al. (2013) in defining staging periods when distance between smoothed positions were smaller than 200 km for at least 3 consecutive days. Subsequently, staging areas were identified by creating a 95 % utilization distribution kernel based on staging positions of all individuals, using the 'adehabitatHR' package for R (Calenge 2011). For this, a Lambert azimuthal equal-area projection was used with a grid cell size of 50 km and a smoothing factor of 200 km. Kernels were estimated for 4 space/time segments of the data: (1) before 1 January, between 25° and 60° N, (2) before 1 January, south of 25° N, (3) after 31 December, south of 25° N and (4) after 31 December, between 25° and 60° N. The split at 1 January is well after arrival at the main wintering areas but before long-distance northward movements (Gilg et al. 2013). The area between 25° and 60° N encompasses the large stopover area in the North Atlantic used by many seabirds, including long-tailed skuas (Sittler et al. 2011, Gilg et al. 2013). Few positions were obtained north of 60° N, in particular for birds breeding at Svalbard or Greenland as they travelled here at times with more or less constant daylight. The area south of 25° N contains all wintering areas.

Consistency in movement patterns

Within- and between-individual consistency was mapped over entire recorded tracks, applying the method used by Guilford et al. (2011) and Dias et al. (2013) to calculate distances between tracks, based on nearest-neighbour analysis. For each position estimate in a focal track, we calculated the great-circle distance to the nearest position estimate in another track. The nearest neighbour was selected from the comparison track within a time window. Using a short time window will retain effects of different timing (hence can be used to test for route and timing consistency, which is not the topic of the current contribution), whereas a longer time window removes the effect of timing (thus tests for route consistency only). We quantified median within-individual intertrack distances for a range of time windows (7 to 121 d, with steps of 6 d) to investigate when the gradual removal of a timing effect on the intertrack distance fades. Next, one time window was selected visually Fig. A1 in the Appendix) and used for the analysis and figures of route consistency. If 2 tracks follow the same route, intertrack distances from the first track will be biased in the part where the comparison track has missing values due to the equinox. Therefore, if the nearest neighbour of the comparison track is a first or last position on either side of the equinox, this measurement is excluded. In this way, only more or less parallel parts of the tracks are compared, reducing bias due to missing positions during equinoxes. For reasons of interpretability, we only included comparisons of each track with tracks from the previous year.

We studied the resulting intertrack distances in 2 ways. First, we calculated the overall median intertrack distance per comparison to get an overall measure of track similarity. To allow for greater spatiotemporal resolution and inference of fidelity to staging areas, we also calculated the median intertrack distance per comparison for 6 'segments'. Median intertrack distances were then calculated within the 4 staging kernels mentioned above. In addition, median intertrack distance was calculated for the southbound (before 1 January) and northbound migration (at or after 1 January) based on all locations that fell outside the staging kernels and south of 50° N. The resulting values were continuous, non-negative and right-skewed. Although such data can be modelled using e.g. gamma or inverse-Gaussian error distributions, we log-transformed the data (a variance-stabilizing transformation) to allow the use of a Gaussian error distribution, for which routines to calculate intra-class correlation coefficients (ICCs or r, repeatability) are readily available (Nakagawa & Schielzeth 2010). Bayesian generalized linear mixed models (GLMMs) were fitted using the package MCMCglmm for R (Hadfield 2010), with 130 000 iterations, a burn-in of 30 000 iterations and a thinning rate of 100. As an indication of significance, we provide p_{MCMC} values, which are twice the probability that the parameter value is above or below zero. A focal individual in each comparison was included as a random effect to account for pseudo-replication and to assess within- and between-individual variance components. If populations differ in migration routes and destinations, they may inflate between-individual intertrack distances. We therefore first explored whether between-individual and within-individual intertrack distances differed between subspecies, then compared within-individual intertrack distances with between-individual intertrack distances of each subspecies.

Second, in order to more precisely illustrate spatiotemporal patterns in within- and between-individual route consistency, we bootstrapped the median of intertrack distances 10 000 times for each calendar day and, separately, in each 5° latitude × 5° longitude grid cell, with only 1 track ind.$^{-1}$ selected in each iteration. We performed this bootstrapping procedure for within-individual and between-individual intertrack distances. To illustrate how the spatial pattern in intertrack distances relates to staging areas, we overlaid it with the staging area kernels (see above). With median intertrack distances visualized on a continuous scale, we aided the eye by using a red outline for grid cells with a median intertrack distance of <500 km.

Individual variation in route flexibility

To test whether individuals differ between consecutive years in their route flexibility, e.g. whether some individuals are repeatedly flexible and others are repeatedly consistent in their routes or whether individuals may be consistent between some years and flexible between others, we calculated ICCs for within-individual median intertrack distances between tracks from subsequent years (i.e. with only 1 yr difference) using the 'rpt.mcmcLMM' function from the 'rptR' package (Schielzeth & Nakagawa 2013). Note that the term 'repeatability' is used here only to refer to ICC values.

RESULTS

Sample size

In Ammarnäs, Sweden, out of 46 geolocators deployed in 2011 to 2014, 27 (59%) were retrieved by 2015. Numbers of retrievals and deployments are 20 out of 30 (67%) for Svalbard, 5 out of 14 (36%) for Zackenberg, 2 out of 6 (33%) for Karupelv and 1 out of 3 (33%) for Hochstetter Forland. Note that some individuals were refitted and recaptured multiple times and that recapturing birds in Sweden and Greenland is hampered by non-breeding years. In total, 97 tracks were obtained from 38 individual long-tailed skuas, of which 24 individuals were tracked over a period of 2 to 5 yr. See Table 1 for further specification of samples relative to subspecies. Due to logger failure or empty batteries, 14 tracks stopped prematurely between 28 December and 1 May; these were included in the analysis.

General movement patterns

All tracks are illustrated in Fig. 1 and in an animation in the Supplement at www.int-res.com/articles/suppl/m578p197_supp/, while some examples of individual tracks are shown in Fig. 2. No systematic differences in non-breeding movements were detected between the 2 subspecies. After departure from the breeding areas, skuas proceeded south-west to stage in the central North Atlantic off Newfoundland. Subsequently, they went south in a relatively narrow corridor to the Canary Current off West Africa. From here, most birds migrated directly to the staging area in the Benguela Current off Namibia and South Africa, whereas 6 individuals (9 tracks) took a westerly loop to approach the Benguela Current from the west. A few proceeded further south-east into the Agulhas Current and the Southern Subtropical Convergence. A single individual (*S. l. longicaudus*) went straight west from the Benguela to the Falkland Current in its second and fourth year of tracking (Fig. 2i). Other individuals lingered along the west side of Africa, in particular off Angola. The most northerly winterer was a (*S. l. longicaudus*) wintering in the Canary Current. Northward movements commenced in January to March and occurred over a broad front, covering a large part of the Atlantic, and included stopovers of varying length off Angola, in the Gulf of Guinea and the Canary Current. After crossing the equator, virtually all birds staged in a large area in the central North Atlantic in April–May (mostly within the North Atlantic Drift Province), which they usually slowly crossed from west to east. Some birds staged for a few days west of Ireland before returning to the breeding grounds.

Table 1. Number of individual long-tailed skuas *Stercorarius longicaudus* (subspecies *S. l. longicaudus* and *S. l. pallescens*) tracked over different numbers of years

No. of years	*S. l. longicaudus*	*S. l. pallescens*	Total
1	9	5	14
2	1	3	4
3	2	4	6
4	11	2	13
5	0	1	1
Total (individuals)	23	15	38
Total (tracks)	61	36	97

Route consistency

Intertrack distances showed a strong seasonal pattern when using a narrow time window for nearest-neighbour selection, with large distances in autumn and late winter, and much smaller distances in early winter and spring. Broadening the time window greatly reduced intertrack distances, in particular in autumn (Fig. A1). For example, median within-individual intertrack distance at 15 August was ca. 3000 km for a time window of 7 d, ca. 2000 km for a time window of 30 d and ca. 800 km for a time window of 61 d (Fig. A1). This was mainly caused by the fact that Swedish birds during non-breeding years had earlier autumn migration schedules, but not different migration routes. As the effect of differential timing was largely removed at a time window of 61 d, intertrack distances obtained using this time window were therefore used in subsequent analyses.

Daily median intertrack distances were smaller within individuals than between individuals during almost the entire year (Fig. 3). Between-individual intertrack distances differed between the subspecies, and therefore 'subspecies' was included as a factor in the models. Note that this does not necessarily indi-

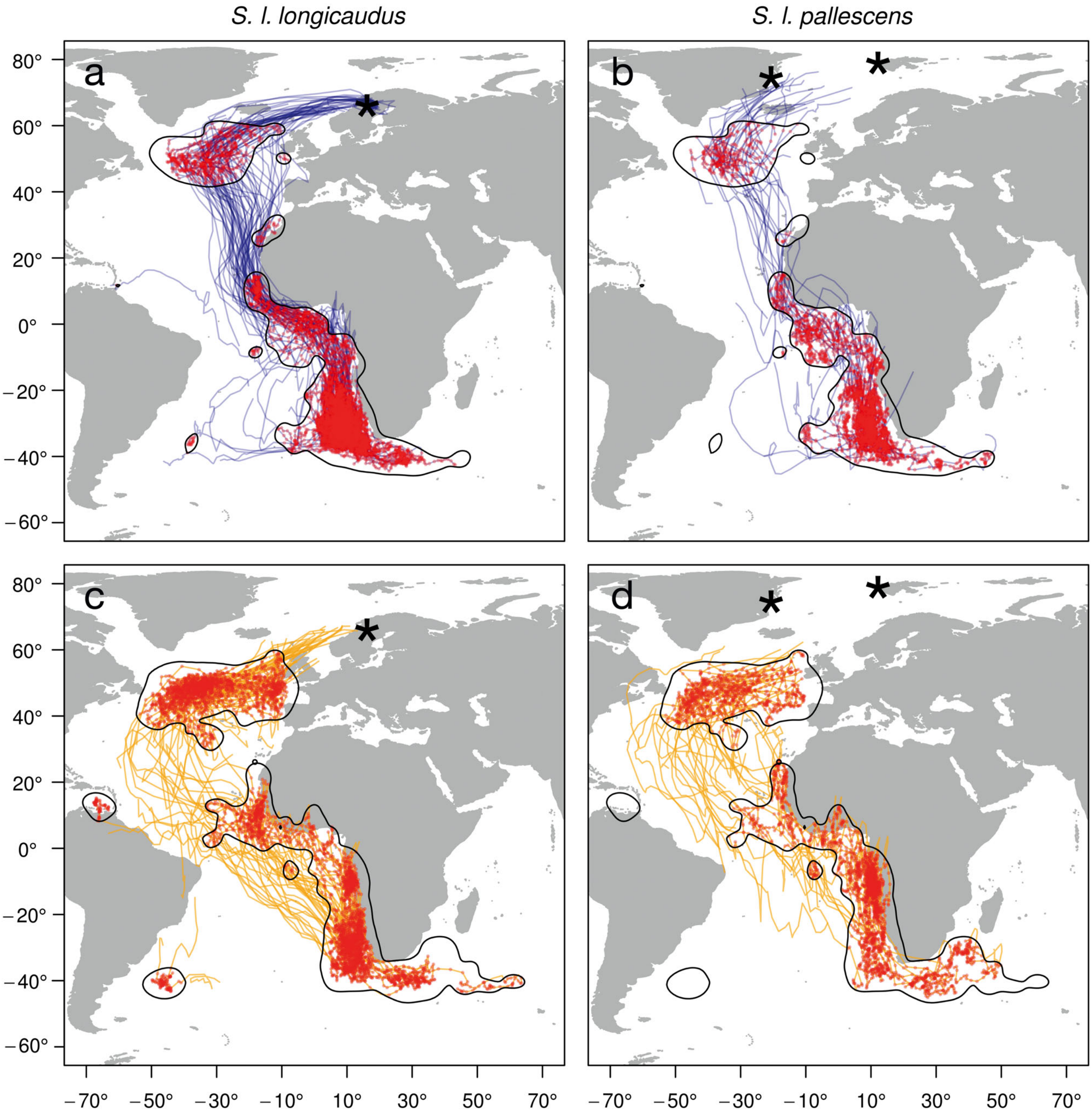

Fig. 1. Movements of the 2 subspecies of long-tailed skuas *Stercorarius longicaudus*, (a,c) *S. l. longicaudus* and (b,d) *S. l. pallescens*, in (a,b) July–December and (c,d) January–June. Red dots indicate staging periods (3 or more consecutive days with <200 km between daily positions). Black stars indicate the sampled breeding sites for each subspecies. The black outlined polygons indicate 95% utilization distribution kernels for staging positions of all birds combined. Inaccuracy of geolocator position estimates is generally ±185 km, but is typically larger close to the equinoxes (Phillips et al. 2004)

cate different routes and site use between the subspecies — it only reflects a difference in the spread in routes and site use (cf. Fig. 1). Overall median intertrack distances were significantly smaller within (model-based, back-transformed posterior mean [μ] and 95% credible intervals [CI]: μ = 274 km, 95% CI = 217–351 km, $p_{MCMC} < 0.001$) than between individuals (Fig. 4; *S. l. longicaudus*: μ = 535 km, 95% CI = 347–835 km, $p_{MCMC} < 0.001$, *S. l. pallescens*: μ = 928 km, 95% CI = 569–1484 km, $p_{MCMC} < 0.001$). This was also true in a model testing the median intertrack distance per segment (Fig. 4; all $p_{MCMC} < 0.001$), except for the North Atlantic staging area during southbound migration (for *S. l. pallescens* only; $p_{MCMC} = 0.370$) and northbound migration (for both *S. l. longicaudus*: $p_{MCMC} = 0.536$, and *S. l. pallescens*: $p_{MCMC} = 0.020$).

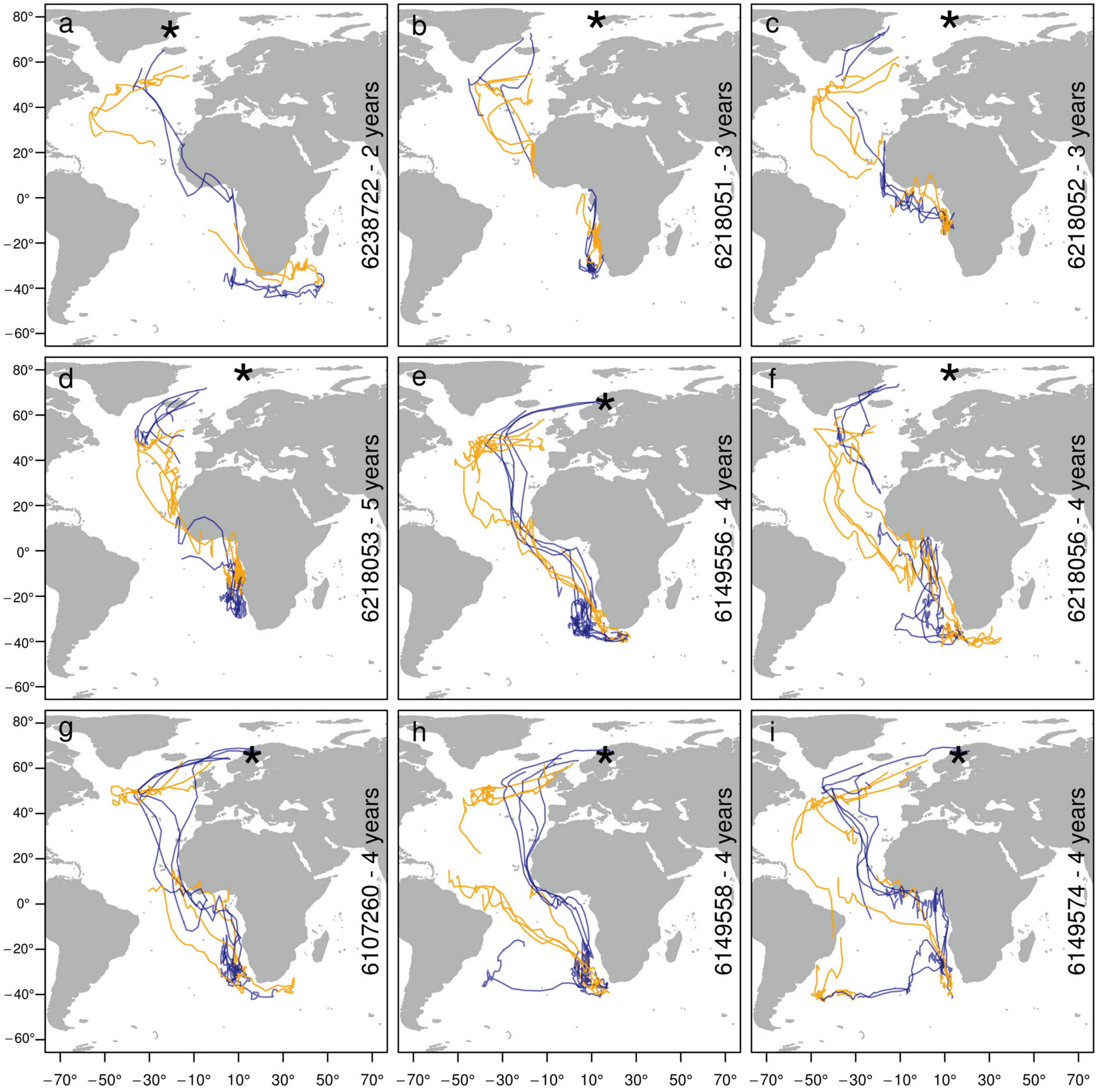

Fig. 2. Nine examples of geolocator tracks of individual long-tailed skuas *Stercorarius longicaudus* tracked over multiple years (blue: July–December, orange: January–June). Numbers on the right are ring numbers, cf. Fig. 6, and number of years tracked. Black stars indicate the breeding site of each individual. Examples include (a–e) individuals with high route consistency and (f–i) individuals with more flexibility in their recorded routes. The individual shown in (h) took a detour along the Falkland Current in one year, while the individual in (i) went to the Benguela Current in all 4 years, but switched mid-winter to the Falkland Current in its second and fourth year of tracking. Inaccuracy of geolocator position estimates is generally ±185 km, but is typically larger close to the equinoxes (Phillips et al. 2004)

Within-individual intertrack distances did not differ between the subspecies and therefore ‘subspecies’ was not included in the models ($p_{MCMC} = 0.448$). Within-individual intertrack distance was largest outside staging area kernels during northbound (Fig. 4; μ = 702 km, 95 % CI = 500–1026 km) and southbound migration (μ = 689 km, 95 % CI = 524–871 km), which were not significantly different ($p_{MCMC} = 0.944$).

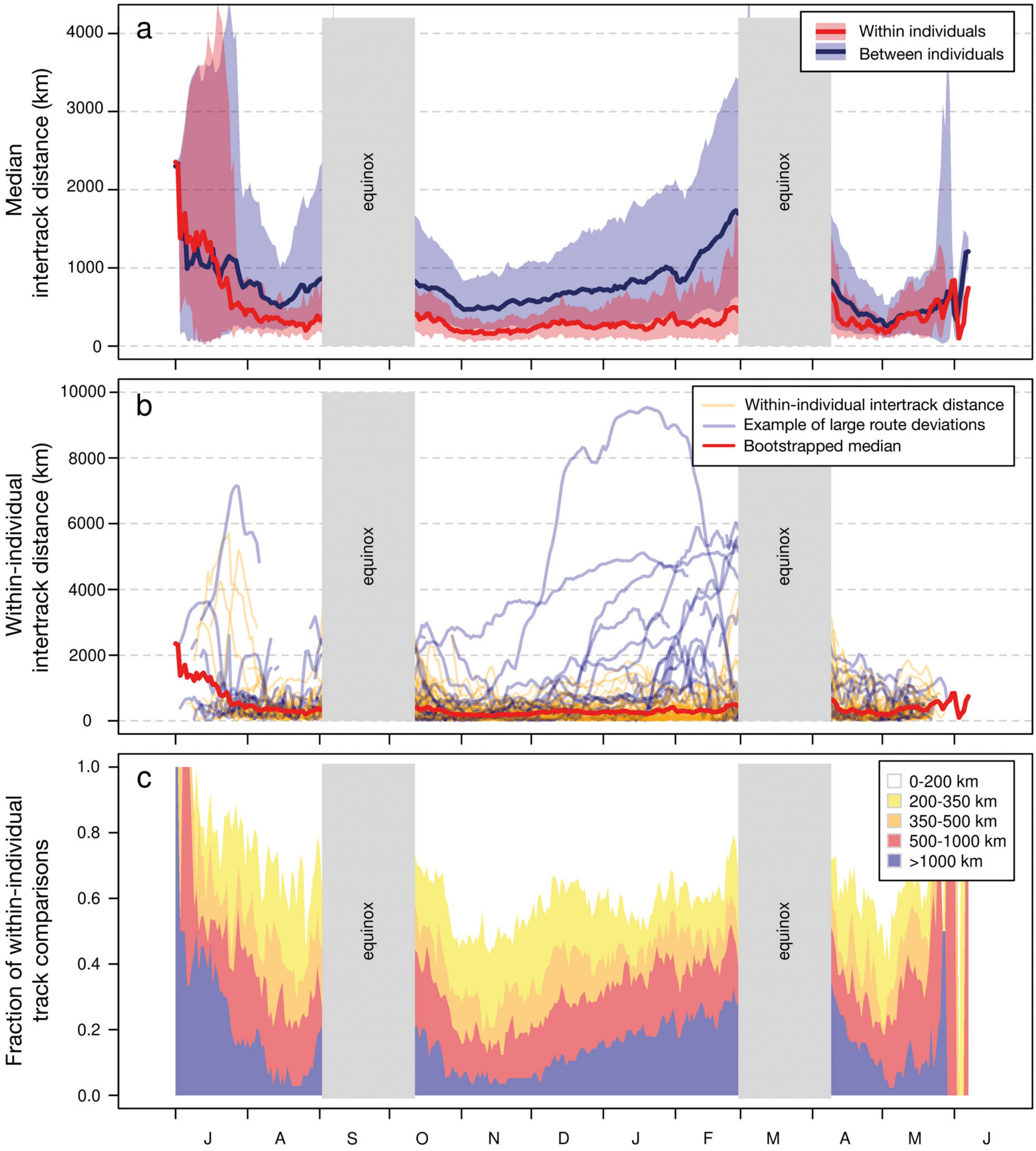

Fig. 3. Daily route consistency per month. (a) Distribution of bootstrapped median intertrack distances (red and blue) for comparisons within (red) and between (blue) individual long-tailed skuas *Stercorarius longicaudus*. Shaded areas represent 90% CI of bootstrapped median intertrack distances, including their overlap (darker red/blue). (b) Within-individual intertrack distances (orange), highlighting examples of large deviations from the previous year's track (blue). The red line shows the bootstrapped median within-individual intertrack distance also shown in panel (a). (c) Fraction of tracks with a certain range of intertrack distances. White represents high route consistency (<200 km); purple reflects large route deviations (>1000 km)

Within-individual intertrack distances outside staging area kernels were larger than within-individual distances within the staging area kernels (Fig. 4; $p_{MCMC} < 0.05$), except for the comparison between southbound migration and the North Atlantic staging area in autumn (p_{MCMC} = 0.084). Considering staging kernels, intertrack distances were larger in the North Atlantic staging area during autumn (μ = 414 km, 95% CI = 299–610 km) than in the staging areas south of 25° N during early winter (μ = 278 km, CI = 160–323 km,

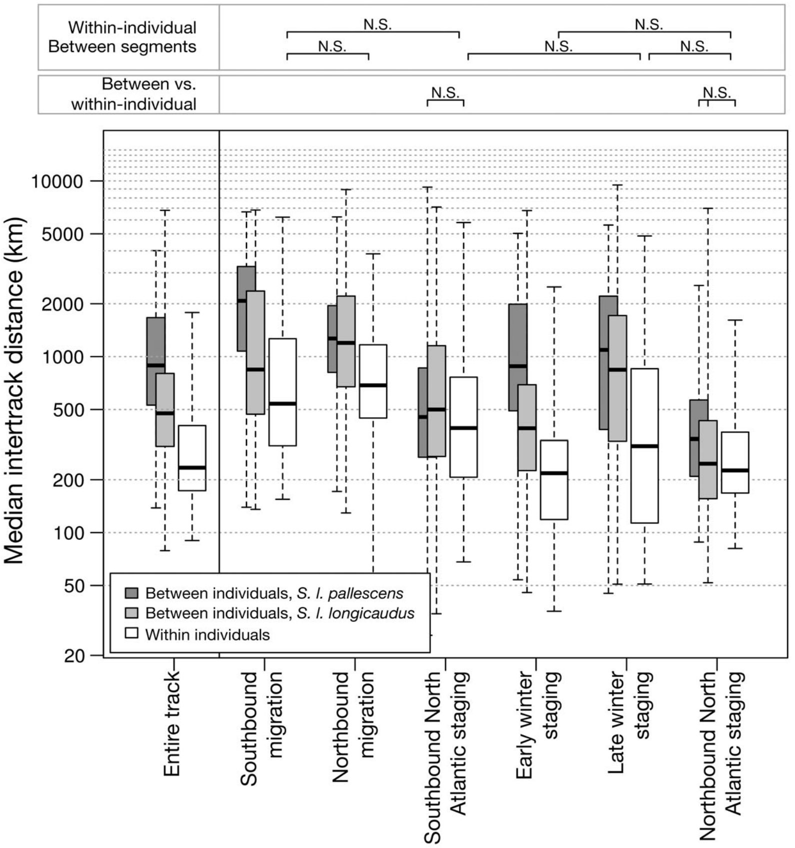

Fig. 4. Median intertrack distance within individual long-tailed skuas *Stercorarius longicaudus*, and between individuals of each subspecies (light/dark grey), calculated for the entire track comparison and for 6 segments (see 'Materials and methods: Consistency in movement patterns'). Note the log scale of the *y*-axis. Bold horizontal lines represent medians, boxes encompass 50% of the values, and whiskers extend to the most extreme values. Above the figure, only non-significant (N.S.) comparisons are indicated; all other comparisons are significant ($p_{MCMC} < 0.05$)

$p_{MCMC} < 0.001$) and in the North Atlantic staging area during northbound migration (μ = 255 km, 95% CI = 175–362 km, $p_{MCMC} = 0.018$), but not different in the staging areas south of 25° N in late winter (μ = 347 km, 95% CI = 248–479 km, $p_{MCMC} = 0.324$). Intertrack distances in staging areas were smaller during early winter than during late winter ($p_{MCMC} = 0.016$). In Fig. 3a, intertrack distances plotted per day over the entire year (irrespective of location) show that within-individual intertrack distances are smallest and individuals thus especially consistent in space and time in August (medians range from 200 to 340 km) and late April/early May (when in the North Atlantic staging area; medians range from 170 to 270 km), and in November (when in the winter quarters; medians range from 160 to 210 km). In the months after November, an increasing number of individuals diverted from their previous year's route; for example in February, about 40% deviated more than 500 km and 20% more than 1000 km. Within-individual intertrack distance did not differ between years (included as a factor).

Spatial patterns in between-individual intertrack distance reflect largely where individuals aggregate at staging areas, for example in the central North Atlantic and in the Benguela Current, and where migration routes converge, such as for example in the East Atlantic during autumn migration (Fig. 5). In July to December, median intertrack distance was smaller within than between individuals in 77% of the grid cells, with some exceptions scattered mainly in the East Atlantic and west of the Benguela Current. Within-individual intertrack distances in this period were generally smaller than 500 km in the North Atlantic staging area, in the Benguela and Agulhas Currents, but also in between. Outside these areas, individuals showed lower route consistency. In January to June, 85% of the grid cells had lower within- than between-individual median intertrack distance. Uninterrupted areas of within-individual intertrack distances below 500 km were apparent again in the same main staging areas (albeit somewhat more restricted). With a few exceptions, intertrack distances were larger outside these areas, in particular between 0 and 40° N.

Of those individuals with at least 3 yr of data (thus having 2 or more sets of intertrack distances), many repeatedly showed intertrack distances around 300 km (Fig. 6). However, several individuals showed small intertrack distances (high consistency) between 1 or 2 pairs of years and large intertrack distances (flexibility) between other set(s) of years. Thereby, within-individual variance of overall median intertrack distances was inflated, causing low ICC values (r = 0.286, 95% CI = 0.048–0.545). The same was found for the parts outside the staging kernels (southbound migration: r = 0.041, 95% CI = 0.010–0.209; northbound migration: r = 0.248, 95% CI = 0.029–0.491) and within the staging kernels (southbound, North Atlantic staging area: r = 0.073, 95% CI = 0.011–0.318, early winter/south: r = 0.225, 95% CI = 0.025–0.508; late winter/south: r = 0.178, 95% CI = 0.011–0.430; spring/north: r = 0.205, 95% CI = 0.025–0.427).

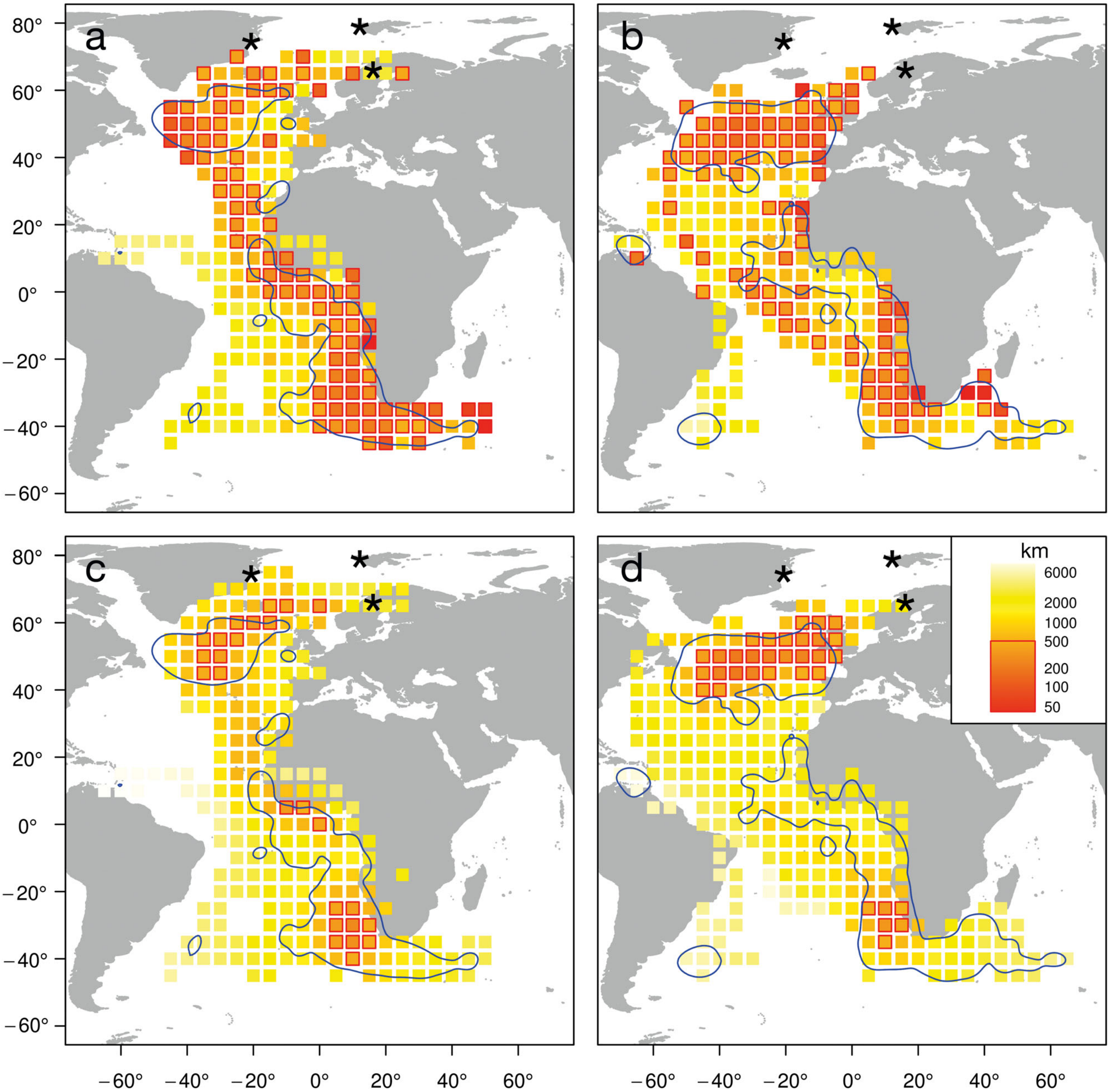

Fig. 5. Median intertrack distance (a,b) within individuals and (c,d) between individuals for (a,c) July–December and (b,d) January–June of long-tailed skuas *Stercorarius longicaudus*. Emphasis is put on grid cells (5° latitude × 5° longitude) with median intertrack distance of less than 500 km by red outlines. Black stars indicate the breeding locations and blue outlined polygons are 95% utilization distribution kernels (see Fig. 1). High route consistency is especially achieved in southbound migration both within and outside staging area kernels

DISCUSSION

We studied consistency of movement patterns at large to meso-scales outside the breeding season in a long-distance migratory seabird, the long-tailed skua *Stercorarius longicaudus*, and generally found large between-individual differences and relatively small within-individual variation. As expected, individuals were faithful to main staging areas in their southbound and northbound migration (off Newfoundland in the central North Atlantic) and winter destination (the Benguela Current off Namibia and South Africa), where they generally followed their previous year's route within about 200 to 300 km, while being more

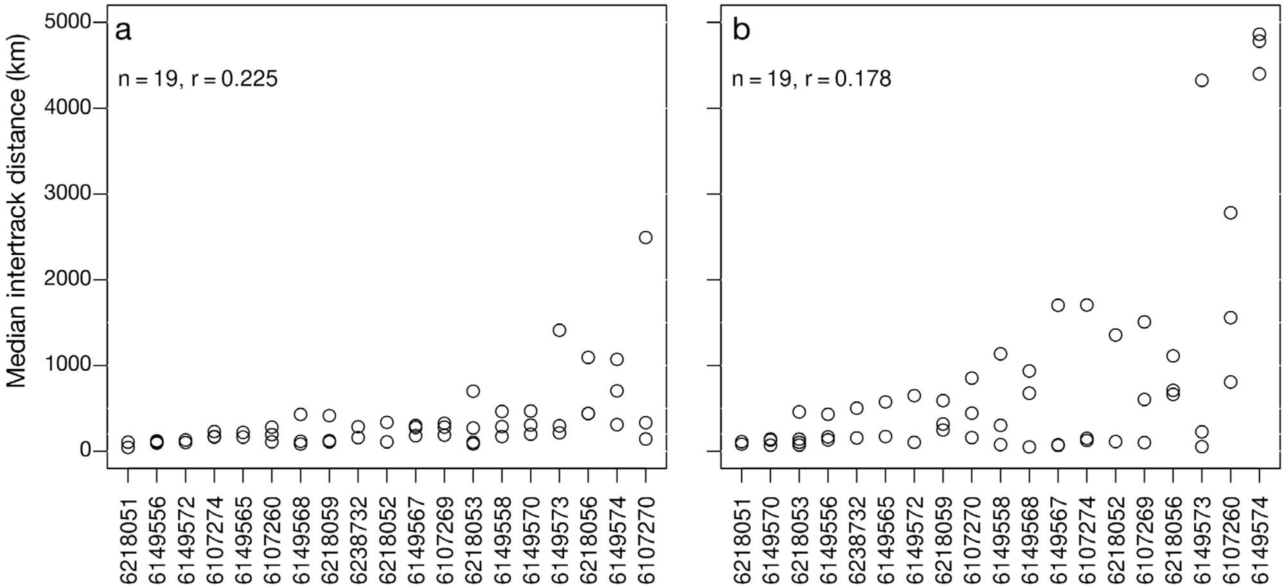

Fig. 6. Within-individual median intertrack distance in staging areas south of 25° N in (a) early winter and (b) late winter for individual long-tailed skuas *Stercorarius longicaudus* with at least 3 tracks, thus at least 2 sets of intertrack distances (*x*-axis labels are individual ring numbers). Most individuals stayed within 500 km of their previous year's route in early winter. Particularly in late winter, some individuals showed large deviations in some years, but not in others. Individual 6149574 (far right; also see Fig. 2i) switched each year in late winter between 2 distinct strategies

flexible during southbound and northbound migration when crossing large areas with low productivity. Surprisingly, over the course of the winter, a minor but increasing part of the individuals started to deviate from their previous year's route. This shows an intriguing combination of general site fidelity and flexibility in subsequent winter movements.

High winter area fidelity has been shown in several seabird species from several families, using both GPS and light-based tracking devices (Phillips et al. 2005, Guilford et al. 2011, Muller et al. 2013, Fifield et al. 2014, McFarlane Tranquilla et al. 2014, Yamamoto et al. 2014). With generally high route consistency within staging areas throughout the winter months, long-tailed skuas fit to this pattern, although their movements are often not restricted to a single, well-defined area (i.e. strategy of itinerancy). The generally high route consistency indicates that, despite a strategy of itinerancy, similar itineraries are followed from one year to the next; thus, although individuals use different staging sites throughout the winter, they use the same staging sites in different years. These staging sites are well-known for their high productivity: the Benguela Current system, offshore Angola, the Gulf of Guinea, the Canary Current and the recently discovered hotspot for seabirds in the central North Atlantic (Longhurst 2006, Chavez & Messié 2009, Stenhouse et al. 2012, Grecian et al. 2016). This is in line with our expectation that area fidelity is favoured when individuals target areas with predictably high productivity.

However, from late December, an increasing number of individuals deviated from the previous year's routes (Figs. 3 & 6). Much of this variation was due to differences in timing (see Fig. A1 and the Supplement), but even when controlling for this, ca. 20% of the tracks deviated more than 1000 km from the previous route in January (Fig. 3c). In extreme cases, the deviations included a transoceanic flight from the Benguela Current to the Falkland Current (ca. 5200 km). The ability to switch wintering areas, sometimes at huge spatial scales, has been reported for a small number of seabird species (e.g. up to 7000 km in Cory's shearwater *Calonectris borealis* and 1300 km in streaked shearwater *C. leucomelas*; Dias et al. 2011, Yamamoto et al. 2014). One of the long-tailed skuas repeated the transoceanic switch even twice (in its second and fourth year of tracking; Figs. 2i & 6) using similar routes and destination, indicating this leap was not just an accidental displacement by severe weather conditions, but likely based on previous experience. In both years, it made the shift after arrival in its usual winter range, the Benguela Current. The same pattern was observed in other individuals, in which deviations increasingly occurred from late December onwards, i.e. after arrival at the wintering areas. This suggests that individual skuas check local conditions at a familiar wintering site before deciding where to go during the following months. In contrast, some Cory's shearwaters directly travelled to a different wintering area than in the previous year, apparently without knowing the conditions at either wintering site (Dias et al. 2011).

Based on individuals with 3 to 5 yr of tracking data, we conclude that individuals do not show the same degree of consistency between each set of subsequent years. Instead, individuals with dissimilar tracks between 2 years could have very similar tracks between other years (Fig. 6). This was already hinted at by Dias et al. (2011), who suggested that 'each individual may have one (or maybe several) 'preferred' migratory strategies (in terms of route and wintering site), but maintains the capacity to choose alternatives.' We can now confirm the intriguing idea of co-occurrence of site fidelity and site-switching within the same individual. In conjunction with the increase in route deviations after arrival at the wintering grounds, this likely indicates that deviations from earlier routes represent individuals' rapid responses to local conditions, for example, weather or foraging conditions (including competition) when arriving in the main wintering area.

What determines whether individuals are faithful to their wintering site or shift over small or large distances? While possibly modulated or constrained by intrinsic factors (genetic background, sex, experience, fat reserves), high variation in individual movement patterns likely results from declining availability, increased patchiness and decreased predictability of resources (Mueller & Fagan 2008), or deteriorating weather conditions preventing efficient foraging. Dias et al. (2011) explored whether site switches of a small number of individuals could be explained by sex, age or reproductive success, or by changes in sea surface temperature and chlorophyll *a*, but found no clear links. Also, what exactly caused the movement deviations observed in long-tailed skuas in this study remains unclear. At-sea foraging behaviour of long-tailed skuas is poorly known, but most authors agree that they probably mostly feed by themselves (e.g. by surface pecking), only rarely kleptoparasitizing other seabirds, as is common in other skua species (Lambert 1980, Cramp & Simmons 1983, Veit 1985, Wiley & Lee 1998). As skuas are unable to dive deep, long-tailed skuas likely depend on mechanisms bringing zooplankton or fish at or very close to the surface. Many individuals aggregated in early winter in the southern Benguela Current. Here, edges of Agulhas rings (bodies of warm water 'leaking' from the Agulhas Retroflection) provide feeding opportunities for seabirds (Camphuysen & van der Meer 2001, Camphuysen 2007), possibly including long-tailed skuas (cf. Ryan 1989). Whereas the occurrence of Agulhas rings within this large area seems predictable, they provide localized, slowly moving foraging areas, resulting in irregular patterns in inter-annual variation of ocean productivity (Chavez & Messié 2009). In addition, sea surface temperature increases and primary productivity of the western part of the Benguela declines during winter (Hardman-Mountford et al. 2003, Longhurst 2006, O'Malley 2016). The skuas seem to respond to this by moving south- or eastwards within the Benguela, into the Agulhas or Angola Current, or to the Canary Current. Particularly these late-winter movements are consistent between most, but differ between some years and cause the observed increase in within-individual intertrack distance from mid-winter onwards. While the onset of these movements may be related to the decrease in productivity, it is unclear what determines the (variation in) flexibility in subsequent destinations. One might argue that flexibility in late-winter movements is promoted by a lower predictability of resources in late winter. Whether this is really the case in our long-tailed skua example is questionable; targeted areas include both areas where they may use wind-driven upwelling areas along shelf-edges (off Angola and Namibia) and areas with eddies and thermal fronts (Agulhas Retroflection) (Ryan 1989), and such habitats do not seem to be notably less predictable in feeding conditions than, for example, the Benguela Current during early winter. Future studies should aim to link positional data with (ephemeral) oceanographic features (Tew Kai et al. 2009, Scales et al. 2014), backed up by field studies of at-sea feeding behaviour and diet. Examining at what conditions individual movement patterns start to deviate offers a promising opportunity to study movement decisions of seabirds.

In line with our expectations, long-tailed skuas showed lower consistency in migration route than in staging area itineraries. Like in many seabird species, migratory routes of long-tailed skuas are closely linked to large-scale oceanic wind patterns. They followed routes that provide tail- or sidewinds, except in the second half of southbound migration when using a narrow corridor hugging the contours of western Africa — against the prevailing wind but avoiding an area with stronger headwinds in the central South Atlantic. The same pattern is shown by Sabine's gulls *Xema sabini* and part of the Arctic terns *Sterna paradisaea* originating from the North

Atlantic (Egevang et al. 2010, Stenhouse et al. 2012), but dissimilar to most Cory's shearwaters which take a westerly roundtrip offering more profitable winds (Felicísimo et al. 2008), a route taken by only a small number of the skuas in this study. Northbound migration towards the North Atlantic staging area occurred over a much broader front, in particular north of the equator, where birds likely experienced easterly winds over a large area. Despite this difference in longitudinal width of the south- and northbound migration, individuals showed a similar degree of consistency, albeit with large variation, generally staying within 300 and 1300 km of their previous year's route. High consistency was observed in particular after departure from the Benguela to the northwest, while more flexibility was shown in the North Atlantic south of the North Atlantic stopover. Higher consistency in northbound than in southbound migration route was also observed in the much shorter migration of streaked shearwaters in the western Pacific (Yamamoto et al. 2014).

Error of position estimates from light-based geolocation using the threshold method (Ekstrom 2004) are typically some 100s of km, which precludes us from any conclusions regarding consistency at smaller scales. Inaccuracy of latitude estimates are largest in proximity to the equinoxes (Phillips et al. 2004, Lisovski et al. 2012) and could lead to noise in derived measures. Indeed, Fig. 3a shows increased variation in median intertrack distances just before and after each equinox, but we do not exclude the possibility of an effect of data gaps around equinoxes. Nevertheless, 2 arguments suggest that the route consistencies as presented here are conservative and therefore our conclusions robust. First, considering that intertrack distances of 2 identical routes would reflect the combined error of the position estimates of both tracks, most within-individual intertrack distances are remarkably close to the typical error of ±185 km of single-position estimates (Phillips et al. 2004). Second, intertrack distances were calculated as point-to-point measurements. Measuring the distance from each position in a focal track to the line between 2 closest positions in the comparison track would lead to even smaller distances, in particular if 2 positions of the comparison track are far apart (e.g. when the bird was migrating).

This study highlights that long-tailed skuas show consistency in non-breeding movements, but, at the same time, a fair amount of flexibility during specific parts of the annual cycle, in particular the late winter period. Variation in itineraries between and within individuals suggests that these birds have the ability to adjust to environmental change. However, as we have a poor understanding about how individual migration patterns arise in the first place, specifically the relative roles of genetics and learning during the ontogeny of individual patterns, and, in addition, to what extent individual migration patterns change over an individual's lifetime (reversible state effects; Senner et al. 2015), it remains unclear how flexible long-tailed skuas really are, and thus how quickly they can respond to environmental change. That an individual skua followed 2 distinct itineraries that were both repeated in later years (Fig. 2i), strongly suggests extensive spatial memory. This spatial memory may have its origin in explorative movements during early life (Pulido 2007, Guilford et al. 2011, Senner et al. 2015), which would enable long-tailed skuas to respond to changes in the distribution of favourable areas relatively quickly, assuming that explorative movements allow for discovery of novel areas. Crucially, the genetic background, as well as the occurrence and extent of exploration behaviour in the first years of life and subsequent life stages, need to be demonstrated for the far majority of seabirds (but see Kooyman et al. 1996, Weimerskirch et al. 2006, Péron & Grémillet 2013), including long-tailed skuas.

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Appendix

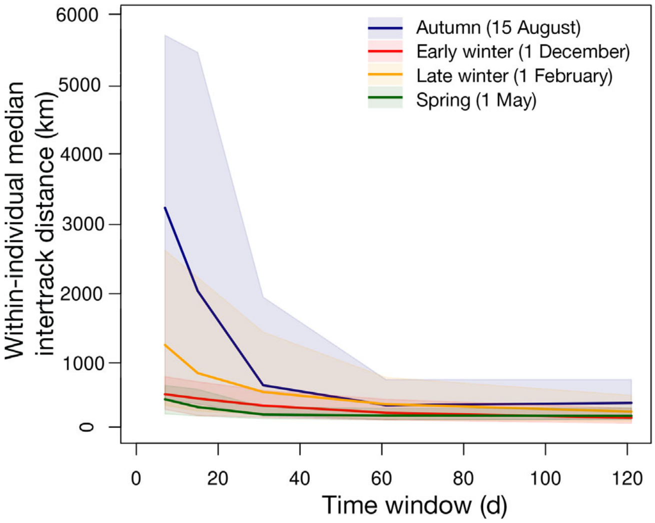

Fig. A1. Effect of widening the time window (from 7 to 121 d) on median within-individual intertrack distances of long-tailed skuas *Stercorarius longicaudus* on 4 example dates. Shaded areas represent 90% CI of bootstrapped medians. Intertrack distances using a time window of 61 d were selected for further analyses

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Contribution to the Theme Section 'Individual varability in seabird foraging and migration'

Consistent variation in individual migration strategies of brown skuas

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ABSTRACT: Seabirds show remarkable variability in migration strategies among individuals and populations. In this study, we analysed 47 migrations of 28 brown skuas *Catharacta antarctica lonnbergi* breeding on King George Island in the Maritime Antarctic. Brown skuas from this population used a large area during the non-breeding period north of 55° S, including parts of the Patagonian Shelf, Argentine Basin and South Brazil Shelf, areas which are characterised by high levels of marine productivity. However, individual birds utilised only a subset of these areas, adopting 1 of 4 distinct migration strategies to which they were highly faithful between years, and showed high repeatability in departure and arrival dates at the breeding ground. Although they spent the majority of the non-breeding season within a particular region, almost all individuals used the same area in the late winter, exploiting its seasonal peak in productivity. Overall, these results indicate consistent individual variation in migration strategies that may reflect a combination of genetic control and individual experience, but with considerable flexibility to shift distribution in response to prevailing environmental conditions.

KEY WORDS: *Catharacta antarctica lonnbergi* · Seabird ecology · Light-level geolocation · Non-breeding distribution · Individual consistency · Ocean primary productivity · Migratory connectivity

INTRODUCTION

Migratory seabirds spend much of the year at sea, far from their breeding grounds, yet have traditionally been studied much more intensively during the breeding than the non-breeding season. However, a growing body of literature demonstrates that these temporally and often geographically distinct periods of the annual cycle are inextricably linked (Harrison et al. 2011). This bias in research towards studies focussing on the breeding season limits our understanding of the ecology of many species, and how individuals and populations are affected by major stressors such as rapid environmental change (Ådahl et al. 2006, Small-Lorenz et al. 2013).

Recent advances in tracking technologies (Bridge et al. 2011) have facilitated numerous studies involving tracking individuals over an extended period of time. This development allows investigation of spatiotemporal consistency in migration strategies within and among individuals and populations (e.g. Phillips et al. 2005, Dias et al. 2011). Although the

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general direction of migration seems to be largely determined by genetics or, in some species, cultural inheritance (Berthold 2001, Mueller et al. 2013), movement patterns of individuals and populations also respond to factors such as food availability (Shealer 2002, Karnovsky et al. 2003). However, prey availability in marine ecosystems is generally characterised by varying degrees of temporal and spatial predictability (Weimerskirch 2007) and hence it cannot be assumed that all areas will be favourable for a particular species in every year. This could ultimately lead to variation in individual migration patterns of seabirds at some spatial scale across years. Indeed, although most species show high individual consistency in non-breeding destinations at a large spatial scale (Phillips et al. 2005, Fifield et al. 2014, Müller et al. 2014), there are exceptions; in addition, in almost all species there is extensive variation both among and within individuals in routes, use of staging areas and timing (Quillfeldt et al. 2010, Dias et al. 2011, McFarlane Tranquilla et al. 2014).

In this study, we analysed the migration strategies of individual brown skuas *Catharacta antarctica lonnbergi* breeding on the South Shetland Islands in the Maritime Antarctic. Migration routes and non-breeding areas were derived using light-level geolocators (also termed global location sensors or GLS loggers), and our dataset included repeated tracks from individuals over 2 to 3 yr. Brown skuas are long-lived and highly opportunistic top predators, with a circumpolar breeding distribution on subantarctic islands and the Antarctic Peninsula (Furness 1987, Ritz et al. 2008). To date, the only detailed distribution data available for brown skuas during the non-breeding period are for birds from the population at South Georgia, migrating to waters between the northern extent of the Subtropical Front and the southern boundary of the Antarctic Circumpolar Current, and between the Argentine and Agulhas (Phillips et al. 2007, Carneiro et al. 2016). In contrast, the limited data for the closely related Falkland skuas *C. a. antarctica*, tracked in different years, suggest a non-breeding distribution mainly in subantarctic waters around the central Patagonian shelf-break (Phillips et al. 2007).

Given the lack of knowledge of the non-breeding ranges of brown skuas from the South Shetland Islands, the adjacent southern population, and the inclusion in our dataset of repeated migration tracks from the same individuals in multiple years, the aims of the study were 2-fold. Firstly, we aimed to reveal the spatiotemporal non-breeding distribution of the tracked population, the degree of variation among individuals, and the effects of sex, year and previous breeding performance. Secondly, we aimed to quantify individual consistency in annual migration strategies. In addition, we used activity (immersion) data recorded by the loggers, and remotely sensed data on net primary production to examine the correlation between this proxy for food availability, and the movement and activity patterns of individual birds.

MATERIALS AND METHODS

Logger deployment and retrieval

Fieldwork was carried out on adult brown skuas at King George Island (Fildes Peninsula, 62° 19′ S, 58° 95′ W) in the Maritime Antarctic. A total of 46 geolocator-immersion loggers were deployed on 33 individuals (which at the time were of unknown sex) over the course of 3 breeding seasons (2006/2007 to 2008/2009). Three types of loggers (manufactured by the British Antarctic Survey) were used in this study: MK5 (n = 20), MK9 (n = 22) and MK15 (n = 4). Total weights were 6.4, 5.3 and 5.3 g, respectively, which included the device, aluminium ring and cable ties used for attachment (together with metal ring of 3 g used for identification, corresponding to ~0.6% of the mean body mass). Besides recording light intensity over time, all loggers tested for saltwater immersion every 3 s and stored the sum of positive tests at 10 min intervals, resulting in values between 0 (entirely dry) and 200 (entirely wet). Birds were recaptured in the subsequent season, and in 11 cases the loggers were replaced by a new device; these devices and others from the initial deployments were retrieved in the third season. A blood sample was taken from each bird (~50 µl), stored at −20°C, and later used to determine sex from DNA (Fridolfsson & Ellegren 1999). All individuals were monitored regularly in the pre- and post-migratory season (from early December to March) to determine breeding status and performance (i.e. success vs. failure).

Departure and arrival date

Since brown skuas switch from a predominantly terrestrial lifestyle to almost exclusively marine habitat after leaving the breeding site (Phillips et al. 2007), departure and arrival dates at King George Island were identified by visual inspection of immersion data. For individuals lacking immersion data because of logger malfunction, these dates were identified from the length and frequency of shading of the light sensor during daylight, which is substantially higher when skuas spend time sitting on land at the breeding ground. The duration of the non-breeding period was based on departure and arrival dates. Some individuals also went on a pre-laying exodus within a few weeks of first return to the colony.

Movement pathway analysis

Positions during the non-breeding season were estimated from raw light intensity data using the threshold method (Lisovski et al. 2012). Twilight events (i.e. sunrise and sunset transitions) were defined using the R package 'BAStag' (Wotherspoon et al. 2013a) based on a light intensity threshold of 2.5. Twilight times that were clearly suspect because of shading of the sensor (i.e. >30 min difference from the previous or subsequent day) were discarded, and the time interpolated with respect to the surrounding twilights. This approach was applied to between 5 and 10 % of all twilights during the annual migration of each individual. Locations from the breeding period were excluded from subsequent analyses. We used a Bayesian framework to refine the initial, rough positions estimated from the threshold method and to derive uncertainty estimates. The R package 'SGAT' (Wotherspoon et al. 2013b) uses Markov Chain Monte Carlo (MCMC) simulations allowing the incorporation of a spatial probability mask, prior definition of the error distribution of twilight events (twilight model) and a flight speed distribution to refine location estimates (for detailed information see Sumner et al. 2009 and Lisovski et al. 2016). The twilight model should reflect the expected error in detecting the real time of sunrise and sunset. Since brown skuas spend a substantial amount of time sitting at the breeding site, which obscures the light sensor, we could not use twilight times from a known location (i.e. breeding site) to parameterise the twilight model. We therefore used a rather conservative prior (log-normal distribution: meanlog = 2, sdlog = 1.2) describing a large variation in the discrepancy between the real and recorded twilight events. The movement behaviour was modelled assuming that over the course of the non-breeding periods, brown skuas are sedentary for the majority of the time (high likelihood of very slow movement speeds) while allowing for occasional fast movements (~80 km h^{-1}) during migration (gamma distribution; shape = 0.7, scale = 0.05). The spatial mask was based on the assumption that the tracked individuals avoid land (10 times lower probability of occurrence on land compared to sea) and that the spatial range was between 10 and 70° S, and 85 and 20° W (based on locations derived using the threshold method).

The threshold method requires a zenith angle to estimate locations, which is usually derived using light intensity recordings from tracked animals of known distributions, or fixed loggers. As these data were unreliable or unavailable for this study, we used an alternative approach, the 'Hill-Ekstrom calibration' (see Lisovski et al. 2012) to estimate the right zenith angle for each annual migration track. First, for all tracks, initial locations were estimated using a zenith angle of 95° (i.e. sun elevation angle of −5°). Next, using the initial locations, a set of MCMC simulations (drawing 2400 samples) was performed using a range of zenith angles between 94 and 96°. The median path for each zenith angle and a total of 2400 chains were then calculated. We then choose the zenith angle that minimised the variance in latitude estimates during periods when the tracked birds were largely sedentary within their non-breeding range. The derived zenith angles varied between individual tracks, and ranged from 94.5 to 95.7°.

Using those zenith angles, a complete MCMC simulation was performed on each individual annual track. An initial 2000 samples were drawn and discarded to allow for both burn-in and tuning of the proposal distribution, i.e. to find an initial path that matches the model assumptions. A final 4000 samples were than drawn to describe the posterior distribution. Convergence of chains, i.e. whether 2 independent simulations produce the same result, was evaluated by visual inspection by comparing the median tracks. The final run provided 4000 chains of possible migration pathways that satisfied the defined sunrise and sunset times, their error distribution, the movement behaviour and the spatial mask. The set of chains were used to generate time-spent maps illustrating the relative probability distribution of an individual at a given time or period, and to calculate most likely tracks.

Activity analysis

Saltwater immersion data recorded by the logger were used to determine activity patterns of brown skuas using the web-based program Actave.net (Mattern et al. 2015). Values of 0 (entirely dry), 1 to 199, and 200 (entirely wet) in each 10 min period were categorised as either 'flight' (as skuas remain at sea during the non-breeding period), 'foraging' or 'sitting on water', respectively, assigned to daylight or darkness periods based on nautical twilight hours and summarised accordingly (see Mattern et al. 2015). Although some intermediate values (from 1 to 199) will reflect non-foraging behaviour, in general this categorisation is assumed to provide a reasonable indication of foraging activity among seabirds (McKnight et al. 2011, Cherel et al. 2016).

Spatial data analysis

We used R (R Core Team 2015) to manipulate and analyse all data. A Lambert Azimuthal Equal Area projection was used for all spatial analyses and mapping. Due to the large error distribution of the twilight times, the MCMC simulation did not perform well in correcting location estimates during the period of the equinox (1 March to 22 April, and 22 August to 9 October), and these locations were therefore excluded from all analyses.

Movement patterns within the non-breeding range were analysed in the context of the Marine Ecoregions of the World (MEOW), biogeographic areas of relatively homogenous and distinct species composition (for details, see Spalding et al. 2007). However, MEOW only characterises costal and shelf areas, and we therefore added the 'Argentine Basin' to be able to categorise the entire non-breeding range of the tracked brown skuas. For each position on the individual median tracks (i.e. the most likely track) we extracted the corresponding MEOW. To quantify the relative use of the various MEOW by each individual, the proportions of time spent inside each region between 22 April and 22 August was calculated. These proportions were used to group individual tracks based on the similarity in the use of each MEOW, using a cluster analysis with Euclidean distance (R package 'vegan'; Oksanen et al. 2015). To exclude individual effects, the analysis was initially performed using the first track of each individual only. Subsequently, and to evaluate the robustness of the groups, all 47 annual tracks were analysed together followed by a repeated analysis using Ward's method (Oksanen et al. 2015).

The relative probability distributions (i.e. time-spent maps) between 22 April and 22 August were used to investigate the spatial overlap of movement paths among and within individuals. Each individual relative probability distribution (D_{XY}) corresponded to a raster with XY grid cells and a resolution of 39.3 × 55.6 km. The values were normalised such that $\Sigma_x\Sigma_y D_{XY} = 1$. The degree of overlap (O) between 2 tracks (a and b) was defined as the sum of the minimal value over all shared (overlapping) grid cells according to:

$$O_{ab} = \Sigma_x\Sigma_y \min(D_{XYa} \mid D_{XYb}) \quad (1)$$

This calculation results in 0 if the 2 tracks share no common grid cell and in 1 if the 2 probability distributions were 100% identical. All combinations of the 47 annual tracks were calculated. The resulting degrees of overlap were arcsine square root transformed to meet statistical assumptions.

To reveal temporal trends in marine productivity (as a proxy of the seasonal dynamics of food availability at a mesoscale level), and to test for relationships with individual distributions, timing of movements and activity patterns of the tracked skuas, we downloaded net primary production data (NPP) from www.science.oregonstate.edu/ocean.productivity/index.php (accessed 5 August 2014), in 8 d intervals and a resolution of 0.17°. Individual brown skua probability distributions were pooled into 8 d intervals to match NPP data format and normalised such that $\Sigma_x\Sigma_y D_{XY} = 1$. If the matched NPP data had missing values corresponding to >50% of the probability distribution, the 8 d interval was excluded from the analysis. The relative probability distributions were then used to weight the NPP data of each corresponding grid cell according to:

$$\text{NPP}_{\text{sum}} = \Sigma_x\Sigma_y (D_{XY} \times \text{NPP}_{XY}) \quad (2)$$

Statistical analysis

We used linear mixed-effect models (R package 'lme4'; Bates et al. 2014) to quantify the effects of sex, breeding performance (i.e. successful [at least one chick fledged] or unsuccessful in the current season) and migration strategy on the subsequent timing of migration (departure date, arrival date, duration) and individual activity patterns (foraging activity, number of dry bouts and duration of dry bouts). To avoid pseudoreplication, individual identity was included as a random intercept. Two individuals with behaviours very different to the others were excluded from specific analysis: ID 108276 departed exceptionally early (15 January) in 2008, and was excluded from the analysis of departure date and duration, and ID 139514 spend several (dry) nights on a vessel or on land, biasing the activity data. To correct for temporal autocorrelation in the model testing for an effect of prey predictability (i.e. NPP) on activity pattern, the random effect was specified as days since the start of the non-breeding season each year (hereafter 'day of the year') nested within individuals. p-values were calculated using the 'lmerTest' package (Kuznetsova et al. 2015). A linear mixed-effect model with the binary fixed factors (1 as 'same' and 0 as 'different') 'same sex', 'same year', 'same breeding performance' and 'same individual', and the random factor 'individual' was used to test for differences among and within groups in the spatial overlaps of the probability distributions.

Individual repeatability, i.e. the intraclass correlation coefficient, which allows the quantification of variance among and within individuals (Lessells & Boag 1987), was calculated for timing of migration and mean activity metrics obtained in different years. Linear mixed-effect models with individual as random effect and year as fixed factor were fitted for each sex. Due to the small sample size, models fitted to the activity metrics were not separated by sex, and sex was instead included as a fixed factor. The adjusted repeatability value, corresponding confidence interval and p-value were calculated using the R package 'rptR' (Nakagawa & Schielzeth 2010).

RESULTS

Logger retrieval details

DNA sexing revealed that the loggers were deployed on 33 females and 13 males. A total of 42 (91%; 31 females, 11 males) of the loggers were retrieved, which provided data on 47 annual tracks of 28 individuals (20 females, 8 males) between 2007 and 2010, including migrations of the same individuals over 2 (n = 13) or 3 (n = 3) non-breeding seasons. Additionally, saltwater immersion data were recorded for 35 of the 47 annual tracks.

Spatiotemporal distribution

During the non-breeding period, the tracked brown skuas were widely distributed north of their breeding sites, over parts of the Patagonian Shelf, the Argentine Basin and, to a lesser extent, the Southern Brazil Shelf (Fig. 1a). This distribution includes regions with heterogeneous levels of productivity: subantarctic, mixed subantarctic–subtropical and subtropical, and open shelf waters. The core area of the distribution overlapped with the Patagonian shelf-break front, the confluence zone of the Falkland and Brazil currents, and offshore of the Rio de la Plata estuary.

Single individuals used distinct portions of the entire area, revealing characteristic spatiotemporal patterns (Fig. 2). Based on the time spent in each MEOW, the annual tracks could be grouped in 4 migration strategies. Applying cluster analyses with different linking methods on all annual tracks, or only

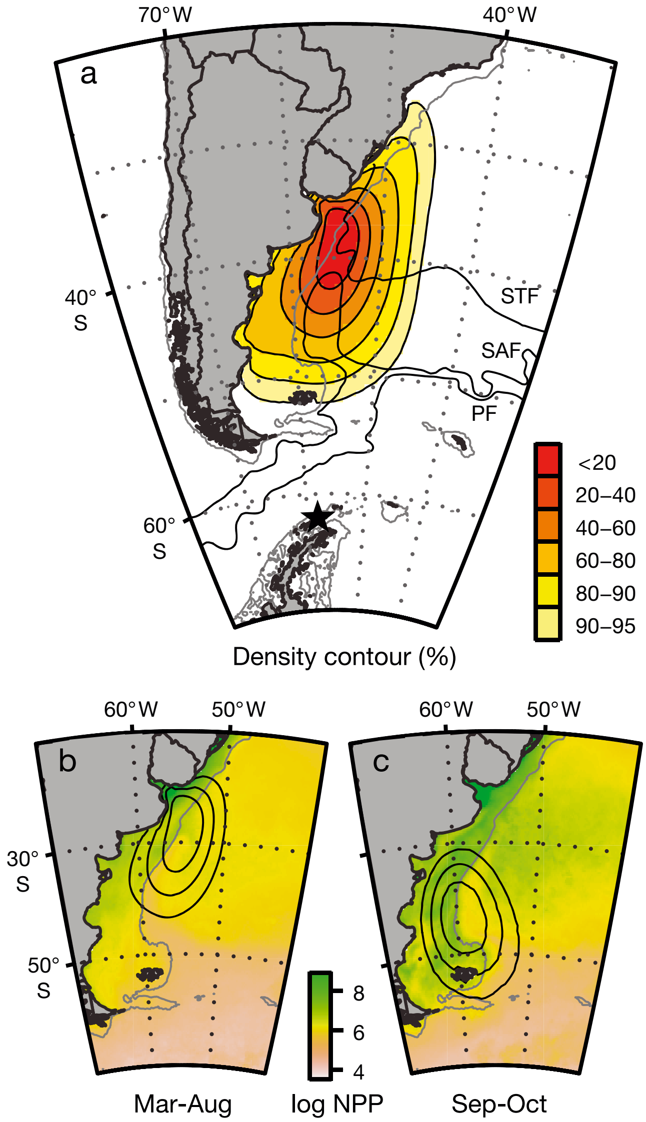

Fig. 1. (a) Density distribution of 28 brown skuas *Catharacta antarctica lonnbergi* from King George Island (black star) during the non-breeding period from 2007 to 2010. Black lines: approximate locations of the Subtropical Front (STF), Subantarctic Front (SAF) and Polar Front (PF) based on Orsi et al. (1995); grey line: 500 m bathymetric contour, indicating the Patagonian shelf-break. (b) Mean net primary production (NPP; in mg C m^{-2} d^{-1}) between the mean departure date of brown skuas (17 March) and August from 2007 to 2010, and (c) NPP (in mg C m^{-2} d^{-1}) between September and the mean arrival date of brown skuas (31 October) from 2007 to 2010, both overlaid by the density distribution (contour lines: 20, 40, and 60%) of brown skuas in the same period

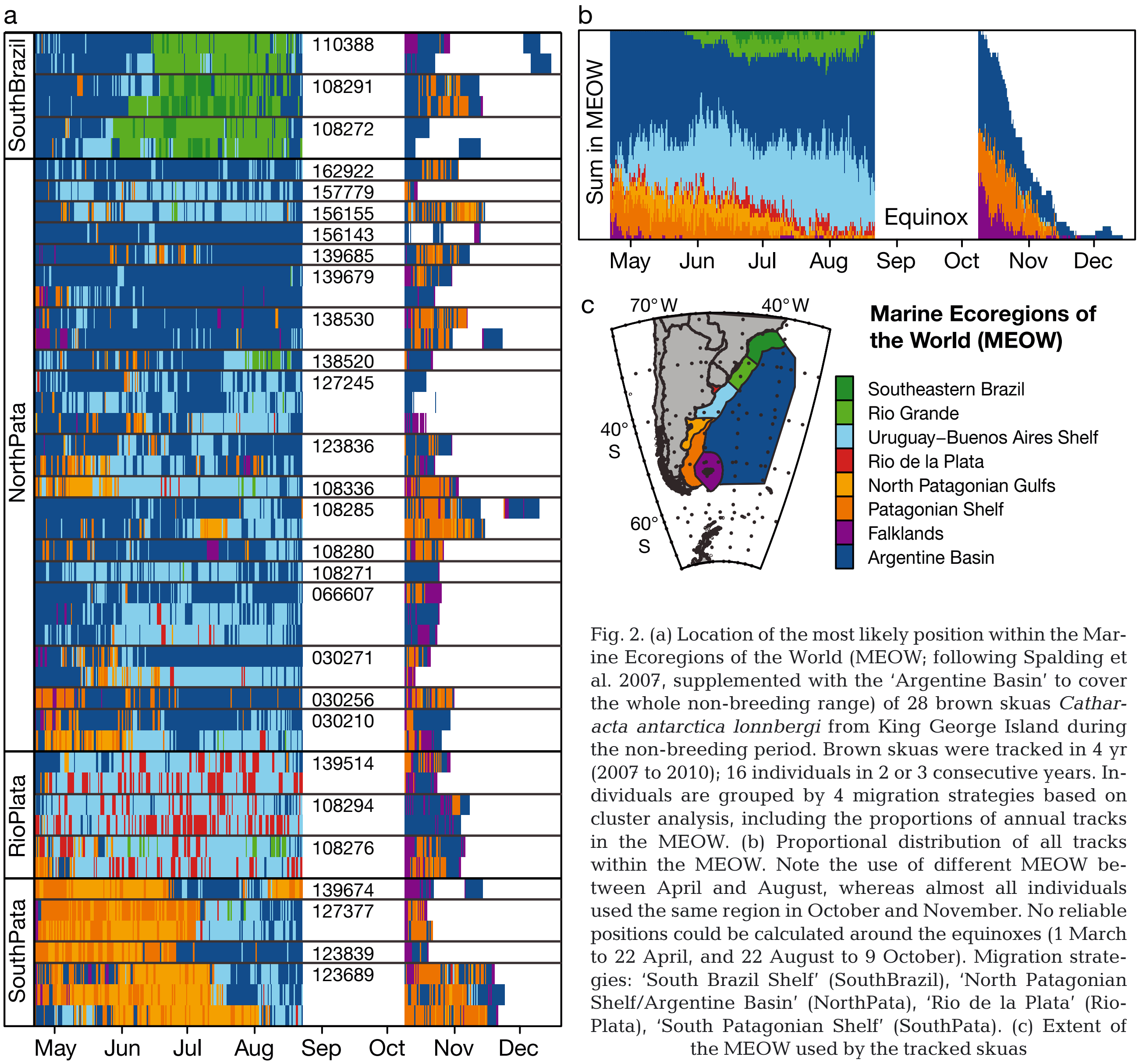

Fig. 2. (a) Location of the most likely position within the Marine Ecoregions of the World (MEOW; following Spalding et al. 2007, supplemented with the 'Argentine Basin' to cover the whole non-breeding range) of 28 brown skuas *Catharacta antarctica lonnbergi* from King George Island during the non-breeding period. Brown skuas were tracked in 4 yr (2007 to 2010); 16 individuals in 2 or 3 consecutive years. Individuals are grouped by 4 migration strategies based on cluster analysis, including the proportions of annual tracks in the MEOW. (b) Proportional distribution of all tracks within the MEOW. Note the use of different MEOW between April and August, whereas almost all individuals used the same region in October and November. No reliable positions could be calculated around the equinoxes (1 March to 22 April, and 22 August to 9 October). Migration strategies: 'South Brazil Shelf' (SouthBrazil), 'North Patagonian Shelf/Argentine Basin' (NorthPata), 'Rio de la Plata' (RioPlata), 'South Patagonian Shelf' (SouthPata). (c) Extent of the MEOW used by the tracked skuas

the first from each individual, distinguished up to 5 groups. However, 3 groups were always identified as clearly distinct, independent of the methods and data background: (1) a group of individuals that utilised the 'Argentine Basin' at the end of April and in May, and, for a shorter period, the 'Uruguay–Buenos Aires Shelf', which corresponds to the use of the Brazil–Falklands confluence. Subsequently, at the beginning of June, these birds moved to the Southern Brazil Shelf, where they primarily utilised the 'Rio Grande' and partly 'Southeastern Brazil'. These annual tracks were assigned to the migration strategy 'South Brazil Shelf' (SouthBrazil), and consisted of 3 individuals (11 %). (2) Individuals that mainly used the 'Uruguay–Buenos Aires Shelf' between April and September as well as the 'Rio de la Plata'. These tracks were assigned to the migration strategy 'Rio de la Plata' (RioPlata), including tracks of 3 individuals (11 %). (3) Individuals grouped across the southern Patagonian Shelf, e.g. the 'North Patagonian Gulfs' and 'Patagonian Shelf', between April and July to August. These tracks were assigned to the migration strategy 'South Patagonian Shelf' (SouthPata) and consisted of 4 individuals (14 %). The cluster analysis could not clearly separate the remaining 2 groups, and assignment of tracks was dependent on method and data background. (4) Individuals that mainly used the 'Argentine Basin' and the 'Uruguay–Buenos Aires Shelf'. Most of these birds moved frequently between these 2 major regions and some were also distributed partly over the southern Patagonian Shelf. These tracks of 18 individuals (64 %) were assigned to migration strategy 'North Patagonian Shelf/Argentine Basin' (NorthPata).

In October, the differences between individual strategies diminished (Fig. 2b), and almost all skuas moved into a highly seasonal and productive area: the transition zone between the 'Argentine Basin', the 'Patagonian Shelf' and the 'Falklands' (Fig. 1c). However, 3 individuals (IDs 127245, 108272 and 156143) did not use this area during this period, but rather were distributed east from the Falkland Islands over mixed water masses of the Antarctic Polar Front and the Subantarctic Front. One other individual (ID 156143) travelled as far east as the waters north of South Georgia.

On 9 occasions, 8 individuals (5 females, 3 males) performed a pre-laying exodus. These birds departed from King George Island after a median of 6 d (min. = 1 d, max. = 36 d) and their first arrival dates were on average 1 wk before the arrival of birds that did not make a pre-breeding exodus. Seven individuals flew back to the north or east of the Falkland Islands, whereas the others remained in the proximity of King George Island or performed an 8 d trip to the Drake Passage.

The degree of overlap of the probability distributions was significantly larger (22 ± 0.3 % SE, $p < 0.001$) within individuals than among individuals (Fig. 3). Only 1 individual (ID 139679) showed an overlap of just 44 %, whereas the within-individual overlap for all the other tracked skuas was 60 to 95 %. This significant overlap in movement paths was reflected in the very high consistency within individuals with respect to their migration strategy (Fig. 2). This was higher in individuals using 'South Patagonian Shelf', 'Rio de la Plata' and 'South Brazil Shelf' than in individuals that adopted the 'North Patagonian Shelf/Argentine Basin' strategy. There was no significant effect of sex (1.6 ± 1.0 % SE, $p = 0.117$), year (0.3 ± 1.0 % SE, $p = 0.796$) or previous breeding performance (0.4 ± 1.0 % SE, $p = 0.691$) on the distribution of the tracked birds.

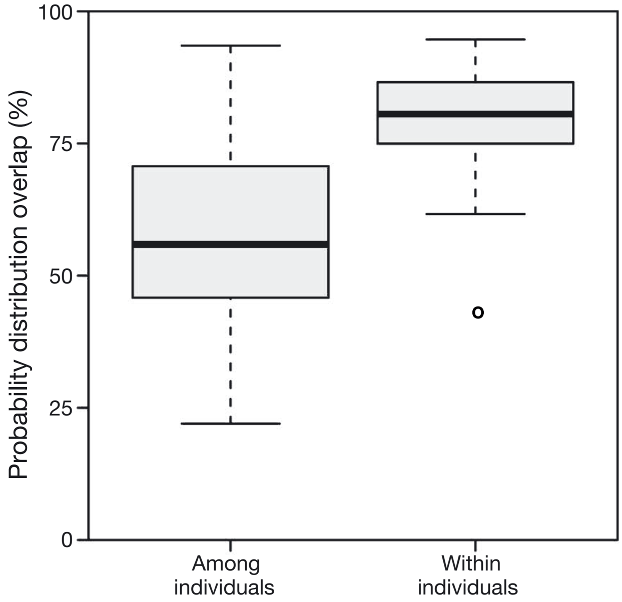

Fig. 3. Overlap among and within individual probability distributions of 28 brown skuas *Catharacta antarctica lonnbergi* from King George Island during the non-breeding periods from 2007 to 2010, including annual migrations of the same individuals over 2 (n = 13) or 3 (n = 3) yr. Line: median; box: 25th–75th percentiles; whiskers: 5th–95th percentiles; circles: outliers

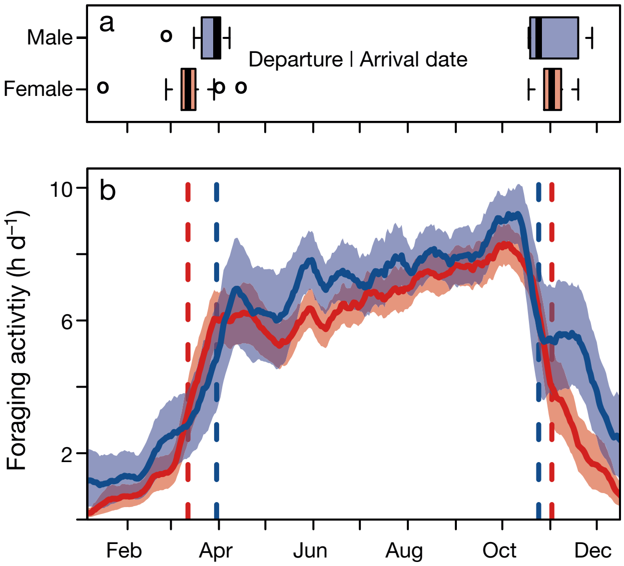

Fig. 4. (a) Departure and return dates of brown skuas *Catharacta antarctica lonnbergi* (20 females, 8 males) from King George Island during 2007 to 2010. Boxplot limits as in Fig. 3. (b) Marine foraging activity (20 d moving average and 95 % CI) of 16 female (red) and 7 male (blue) brown skuas, throughout the years 2007 to 2010. Foraging activity was approximated by saltwater immersion data with intermediate (wet and dry) 10 min intervals. Note that brown skuas fed mainly on terrestrial prey during the breeding season and switched to a pelagic distribution after they left the breeding site. Dashed lines: median departure and return dates

Timing of migration

The mean departure date from King George Island was 17 March (±12 d SD; 25 February to 13 April, n = 28). Females departed around 2 to 3 wk earlier than males (17.38 ± 2.75 d SE, $t = 6.32$, $p < 0.001$; Fig. 4a). 'SouthPata' individuals departed significantly earlier than 'NorthPata' (17.7 ± 3.47 d SE, $t = 5.08$, $p < 0.001$), 'RioPlata' (11.0 ± 4.96 d SE, $t = 2.22$, $p = 0.03$) and

'SouthBrazil' individuals (11.8 ± 4.50 d SE, t = 2.6, p = 0.01). Besides the significant differences between these particular strategies, departure date was not influenced by previous breeding performance (1 or 2 chicks fledged vs. unsuccessful; 3.41 ± 2.39 d SE, t = 1.42, p = 0.16) or year (−0.61 ± 1.21 d SE, t = 0.5, p = 0.61). The repeatability value of the departure date was moderate in both sexes (Table 1).

Brown skuas returned to King George Island around 31 October (±10 d; 17 October to 23 November, n = 28). The arrival date did not differ significantly between sexes (1.46 ± 4.30 d SE, t = 0.34, p = 0.73), but was highly repeatable at the individual level (Table 1), and there were significant differences between years (2007–2010: 2.07 ± 0.80 d SE, t = 2.57, p = 0.016).

The mean (±SD) duration of the non-breeding period was 228 d (±17 d; 197 to 272 d, n = 28), and was highly repeatable within individuals (Table 1). Males spent less time away from the breeding site than females (18.37 ± 5.21 d, t = 3.52, p = 0.001) independent off year (2.53 ± 1.7 d, t = 1.48, p = 0.14) and breeding performance (6.04 ± 3.7 d, t = 1.62, p = 0.11). Additionally, 'SouthPata' individuals had a significantly shorter non-breeding period (20.2 ± 6.68 d, p = 0.006) than 'NorthPata' individuals.

Activity patterns

During the non-breeding period, tracked brown skuas spent a large proportion of the day sitting on water (females: 57 ± 4.40 % SD, n = 16; males: 55.38 ± 6.08 % SD, n = 7) and a much smaller proportion in flight (females: 14.71 ± 3.45 % SD, n = 16; males: 12.46 ± 4.10 % SD, n = 7). The length of time categorised as foraging was significantly higher in males than females (0.93 ± 0.30 h SE, t = 3.06, p = 0.006; Table 1), and was concentrated mainly during the day (females: 67.21 ± 8.08 % SD, n = 16; males: 69.45 ± 8.45 % SD, n = 7) rather than at night (females: 22.34 ± 5.98 % SD, n = 16; males: 21.37 ± 4.70 % SD, n = 7). Foraging activity differed significantly between years (−0.20 ± 0.07 h SE, t = 2.61, p = 0.009) and over the non-breeding period (0.07 ± 0.009 h SE, t = 8.06, p < 0.001), but there was no significant repeatability within individuals (Table 1). Within the non-breeding period, the foraging activity peaked in early October (Fig. 4b), before the brown skuas returned to King George Island.

The number of flight bouts per day did not differ significantly between males (4.16 ± 1.02 SD) and females (3.86 ± 0.65 SD) (0.35 ± 0.24 SE, t = 1.44, p = 0.16). Day of the year had a significant effect (0.16 ± 0.01 h SE, t = 9.02, p < 0.001) on the number of flight bouts, but there was no effect of year (−0.07 ± 0.08 h SE, t = 0.83, p = 0.40). However, the number of flight bouts was not repeatable within individuals (Table 1). In contrast, there was a significant effect of sex (females: 63.53 ± 19.04 min SD, males: 45.97 ± 8.45 min SD; difference: 15.10 ± 7.10 min SE, t = 2.11, p = 0.049) and year (−5.81 ± 2.16 min SE, t = 2.68, p = 0.009) on the duration of flight bouts, which was independent of

Table 1. Migration characteristics (mean departure date, arrival date and duration) and activity patterns (foraging activity, number and duration of flight bouts) of brown skuas *Catharacta antarctica lonnbergi* during the non-breeding periods from 2007 to 2010, and their individual repeatability (R, lower and upper 95 % CIs and p-values). Mean values were calculated using only data from the first migration track from every individual (N_{ind}) and repeatability values, using repeated migrations (N_{rep}) over 2 or 3 yr

	Sex	N_{ind}	Value ± SD	N_{ind}/N_{rep}	R	Lower CI	Upper CI	p-value
Departure date from breeding site	Female	20	13 March ± 10 d	11/23	0.477	0.009	0.821	0.002
	Male	8	26 March ± 13 d	4/10	0.490	0.035	0.747	<0.001
Arrival date at breeding site	Female	20	31 October ± 8 d	12/25	0.871	0.729	0.995	<0.001
	Male	8	30 October ± 15 d	4/10	0.972	0.939	0.991	<0.001
Duration of the non-breeding period	Female	20	232 ± 12 d	12/25	0.814	0.590	0.937	<0.001
	Male	8	218 ± 24 d	4/10	0.859	0.542	0.974	<0.001
Daily foraging time in h d^{-1} (%)	Female	16	6.72 ± 0.75 (28.00 ± 3.14)	7/16	0.623	0.080	0.895	0.066
	Male	7	7.71 ± 0.80 (32.16 ± 3.34)					
Daily flight bouts (n)	Female	16	3.86 ± 0.65	7/16	0.207	0.000	0.750	1.000
	Male	7	4.16 ± 1.02					
Flight bout duration (min)	Female	16	63.53 ± 19.04	7/16	0.656	0.178	0.916	<0.001
	Male	7	45. 97 ± 8.45					

day of the year and significantly repeatable within individuals (Table 1). NPP and breeding performance had no effect on the foraging activity, or the number and duration of flight bouts.

DISCUSSION

During the non-breeding season, the tracked brown skuas from King George Island (Maritime Antarctic) were widely distributed over the Patagonian Shelf and shelf-break and the Argentine Basin, particularly in the area of the Brazil–Falklands Confluence. The northern end of this range is substantially further north than the distribution indicated for this species in Furness (1987), but more consistent with subsequent at-sea observations (Olmos 2002). The use by some individuals of the Southern Brazil Shelf contrasts the tracking data from brown skuas at South Georgia, which mostly spent the non-breeding season further south in the Argentine Basin (Phillips et al. 2007, Carneiro et al. 2016). Hence, the distributions of the 2 brown skua populations overlap only at the Brazil–Falklands Confluence — and indeed, there seems to be greater overlap of the birds from South Georgia with those of the closely-related Falkland skua in the area of the southern Patagonian shelf-break (Phillips et al. 2007). However, given the few Falkland skuas (n = 4) that have been tracked and the different study periods (2002), this conclusion should be viewed with some caution.

Within the entire (population-level) non-breeding range, individuals were continuously distributed across space, suggesting a large contiguous area of suitable habitat (Fig. 1a). However, particular individuals only used distinct portions of the overall range and in a rather consistent manner within and across years (Figs. 2 & 3). Individual consistency in migration strategies was also recorded for 17 south polar skuas *Catharacta maccormicki* and 3 great skuas *C. skua* tracked in 2 and 3 consecutive non-breeding seasons (Kopp et al. 2011, Magnúsdóttir et al. 2012, Weimerskirch et. al. 2015), and suggests that individual consistency in migration strategies is widespread in skuas.

The 4 migration strategies identified within this brown skua population matched the seasonal shift in productivity in the wintering area. The majority of the individuals ('NorthPata' strategy) utilised the year-round, highly productive Brazil–Falklands Confluence (Garcia et al. 2004). Moreover, a small group of 3 individuals ('RioPlata' strategy) regularly switched between the highly productive region influenced by the outflow of Rio de la Plata (Acha et al. 2008) and the more open waters towards the Patagonian shelf-break. Individuals from the southern and northern end of the range ('SouthPata' and 'SouthBrazil' strategies) used the highly productive but seasonal frontal systems of the southern Patagonian Shelf (Acha et al. 2004, Rivas et al. 2006), and the South Brazil Shelf (Acha et al. 2004), respectively. During this period, the tracked individuals spent only a small proportion of the day flying, a pattern found in brown, great and south polar skuas (Phillips et al. 2007, Magnúsdóttir et al. 2014, Weimerskirch et al. 2015, Carneiro et al. 2016). A clear diurnal pattern was apparent, with multiple landings during the day, interspersed by 3 to 4 short flight bouts of approximately 1 h. On average, females made longer flight bouts than males and spend less time foraging (Table 1). The sex-specific differences might be explained by the reversed sexual size dimorphism in brown skuas (Phillips et al. 2002). Males are likely to have lower wing loading, greater manoeuvrability and a lower cost of take-off, which can lead to sex-specific differences in habitat use and behaviour (Phillips et al. 2004). The level of foraging activity and number of flight bouts was not repeatable at the individual level, suggesting that brown skuas adjust their feeding behaviour depending on local food availability. However, there was a degree of individual consistency in the duration of flight bouts, which might also relate to differences between wintering regions in the distance between prey patches, or be associated with the animals' personality, since roaming behaviour and exploration is often considered as a repeatable individual trait (e.g. Dingemanse et al. 2002, Réale et al. 2007, Patrick & Weimerskirch 2014). The lack of correlation between activity patterns and absolute NPP is most likely attributed to the coarse spatial scale, and the time lag for changes in productivity to propagate through trophic levels to affect prey abundance for higher predators such as skuas (Frederiksen et al. 2006). However, we still consider NPP values, in combination with frontal systems, to be a valuable indirect measure of large-scale food predictability and availability that can be linked to population-level distributions (see also Zainuddin et al. 2006, Pinaud & Weimerskirch 2007, Humphries et al. 2010, Thompson et al. 2012).

Following breeding, the tracked skuas travelled to one of several alternative wintering areas within the overall range according to their particular migration strategy. In contrast, in the late non-breeding season, most tracked birds moved towards the same area around the central Patagonian shelf-break, where they remained for several weeks before returning to the breeding ground (Fig. 2). This area is particularly known for its strong seasonality (Signorini et al. 2006), and the increased foraging activity of the brown skuas suggests they exploit the local spring peak in primary production (Figs. 1 & 4b). The diversity of migration strategies means that birds experience different environmental conditions during the winter, which could presumably affect body condition, laying date, breeding probability and success (e.g. Bogdanova et al. 2011, Fayet et al. 2016) and the degree of exposure to pollutants (e.g. Leat et al. 2013). The high spatial and temporal migratory connectivity (here defined as the spatial extent of one population at any given time; see Bauer et al. 2016 and Lisovski et. al 2016) shown by the tracked birds, particularly the aggregation of most individuals in the same area at the end of the winter, makes the population susceptible to oceanographic or other changes within the region.

It should be noted that 3 of the tracked skuas did not join the others on the central Patagonian shelf-break but moved further offshore before returning to King George Island. Based on a discriminant analysis (including bill depth at the gonys, along with tarsus, culmen, wing and head length), these 3 individuals were significantly smaller than the others (authors' unpubl. data). This suggests that they might have been hybrids between brown skuas and the smaller south polar skua, as hybridisation between these closely-related species occurs frequently (Ritz et al. 2006). This might explain their distinctive migration pattern, as south polar skuas are trans-equatorial migrants (Kopp et al. 2011, Weimerskirch et al. 2015), and hybridisation is known to alter migration behaviour in other species (e.g. Helbig 1991).

Timing of migration, like distribution, differed between sexes and was consistent within individuals (Table 1). Repeatability in the arrival date at the breeding grounds was notably high, particularly given the extensive variation among individuals (within a 48 d range). This could reflect the varying costs and benefits of the timing of migration between individuals (Møller 1994), or among birds of different age-classes or experience levels (Jaeger et al. 2014). For example, competitive individuals can evict weak competitors from territories even if they arrive latter, and might consequently benefit from a shorter overall attendance period at the breeding grounds (Forstmeier 2002). There was some variation between years, indicating a degree of flexibility in response to local environmental conditions, as has been demonstrated across a large range of taxa (e.g. Marra et al. 1998, Gill et al. 2001, Norris et al. 2004).

As arrival date is subject to much stronger selection pressures (Both & Visser 2001, Brown et al. 2005), we expected that individual repeatability in departure dates from King George Island would be lower. Previous studies of brown skuas, as well as other seabird species, have shown that non-breeders or failed breeders depart earlier because they are not constrained by reproductive duties (Phillips et al. 2005, 2007, Bogdanova et al. 2011, Fifield et al. 2014). However in our data there was no such relationship, although the sample size was high (18 successful and 29 unsuccessful individuals). The later departure of male brown skuas in comparison with females can be explained with their higher degree of nest-site fidelity (Parmelee & Pietz 1987) and the benefits of a longer defence period that might increase their chance of retaining the same territory in consecutive breeding seasons.

Eight tracked individuals, most of which returned relatively early to the breeding grounds, went on a pre-laying exodus of ca. 1000 to 1500 km back to their non-breeding ranges. The majority of brown skuas tracked from South Georgia, particularly females, also went on a pre-laying exodus (Phillips et al. 2007, Carneiro et al. 2016). There are obvious benefits of early arrival; brown skuas are highly territorial and their reproductive success depends on the quality of the acquired territory (Hahn & Bauer 2008). However, there might also be costs, such as the increased risk of encountering adverse weather during the early season (Møller 1994). It appears that a pre-laying exodus is discretionary, presumably depending on conditions at the breeding colony, as only 1 of the 5 individuals tracked in multiple years performed such a trip twice.

In conclusion, we recorded highly consistent individual migration strategies in brown skuas from King George Island; this reflected considerable variation in timing of migration, non-breeding distributions and activity patterns. The tracked birds differed extensively in their arrival dates at the breeding ground, a migratory trait that is supposed to be under strong selection (e.g. Kokko 1999), whereas the arrival dates within individuals were highly repeatable. Based on the high levels of primary production, the tracked brown skuas mainly exploit one of a number of alternative wintering areas within the overall non-breeding range. However, almost all individuals moved to take advantage of a seasonal peak in marine productivity in a particular area for several weeks before the final return to the colony; these birds are presumably returning to this area of high resource abundance that they experienced during an initial early-life exploration–refinement phase (Guilford et al. 2011). The 3 individuals that showed a different late-winter distribution may not have visited this otherwise common area in previous years, or may be hybrids exhibiting an alternative migration strategy that reflects genetic differences. We were unable to disentangle the relative contribution of genetic control versus past experience in determining individual migration strategies. To this end, we would need to track movements of juvenile brown skuas during their first years at sea, and ideally, also track their parents. Such data would also be extremely valuable for determining the flexibility in migration strategies within and across generations, and provide an indication of how quickly seabirds can adapt to rapid changes in the environment.

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Contribution to the Theme Section 'Individual variability in seabird foraging and migration'

Intra- and inter-individual variation in the foraging ecology of a generalist subantarctic seabird, the gentoo penguin

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ABSTRACT: Individual specialisations have been suggested to improve foraging efficiency by optimising individual capacity (physiological and behavioural) and reducing intra-specific competition in exploiting prey resources. In this study, we investigated the inter- and intra-individual variation in behaviour in an opportunistic forager, the gentoo penguin *Pygoscelis papua*, at Kerguelen Island, southern Indian Ocean. We used complementary bio-logging and stable isotope analyses, coupled with morphometric measurements, to: (1) determine the inter-individual variation in morphology and foraging behaviour; (2) quantify intra-individual variation in foraging behaviour; (3) investigate the links between consistency in foraging, distances travelled and body condition; and (4) determine if dietary specialisations exist and are maintained outside the breeding season. We show that this species exhibits a large inter-individual variation in foraging behaviour, with some individuals conducting very short trips close to the colony while others travelled considerably farther. Heavier individuals tended to forage in more distant locations, dive deeper and perform more benthic dives. Individual specialisation in behaviour was low to moderate at the population level, yet some individuals were very consistent. The rate of travel was not influenced by consistency, and there was a lack of correlation between body condition and foraging consistency. High inter-individual variation in feeding ecology and dietary specialisations outside of a single breeding season were observed, consistent with gentoo penguins being Type 'B' generalists (i.e. generalist populations composed of individuals each consuming a different range of foods).

KEY WORDS: Behavioural consistency · Diving behaviour · Feeding ecology · Foraging behaviour · Individual specialisations · *Pygoscelis papua* · Stable isotopes

INTRODUCTION

According to the optimal foraging theory, individuals implement feeding strategies aimed at maximizing energetic gains while minimizing costs (Stephens & Krebs 1986). Individual specialisations have been suggested to improve feeding efficiency by reducing intra-specific competition or allowing individuals to catch prey they can handle and digest most efficiently (Bolnick et al. 2003, Estes et al. 2003). Food consumption rates and body condition differ among diet specialists, and these differences may reflect differences in an individual's intrinsic quality (dit Durell et al. 2001, Bolnick et al. 2003, Anderson et al. 2009, Svanbäck & Persson 2009, Cucherousset et al. 2011). Specialisations in foraging, involving the repetition of specific behaviours to acquire food or dietary choices over time, have until recently been poorly investigated

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(Bolnick et al. 2003, Estes et al. 2003, Cook et al. 2006). Individual specialists have been defined as 'individuals whose niche is substantially narrower than their population's niche for reasons not attributable to their sex, age or discrete morphological group' (Bolnick et al. 2003, p. 3). Even populations usually thought to be generalists can actually be composed of individual specialists, referred to as Type 'B' generalists (individuals each specialising on a different but narrow range of food types) as opposed to Type 'A' generalists (individuals all taking a wide range of food types) (Araújo et al. 2011, Loxdale et al. 2011, Layman & Allgeier 2012, Fodrie et al. 2015).

Information on individual specialisations is crucial, as they may have significant ecological consequences at the individual and population levels, and may impact ecological processes and foraging dynamics (Bolnick et al. 2003, Matich et al. 2011, Ceia & Ramos 2015). Thus, it is of importance to identify the mechanisms generating inter-individual variation and study the wider implications of variation in foraging behaviour to understand trophic relationships between the animals and their environment (Bolnick et al. 2003, Baylis et al. 2015, Ceia & Ramos 2015, Kernaléguen et al. 2015). The study of individual specialisations requires longitudinal sampling, in which the same individuals are sampled over time (Bolnick et al. 2003, Araújo et al. 2011). Ideally, the use of complementary techniques that represent different timescales and resolutions should be implemented to accurately describe individual specialisations and their persistence (Kernaléguen et al. 2016). Seabirds are suitable models to study individual specialisations, as most species nest in large colonies that allow for easy access to individuals that use the same environment, are strongly constrained during breeding as central place foragers and may compete for the same resources (Ratcliffe et al. 2013).

Gentoo penguins *Pygoscelis papua* are among the most widespread penguin species, distributed from the northern subantarctic islands (Crozet; 46° S) to the Antarctic Peninsula (62 to 69° S; Williams 1995). These birds are considered inshore opportunistic foragers, consuming both benthic and pelagic species, and exhibiting high plasticity in their diet, marine habitat use and dive behaviour (Bost & Jouventin 1990, Woehler 1995, Lescroël & Bost 2005, Miller et al. 2009). They consume patchy prey encompassing a large size range, from small crustaceans to large fish species (Hindell 1989, Robinson & Hindell 1996). Accordingly, their diets vary substantially among breeding locations, within colonies and also within individuals of the same colony (Croxall et al. 1988, Bost & Jouventin 1990, Robinson & Hindell 1996, Lescroël et al. 2004, Polito et al. 2015).

As gentoo penguins are long-lived and sedentary (Williams & Rodwell 1992), individuals are expected to learn to apply efficient foraging tactics throughout their lifetime and, thus, increase their individual efficiency when foraging under situations of competition or food limitation (Estes et al. 2003). Indeed, recent studies suggest that individuals exhibit some degree of prey selection and specialisation, as judged by stomach content analysis and stable isotope values (Polito et al. 2015). However, there is little information on individual consistency in foraging behaviour and on whether such specialisations are linked to diet in this species.

In the present study, we investigated inter- and intra-individual variation in the foraging ecology of gentoo penguins. We used complementary bio-logging and stable isotope analysis, coupled with morphometric measurements to: (1) describe their inter-individual variation in morphology, spatial use and dive behaviour; (2) quantify their intra-individual variation in foraging behaviour; (3) investigate the links between consistency in foraging behaviour, distances travelled and body condition; and (4) describe their inter-individual variation in feeding ecology, and determine if dietary specialisations exist and are maintained outside of the breeding season. We predicted that: (1) individuals would differ greatly in foraging metrics, as gentoo penguin diet and behaviour are known to vary among colonies and between individuals of the same colonies, and that such variation would be attributed to differences in body mass, which influences dive depth (Lescroël et al. 2004, Lescroël & Bost 2005, Cook et al. 2013, Polito et al. 2015, Camprasse et al. 2017); (2) dietary and behavioural consistency would be detected, as populations usually considered generalists are increasingly shown to be composed of individual specialists (Woo et al. 2008, Araújo et al. 2011, Loxdale et al. 2011, Layman & Allgeier 2012, Fodrie et al. 2015); and (3) individuals displaying higher consistency in foraging behaviour would travel shorter distances and have higher body condition, as such consistency is thought to allow individuals to forage more efficiently (Bolnick et al. 2003, Estes et al. 2003).

MATERIALS AND METHODS

Study site and instrumentation

The study was performed at Kerguelen Island in the southern Indian Ocean, one of the major breed-

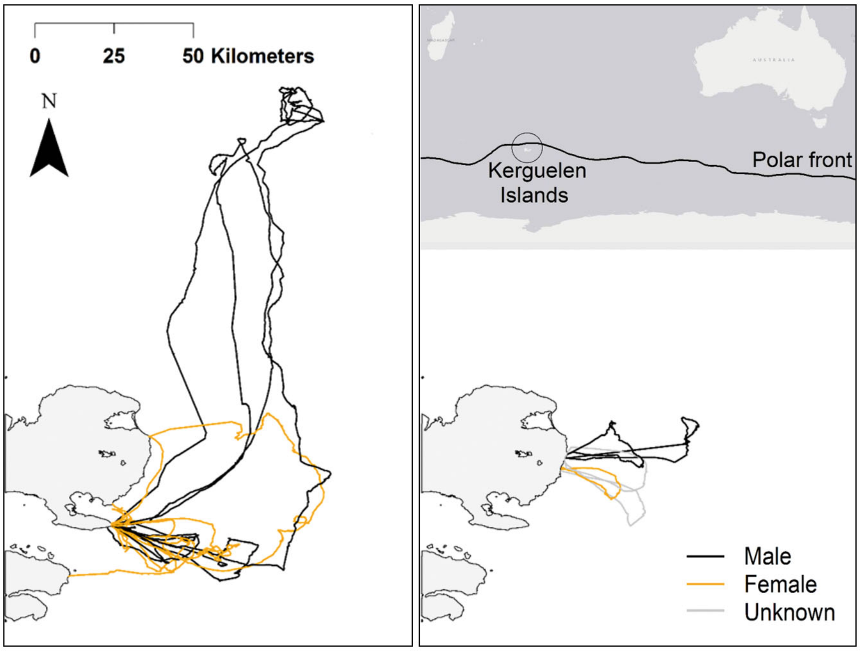

Fig. 1. One track per gentoo penguin *Pygoscelis papua* instrumented at Pointe Suzanne (left panel) and Estacade (right panel), Kerguelen Islands, Indian Ocean, during the crèche period in December 2014 to January 2015

ing grounds for gentoo penguins (hereafter referred to as gentoos) with 40 000 pairs (Lescroël et al. 2004, Lynch 2013). Gentoos breed along most of the Kerguelen coastline in many small to medium-sized colonies ranging from 15 to >400 pairs). As the diet and foraging behaviour of this species are known to vary substantially among colonies and within breeding locations, especially on Kerguelen Island (Lescroël et al. 2004, Lescroël & Bost 2005), 2 colonies were selected to ensure that the patterns observed were not solely dependent upon colony location. Accordingly, field work was conducted at the Pointe Suzanne and Estacade colonies (ca. 20 km apart, 49° 26′ S, 70° 26′ E and 49° 15′ S, 70° 33′ E, respectively, with ca. 50 and 25 chicks, respectively; Fig. 1). Both colonies face the open ocean. The Pointe Suzanne colony, however, faces a wider range of foraging habitats due to its proximity to a more sheltered bay (Baie Norvégienne). The Estacade colony is localized westward of the Polar Front, a productive frontal zone, on the eastward side of the Kerguelen shelf. Gentoos were in the late chick-rearing (i.e. crèche) stage at both study sites. Logistical constraints prevented sampling other colonies, as well as greater sample sizes, and so our results on site effects must be interpreted with caution.

We deployed data loggers on breeding gentoos during the late chick-rearing period (crèche stage: chicks >4–5 wk old), in the 2014/15 breeding season (Table 1). To determine the at-sea movements and diving behaviour of the penguins, we used Fastloc GPS loggers (F2G 134A; FastLoc®; Sirtrack; 69 × 28 × 21 mm, 39 g in air), alone or in combination with time-depth recorders (TDR, LAT1800S, Lotek Wireless; 36 × 11 × 7.2 mm, 4.8 g in air). GPS loggers were programmed to sample position every 5 min. The TDR units were set to record depth and temperature at 1 s intervals. All attached devices, alone or in combination, weighed <1 % body mass.

At Pointe Suzanne, sampling occurred between 24 November and 9 December 2014. In total, 24 birds were instrumented for 4 to 16 d according to the possibilities of recapture. We used either 2 kinds of instruments (GPS+TDR: n = 18), or only 1 instrument (GPS: n = 4, TDR: n = 2). At Estacade, 9 birds were instrumented between 20 December 2014 and 4 January 2015 with GPS+TDR for 4 to 15 d.

All instrumented birds were confirmed breeders, with only birds that were observed feeding chicks being sampled. Individuals were weighed in a cloth bag using a suspension scale (±25 g, Pesola) before data loggers were attached to the dorsal feathers using waterproof tape (Tesa 4651) and cyanoacrylate glue (Loctite 401 Instant Adhesive). Individuals were then released and resumed normal behaviours. With the exception of 3 individuals from Estacade that were recaptured on the beach a few kilometres north or south of the colony, all birds were recaptured at the colony after several foraging trips. The data loggers were removed and individuals were weighed again. Measurements of bill length and depth were taken with Vernier callipers (±0.05 mm) and flipper length with a

Table 1. Summary of bio-logging deployments for gentoo penguins *Pygoscelis papua* instrumented and retrieved at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015; F: female, M: male, –: missing data

Bird	Sex	Body condition index	Initial mass (kg)	Bill depth (mm)	Bill length (mm)	Flipper length (mm)	Tracking time (d)	Total no. of trips
Pointe Suzanne								
4	F	0.4	5.0	13.4	81.0	225.0	8.3	15
7	F	−0.4	5.8	16	95.0	244.0	6.9	4
9	F	−0.4	3.6	13.3	76.0	215.0	10.9	11
10	F	−0.4	4.4	15.6	81.0	220.0	7.0	9
13	F	−0.4	4.4	15.8	80.0	221.0	10	3
15	F	−0.3	5.2	15.1	88.0	232.0	4.0	3
20	F	0.2	5.0	14.9	75.0	230.0	4.5	3
22	F	0.0	4.5	15.5	81.0	210.0	13.3	6
24	F	0.4	5.1	14.3	84.0	220.0	4.4	3
1	M	−1.7	4.3	16.7	95.0	234.0	6.5	9
2	M	–	5.9	11.8	–	235.0	8.2	12
3	M	0.4	6.8	18.1	91.0	245.0	7.9	2
5	M	–	6.1	16.5	–	235.0	6.1	3
6	M	0.4	5.9	18.4	79.0	231.0	–	–
11	M	−0.1	5.8	16.5	89.0	238.0	8.7	3
12	M	0.3	5.7	17.6	85.0	225.0	8.0	2
14	M	−0.2	5.3	16.5	90.0	228.0	4.4	4
17	M	−0.1	5.3	16.8	85.0	230.0	5.4	3
19	M	−0.2	5.7	18.2	89.0	232.0	–	–
23	M	−0.3	5.8	17.3	95.0	232.0	–	–
Estacade								
26	–	–	4.5	–	–	–	6.1	2
28	–	–	6.4	–	–	–	15.4	3
27	F	–	5	17.1	82.0	220.0	4.0	3
25	M	–	6.6	–	91.0	234.0	5.9	2
30	M	1.4	7.8	19.5	92.0	235.0	6.2	6
33	M	1.1	6.3	16.4	85.0	224.0	–	–

metal ruler (±1 mm). In addition, a blood sample (0.5–1.5 ml) was obtained by venipuncture of a tarsal vein for stable isotope analysis and molecular sex determination. Feathers (n = 3–6) were plucked from the thorax region for stable isotope analysis. Handling times ranged from 15 to 20 min, during which the bird's head was covered with a hood to reduce stress. Of the 33 birds instrumented at the 2 study sites, 28 birds were recaptured, of which 4 did not go to sea to forage and 2 individuals had TDRs that malfunctioned. Overall, 22 individuals provided data which were analysed (Pointe Suzanne: n = 17, Estacade: n = 5). All 22 individuals conducted more than 1 trip, with 19 providing both TDR and GPS data.

Isotopic analyses

The δ^{13}C values of seabirds reflect their foraging habitats (Cherel & Hobson 2007, Jaeger et al. 2010), while their δ^{15}N values increase with trophic level (Cherel et al. 2010). Isotopic values were measured on whole blood and feathers. The rationale is that the 2 complementary tissues integrate different periods of information, due to the fact that the keratin in feathers is inert after synthesis (details in Cherel et al. 2008). Blood is a metabolic active tissue that integrates a period of weeks before sampling, whereas feathers reflect the diet at the time they were grown, as feathers are metabolically inert after they are grown (Cherel et al. 2000). In the present study, blood isotopic values integrated a few weeks before sampling, thus corresponding to the breeding period (Bearhop et al. 2006). In contrast, gentoos moult once a year, at the end of the breeding period, after a period of 10 d at sea dedicated to replenishment of body reserves (Croxall & Davis 1999, Polito et al. 2011). They then fast ashore for about 3 wk, using their body reserves to cover the energetic and nutrient needs for moulting and fasting (Croxall & Davis 1999). Hence, the isotopic values of feathers document the foraging ecology of penguins during the pre-moult period of hyperphagia at sea during which they build up energy reserves (Cherel et al. 2008), here almost 1 yr before sampling the instrumented gentoos.

In the laboratory, blood samples were freeze-dried and powdered. Lipid extraction was unnecessary, as the C:N mass ratio was <3.5 for all blood samples (Cherel et al. 2005b); C:N mass ratios ± SD were 3.29 ± 0.06 (whole blood, n = 25) and 3.17 ± 0.05 (feathers, n = 27). A pool of 3 feathers bird^{-1} was cleaned of surface lipids and contaminants using a 2:1 chloroform:methanol bath, air-dried and cut into small pieces. For each feather, the rachis and the top 5 mm of the feather synthesised at sea were discarded before analysis so that the remaining feather sections were homogeneous and corresponded to the fasting period (Cherel et al. 2005a).

Nitrogen and carbon isotopic ratios were measured on aliquots of 0.2 to 0.4 mg with a continuous-flow isotope-ratio mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite (VPDB) for carbon and atmospheric N_2 (AIR) for nitrogen. Replicate measurements of internal laboratory standards (acetanilide and peptone) indicated measurement errors <0.15‰ for both $\delta^{13}C$ and $\delta^{15}N$. Blood and/or feather sampling was not possible on all individuals instrumented, resulting in the collection of either no samples, only feathers, only blood, or both samples for each individual. Stable isotope values were obtained from 25 individuals for blood (11 females, 14 males), and 27 individuals for feathers (11 females, 13 males, 3 unknown). Both tissues were sampled in 24 individuals (11 females, 13 males). Of these 24 individuals, 16 also had both GPS and TDR data, 1 had TDR data only, 3 had GPS data only, and 4 did not have any bio-logging data.

Data processing

All data analyses were conducted in the R Statistical Environment in version 3.3 (R Core Team 2015). The GPS records for each bird were visually inspected to identify individual foraging trips. As some birds hauled out in some locations distant from the colony for a few hours to several days, foraging trips were defined as the time between when an individual left a land-based position until it came back ashore. The *diveMove* package (Luque 2007) was used to apply a speed filter to the GPS data to remove erroneous locations (with a speed threshold of 1.5 m s^{-1} based on the 95th percentile of swim speeds for all individuals). The GPS records were interpolated to 1 s intervals in the *adehabitatLT* package (Calenge 2015) to provide spatial information for the dive records. Furthermore, the packages *trip* (Sumner 2009) and *sp* (Pebesma & Bivand 2005) were used to obtain summaries of at-sea movements and investigate the consistency in habitat use. Individual tracks were overlaid with a grid comprised of 2 × 2 km cells, where the number of grid cells used were calculated for each trip. Means and coefficients of variation for each individual were calculated for trip duration, maximum range, and horizontal distance travelled per trip and per hour. Bearing for each trip was calculated as the angle between the colony and the most distal point of the tracks, and standard deviation in bearing was calculated for each individual using the *circular* package (Agostinelli & Lund 2011).

The *diveMove* package was used to obtain summaries of diving metrics from TDR records (only dives deeper than 2 m were considered to be foraging dives, following Lescroël & Bost 2005). The *lubridate* package (Grolemund & Wickham 2011) was used to identify night and day dives based on sunset and sunrise times at the relevant sites. Benthic and pelagic dives were determined based on the proportion of dive time that was spent in the bottom phase for each dive (phase detected by the 'diveStats' function after descent and before ascent), and the depth achieved on consecutive dives. If the dive depth stayed within 5% of the maximum depth for this dive for more than 15 s, and if the dive was within 5% of the maximum depth achieved during the last 15 min of diving, the dive was labelled as 'flat-benthic'. If the dive was within 5% of the maximum depth achieved for 'flat-benthic' dives during the last 15 min of diving, but the other criterion was not met, the dive was labelled as 'V-benthic'. If the dive met neither of these criteria, the dive was labelled as 'pelagic'. The proportion of pelagic dives was then determined. Means and standard deviations per trip were calculated for bottom time and mean bottom depth of each dive, the total vertical distance travelled per trip and per hour, and the proportion of pelagic and night diving. Horizontal and vertical distances travelled were summed to provide an index of foraging energy expenditure per trip and per hour (Wilson et al. 1986).

An index of consistency in habitat use was calculated for each animal. For each trip, the number of grid cells used by the individuals was identified. The number of shared grid cells between each pair of trips (e.g. trip 1 and trip 2, trip 2 and trip 3, trip 1 and trip 3 etc.) was determined and the average of these calculated. This number was then divided by the average number of grid cells used per trip. Different grid cell sizes were tested to calculate the index of consistency in habitat use (from 1 × 1 km to 10 × 10 km) to check the influence of grid cell size on our estimate of spatial consistency. Indices obtained, regardless of cell grid sizes, were highly correlated, and data from the 2 × 2 km grid cell size are presented.

Statistical analyses

Body mass and morphometric measurements were correlated (linear regressions: beak depth: $F_{1,18} = 14.62$, $R^2 = 0.42$, $p = 0.001$; flipper length: $F_{1,18} = 14.15$, $R^2 = 0.65$, $p = 0.001$) and therefore, only relationships with body mass were further investigated in models. A principal component analysis was run on flipper and bill length and bill depth with the *FactoMineR* package (Lê et al. 2008). Residuals from a linear regression of the first principal component against body mass were then used as an index of body condition (Cuervo et al. 2009). The first principal component of the morphometric measurements explained 72.2% of the total variation and was therefore used as an estimate of structural size. There was no significant difference between the sexes in the slopes or elevations of the linear regressions of body mass on this estimate of structural size. Therefore, data were pooled to estimate individual body condition.

The following spatial metrics were highly correlated: trip duration and maximum range (linear mixed effects models: $F_{1,17} = 61.17$, $R^2 = 0.78$, $p < 0.001$); and maximum range and total distance travelled (linear mixed effects models: $F_{1,17} = 285.7$, $R^2 = 0.94$, $p < 0.001$). Consequently, only maximum range was used in linear mixed effects models. Similarly, the following diving metrics were highly correlated: bottom depth and total vertical distance travelled (linear mixed effects models: $F_{1,17} = 41.41$, $R^2 = 0.69$, $p < 0.001$); and dive time and bottom depth (linear mixed effects models: $F_{1,17} = 91.04$, $R^2 = 0.83$, $p < 0.001$). Thus, only bottom depth was included in further analyses.

Following a preliminary analysis to remove outliers, we used linear regressions, and linear mixed effects models in the package *lme4* (Bates et al. 2014) where individuals had repeated samples, to investigate relationships between morphometric measurements, consistency in foraging strategies and stable isotope values. For all models, backward-stepwise model selection was used to select the most parsimonious model (Ratcliffe et al. 2013). First, the most appropriate random effects structure was identified with the restricted maximum likelihood (REML), then the best fixed effects structure was determined using maximum likelihood (ML) after models were compared with the ANOVA function, and the most parsimonious models were found based on their Akaike's Information Criteria. For models in which 1 observation per trip was used (i.e. for spatial use metrics), individuals were included in the random effects. For models in which multiple observations per trip were used (i.e. for diving behaviour metrics), trip nested within individuals was included in the random effects. The selected models were refitted with REML to estimate the model parameters (Zuur et al. 2009). The residuals of the models were inspected, and whenever there was evidence of heterogeneity in the residuals, a sex- and/or site-specific variance structure was applied (Zuur et al. 2009).

More specifically, in order to describe the inter-individual variation in morphology and foraging behaviour, we investigated the effects of sex and stage on morphometric measurements, and the effects of sex, site and body mass on foraging metrics (interactions between fixed effects could not be investigated due to small sample sizes). A *k*-means clustering analysis was performed to determine whether individuals clustered according to their foraging behaviour. In order to quantify the intra-individual variation in diving behaviour and spatial use, we used the R package *ape* (Paradis et al. 2004) to perform a variance component analysis. This method calculates the variance, standard deviation and proportion of total variance occurring at the levels of individual, and trip within individual when multiple observations per trip were obtained, as well as the residual variation (Ratcliffe et al. 2013, Harris et al. 2014). An estimate of individual specialisation is given by the proportion of variance explained by the individual variance component (Bolnick et al. 2003, Dingemanse & Dochtermann 2013, Ratcliffe et al. 2013). When models including sex, site or body mass were better than the equivalent models without fixed effects (i.e. null models), the variance component analysis was run on both null and optimal models to quantify the reduction in variance explained by the individual, or the trip effects after the inclusion of the fixed effects (Ratcliffe et al. 2013). In order to investigate the links between consistency in foraging behaviour, vertical and horizontal distances travelled, and body condition, linear regressions were used. In order to quantify the inter-individual variation in trophic niche and foraging behaviour, and determine if dietary specialisations were maintained outside of a single breeding season, relationships between carbon and nitrogen values in blood and feathers, respectively, were investigated. Results presented are means ± SD, unless stated otherwise.

RESULTS

Inter-individual variation in morphometry and at-sea behaviour

Gentoo penguins varied considerably in their body condition, mass and morphometric measurements (Tables 1 & 2). Body condition indices were lower at Pointe Suzanne (linear regression: $F_{1,18} = 14.42$, $R^2 = 0.4$, $p = 0.001$) compared to Estacade but similar between sexes (linear regression: $F_{1,18} = 0.37$, $R^2 = -0.03$, $p = 0.5$). Lastly, females had smaller bill lengths than males (linear regression: $F_{1,18} = 32.68$, $R^2 = 0.63$, $p < 0.001$), as well as flipper lengths (linear regression: $F_{1,18} = 4.96$, $R^2 = 0.2$, $p = 0.04$).

Table 2. Summary of morphometric measurements for gentoo penguins *Pygoscelis papua* instrumented and retrieved at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015; F: female, M: male

		Mean ± SD	Minimum	Maximum
Body condition index	Pointe Suzanne	−0.1 ± 0.5	−1.7	0.4
	Estacade	1.3 ± 0.2	1.1	1.4
	F	−0.1 ± 0.4	−0.4	0.4
	M	0.1 ± 0.8	−1.7	1.4
Body mass (kg)	Pointe Suzanne	5.2 ± 0.8	3.7	6.8
	Estacade	7.1 ± 1.0	6.4	7.8
	F	4.8 ± 0.6	3.7	5.8
	M	5.9 ± 0.9	4.3	7.8
Bill depth (mm)	Pointe Suzanne	16.1 ± 1.5	13.3	18.4
	Estacade	18.0 ± 2.2	16.4	19.5
	F	14.9 ± 1.0	13.3	16.0
	M	17.5 ± 1.0	16.4	19.5
Bill length (mm)	Pointe Suzanne	85.5 ± 6.3	75.0	95.0
	Estacade	88.5 ± 4.9	85.0	92.0
	F	82.3 ± 6.1	75.0	95.0
	M	88.7 ± 4.7	79.4	95.0
Flipper length (mm)	Pointe Suzanne	228.4 ± 9.2	210.0	245.0
	Estacade	229.0 ± 7.8	224.0	235.0
	F	224.1 ± 10.1	210.0	244.0
	M	232.2 ± 5.9	224.0	245.0

Overall, a total of 113 foraging trips were obtained (16 from Estacade, 97 from Pointe Suzanne) with 2 to 15 trips recorded per individual (mean = 5) lasting 4.0 to 15.4 d each (mean = 7.3; Table 1). Individuals varied considerably in their spatial use of the marine environment (Table 3), even within the same colony, with some individuals foraging close to the shore, while others travelled towards the continental shelf. Individual maximum distances from the colony averaged 21.6 ± 18.7 (3.3–78.3) km, trip durations averaged 26.6 ± 22.8 (5.1–77.6) h, total horizontal distances covered averaged 65.0 ± 56.7 (9.9–217.4) km, and horizontal distances per hour averaged 2.7 ± 0.5 (1.8–3.7) km. Furthermore, individual birds exploited different areas around the colony (Fig. 1). Six birds hauled out in locations away from the colony for periods of 10 to 57 h. Birds did not go on 2 consecutive long trips, but rather tended to alternate long and short trips. A *k*-means clustering analysis revealed 3 different foraging strategies: birds that travelled farther, dived deeper and were less pelagic (n = 5, means ± SE: 49.3 ± 19.3 km, 40.2 ± 15.8 m, 70.9 ± 11.4 %, respectively); birds that stayed close to colony had the shallowest dives and displayed the highest percentage of pelagic diving (n = 8, means ± SE: 8.1 ± 4.6 km, 13.6 ± 7.1 m, 89.7 ± 6.9 %, respectively); and birds with intermediate foraging metrics (n = 6, means ± SE: 22.0 ± 5.0 km, 30.7 ± 5.4 m, 73.7 ± 10.2 %, respectively). Both sexes and sites were represented in each cluster. Lastly, sex and site did not influence spatial metrics (Table 4).

There was also considerable inter-individual variation in the diving behaviour of the instrumented birds, irrespective of colony. Some individuals performed very short and shallow dives and travelled short vertical distances,

Table 3. Summary of spatial use metrics for gentoo penguins *Pygoscelis papua* instrumented and retrieved at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015 (values are means ± SD); F: female, M: male

Bird	Sex	Mean bearing (°)	Trip duration (h)	Maximum range (km)	Total horizontal distance (km)	Horizontal distance h^{-1} (km)
Pointe Suzanne						
4	F	98.8 ± 0.6	6.6 ± 5.1	3.3 ± 1.7	9.9 ± 5.8	1.8 ± 0.8
7	F	116.9 ± 0.3	26.4 ± 25.7	17.2 ± 10.8	54.3 ± 43.1	2.9 ± 1.2
9	F	55.5 ± 1.1	5.1 ± 3.1	4.0 ± 1.0	11.0 ± 6.0	2.3 ± 0.6
10	F	129.9 ± 0.2	7.9 ± 4.5	5.7 ± 2.1	17.5 ± 8.6	2.4 ± 0.5
13	F	11.5 ± 1.5	66.0 ± 61.7	39.4 ± 18.7	133.8 ± 98.7	2.5 ± 0.8
15	F	127.5 ± 0.2	11.5 ± 7.5	13.9 ± 3.4	35.0 ± 16.7	3.3 ± 0.6
20	F	127.0 ± 0.1	8.2 ± 8.3	10.0 ± 8.9	24.9 ± 25.3	3.0 ± 0.1
22	F	90.4 ± 0.4	33.8 ± 35.4	17.4 ± 15.4	72.4 ± 70.2	2.2 ± 0.4
24	F	162.2 ± 0.0	14.6 ± 7.4	9.9 ± 1.5	29.3 ± 8.6	2.3 ± 0.8
1	M	106.0 ± 0.4	4.8 ± 3.8	4.7 ± 2.8	10.9 ± 6.2	2.6 ± 1.0
2	M	66.3 ± 0.5	8.5 ± 5.7	7.7 ± 4.6	22.4 ± 15.1	2.9 ± 0.6
3	M	56.3 ± 0.8	77.6 ± 43.7	78.3 ± 62.8	217.4 ± 187.3	2.5 ± 1.0
5	M	125.2 ± 0.1	20.2 ± 16.5	25.4 ± 10.8	67.1 ± 41.3	3.7 ± 0.7
11	M	56.4 ± 0.5	56.0 ± 75.2	59.4 ± 70.2	164.4 ± 211.0	3.2 ± 0.4
12	M	107.0 ± 0.1	70.0 ± 38.6	32.3 ± 3.8	140.5 ± 60.9	2.1 ± 0.3
14	M	91.2 ± 0.1	18.8 ± 10.7	21.9 ± 10.2	53.2 ± 28.2	2.9 ± 0.3
17	M	114.4 ± 0.1	19.8 ± 17.1	17.6 ± 12.2	49.5 ± 38.8	2.5 ± 0.4
Estacade						
27	F	127.9 ± 0.2	11.1 ± 12.8	9.5 ± 6.3	23.3 ± 16.8	3.1 ± 1.4
25	M	79.7 ± 0.2	44.8 ± 5.3	28.7 ± 2.4	89.4 ± 2.4	2.0 ± 0.3
30	M	77.3 ± 0.3	17.9 ± 1.0	16.9 ± 2.1	48.9 ± 3.4	2.7 ± 0.2
26	–	137.2 ± 0.1	12.9 ± 7.7	15.4 ± 12.3	35.1 ± 29.0	2.5 ± 0.8
28	–	86.3 ± 0.8	42.9 ± 61.0	36.9 ± 42.9	120.7 ± 164.5	3.5 ± 1.0

Table 4. Model ANOVA testing the effect of gentoo penguin *Pygoscelis papua* sex and site on maximum range, bottom depth and repeatability, including bird as a random factor or trip nested within bird (likelihood ratio [LR] for linear mixed effects models and *F* values for simple linear regressions). The last row reports on the linear mixed effects model testing the effect of dive depth on the proportion of pelagic dives. Values in **bold** are significant

Variable	Type of model	Parameters	LR/*F* test	df	p
Maximum range	Linear mixed effects	**Random effect: bird**	33.21	6	**<0.0001**
		Fixed effects			
		Sex	3.21	8	0.07
		Site	0	8	0.98
		Body mass	3.15	8	0.08
Bottom depth	Linear mixed effects	**Random effect: bird/trip**	1236.29	9	**<0.0001**
		Fixed effects			
		Sex	3.2	8	0.07
		Site	0.46	8	0.5
		Body mass	7.29	8	**0.01**
Repeatability indices	Linear model	Sex	1.42	2, 18	0.27
		Site	0.04	1, 18	0.84
Proportion of pelagic dives	Linear mixed effects	**Fixed effects** Dive depth	84.83	4	**<0.0001**

while others dived for much longer and deeper, and travelled much greater vertical distances (Table 5). On average, individuals spent 70.9 ± 20.1 (29.5–106.8) s at the bottom of dives, dived to bottom depths of 26.0 ± 14.7 (5.1–61.6) m, and travelled total vertical distances of 26.6 ± 23.2 (2.1–74.5) km, and hourly vertical distances of 0.8 ± 0.2 (0.4–1.1) km. Accordingly, the distance travelled (both horizontal and vertical) varied between individuals (mean distance per trip: 96.6 ± 81.0 [13.3–279.6] km; mean distance per hour of foraging: 3.5 ± 0.6 [2.3–4.8] km).

Sex and site did not significantly influence dive depth (Table 4). Some individuals performed almost entirely pelagic dives while, for others, benthic dives represented up to 48% of all dives (Table 5). Furthermore, individuals varied in their diving schedule, with some individuals diving half of their time at night, and other individuals diving mostly during the day (Table 5, Fig. 2). Daylight dives were on average 30.3 ± 37.5 m deep and 68.5 ± 53.2 s long (n = 24 336, 75% of dives recorded) while night dives were on average 9.2 ± 10.2 m deep and 52.3 ± 39.9 s long (n = 8298, 25% of dives recorded). Several individuals dived at night during multiple-day trips while other birds performed short trips (ca. 10 km from the colony) and dived predominantly at night. The frequency of night diving increased with the proportion of pelagic diving, which averaged 76.8% during the day and 92.9% at night (Fig. 2).

Table 5. Summary of dive metrics and distances travelled for gentoo penguins *Pygoscelis papua* instrumented and retrieved at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015 (values are means ± SD); F: female, M: male, –: unsexed

Bird (%)	Sex	Bottom time (s)	Bottom depth (m)	Total vertical distance (km)	Hourly vertical distance (km)	Total (horizontal + vertical) distance travelled Per trip (km)	Total (horizontal + vertical) distance travelled Per hour (km)	Pelagic diving	Night diving (% of all dives)
4	F	29.5 ± 15.1	5.1 ± 2.0	3.4 ± 2.1	0.5 ± 0.2	13.3 ± 7.5	2.3 ± 0.8	93.8 ± 3.8	43.8 ± 27.3
7	F	71.8 ± 30.3	32.6 ± 26.1	33.3 ± 35.8	0.9 ± 0.5	87.6 ± 78.5	3.8 ± 0.7	75.4 ± 20.3	22.5 ± 19.2
9	F	33.9 ± 14.7	5.2 ± 1.8	3.4 ± 3.5	0.6 ± 0.3	14.4 ± 9.5	2.8 ± 0.8	89.3 ± 9.9	40.9 ± 34.3
10	F	51.6 ± 20.5	11.1 ± 5.4	7.6 ± 5.3	0.9 ± 0.3	25.0 ± 13.9	3.3 ± 0.4	92.0 ± 5.6	39.7 ± 33.8
13	F	86.4 ± 10.7	40.1 ± 8.9	72.3 ± 66.2	1.1 ± 0.1	206.1 ± 164.8	3.6 ± 0.7	77.9 ± 7.2	15.6 ± 9.4
15	F	88.2 ± 31.6	17.5 ± 11.9	9.9 ± 10.1	0.7 ± 0.3	44.9 ± 26.8	4.0 ± 0.2	96.1 ± 5.1	24.4 ± 18.3
20	F	68.3 ± 32.2	18.6 ± 15.1	8.8 ± 11.7	0.8 ± 0.5	33.7 ± 36.9	3.8 ± 0.5	87.6 ± 11.7	52.4 ± 42.9
22	F	79.5 ± 28.3	26.6 ± 13.9	31.0 ± 30.3	0.8 ± 0.4	103.5 ± 99.3	3.1 ± 0.6	80.4 ± 14.7	14.5 ± 5.8
1	M	54.8 ± 17.0	9.7 ± 5.5	2.1 ± 1.9	0.4 ± 0.3	13.0 ± 8.1	3.1 ± 1.2	95.7 ± 5.3	36.5 ± 25.9
2	M	89.6 ± 13.8	15.7 ± 8.2	7.2 ± 7.3	0.8 ± 0.2	29.6 ± 22.3	3.6 ± 0.7	88.2 ± 9.5	54.8 ± 17.9
3	M	101.6 ± 3.2	61.6 ± 8.8	62.2 ± 51.4	0.7 ± 0.3	279.6 ± 238.7	3.3 ± 1.2	52.7 ± 6.9	15.4 ± 5.7
5	M	69.5 ± 5.3	26.2 ± 6.6	23.2 ± 20.2	1.1 ± 0.3	90.4 ± 61.5	4.8 ± 0.8	86.5 ± 5.1	6.3 ± 5.5
11	M	53.8 ± 11.3	22.5 ± 6.9	48.3 ± 67.3	0.8 ± 0.1	212.7 ± 278.3	4.1 ± 0.4	80.6 ± 6.6	24.1 ± 5.2
12	M	106.8 ± 8.9	48.8 ± 3.6	74.5 ± 45.1	1.0 ± 0.1	215.0 ± 106.0	3.1 ± 0.2	66.8 ± 4.8	15.2 ± 4.8
14	M	57.6 ± 12.0	25.3 ± 8.7	17.7 ± 14.0	0.8 ± 0.3	70.9 ± 42.2	3.7 ± 0.3	74.6 ± 3.9	12.9 ± 6.9
25	M	72.7 ± 5.3	36.9 ± 9.5	37.1 ± 12.0	0.9 ± 0.4	126.5 ± 14.4	2.9 ± 0.7	68.1 ± 7.3	6.0 ± 2.7
30	M	88.0 ± 11.6	36.5 ± 10.0	18.6 ± 6.9	1.0 ± 0.3	67.4 ± 6.7	3.8 ± 0.2	57.0 ± 12.4	15.5 ± 3.6
26	–	65.1 ± 15.5	25.6 ± 19.8	12.9 ± 15.2	0.8 ± 0.7	48.0 ± 44.2	3.3 ± 1.5	74.7 ± 13.0	5.7 ± 8.1
28	–	78.0 ± 52.1	28.0 ± 24.4	32.5 ± 43.5	0.7 ± 0.5	153.2 ± 208.0	4.2 ± 0.7	76.6 ± 26.8	17.0 ± 16.1

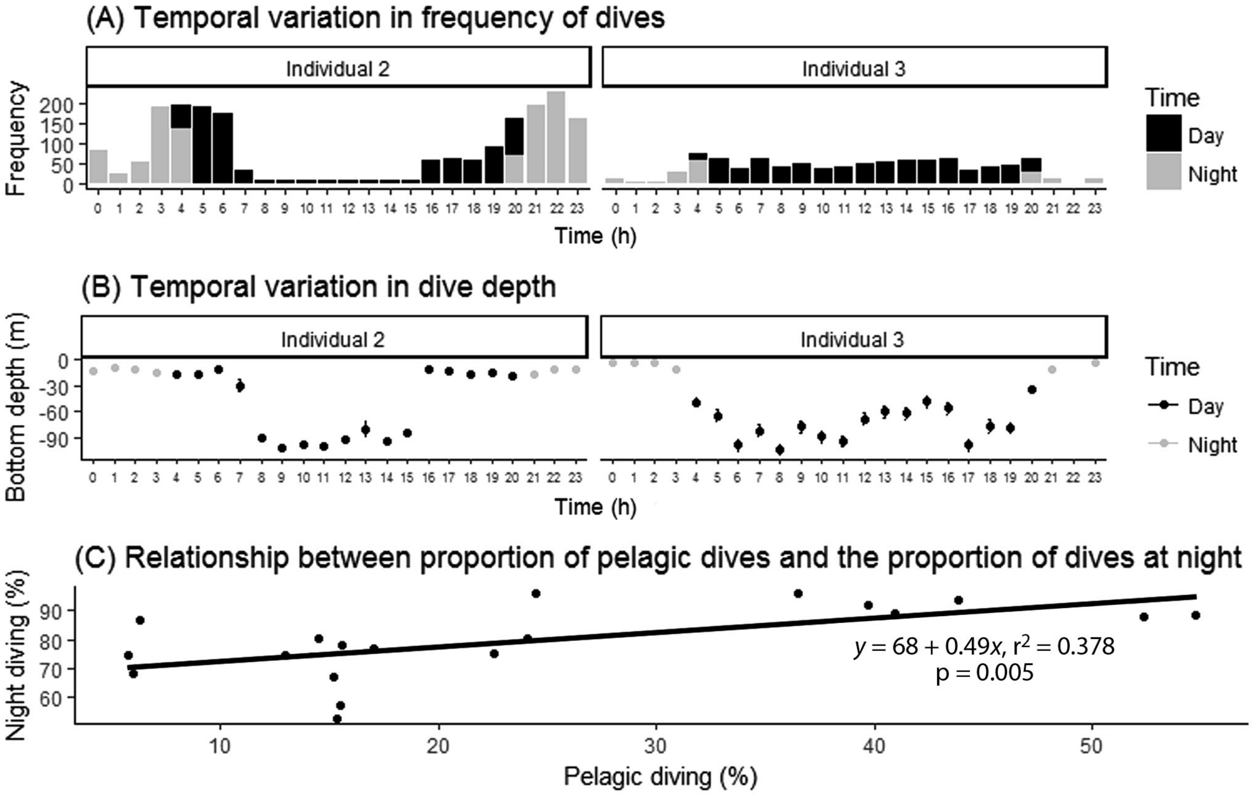

Fig. 2. (A) Frequency of night diving, (B) distribution of dive depths across time of day and (C) relationship between night and pelagic diving in gentoo penguins *Pygoscelis papua* (panels A and B show individuals representative of the most benthic and the most pelagic individuals) instrumented at Pointe Suzanne during the crèche period in December 2014 to January 2015

Intra-individual variation and consistency in foraging behaviour

The large differences in standard deviations between individuals indicate a substantial degree of intra-individual variation both in spatial use and dive metrics (Tables 3–5, respectively). At the population level, the variance component analysis showed low to moderate individual specialisations both in dive behaviour and spatial use (Table 6). The indices of consistency in habitat use were not influenced by sex or site (Table 4, mean 0.37 ± 0.20, range: 0.05–0.73, Fig. 3). Some penguins were very consistent in the proportion of pelagic or benthic dives they performed (e.g. individual 14 stayed within 10% of its own values) while others varied greatly (e.g. individual 28 ranged from 47 to 98% of pelagic dives between trips; Fig. 4). The total (horizontal + vertical) distance travelled per hour was not correlated with repeatability indices (linear regression: $F_{1,17} = 0.97$, $R^2 = -0.002$, $p = 0.34$). Lastly, body condition did not vary with consistency in habitat use (linear regression: $F_{1,12} = 0.16$, $R^2 = -0.07$, $p = 0.70$).

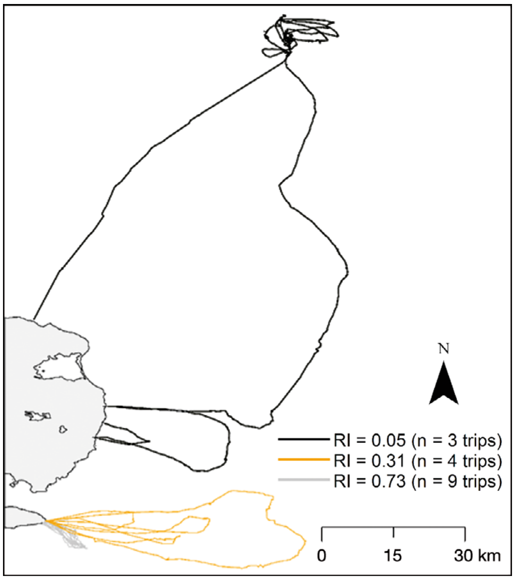

Fig. 3. Representative examples for 3 individual gentoo penguins *Pygoscelis papua* of spatial use and repeatability index (RI) for a highly repeatable individual (grey), a moderately repeatable one (orange) and an individual with limited repeatability (black) among instrumented birds at Pointe Suzanne and Estacade during the crèche period in December 2014 to January 2015

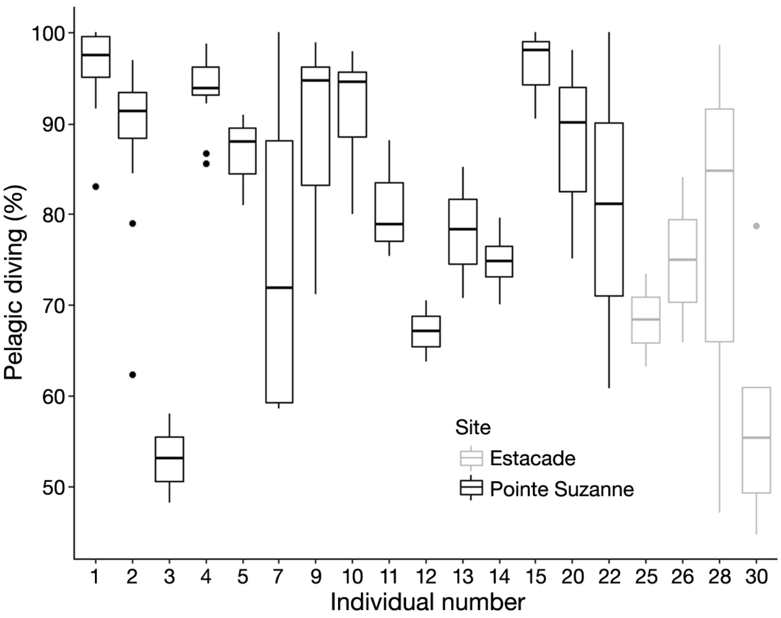

Fig. 4. Boxplots for the proportion of pelagic diving performed in subsequent trips by individual gentoo penguins *Pygoscelis papua* instrumented at Pointe Suzanne and Estacade during the crèche period in December 2014 to January 2015. Bold horizontal line: median of the distribution; box: interquartile range, IQR (first quartile Q1 to third quartile Q3); whiskers: (Q1 + 1.5 × IQR) to (Q3 + 1.5 × IQR); points: outliers

Stable isotope values and link with foraging metrics

Tissue isotope values varied widely among individuals, with $\delta^{13}C$ and $\delta^{15}N$ ranges of 4.0 and 5.8‰ in blood and 4.2 and 4.4‰ in feathers, respectively (Table 7). Values for $\delta^{13}C$ and $\delta^{15}N$ co-varied positively in both tissues (linear regression: $F_{1,23} = 31.94$, $R^2 = -0.56$, $p < 0.001$ and $F_{1,22} = 38.72$, $R^2 = -0.62$, $p < 0.001$ in blood and feathers, respectively; Fig. 5). There was no significant difference between the sexes in their $\delta^{13}C$ values, but males had higher $\delta^{15}N$ values in blood and feathers (linear mixed effects models: $t_{23} = 3.4$, p = 0.002 and $t_{23} = 0.9$, p = 0.4, for nitrogen and carbon, respectively). Site did not influence $\delta^{15}N$ and $\delta^{13}C$ values ($t_{23} = -0.6$, p = 0.5, and $t_{23} = -0.5$, p = 0.6, respectively). Isotopic values in blood and feathers were positively and linearly correlated. Excluding an outlier (that was depicted by a preliminary statistical analysis) increased the strength of the relationships

Table 6. Variance component analysis of dive depths, total distances travelled and bearings to most distal point for gentoo penguins *Pygoscelis papua* instrumented at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015. σ^2 % is an estimate of individual specialisation (see 'Materials and methods' for details)

Variance component	σ^2	Σ	σ^2 %
Maximum range			
Individual	127.6	11.3	13.7
Residual	802.6	28.3	86.3
Bearings to most distal point			
Individual	1572.7	39.7	52.9
Residual	1397.6	37.4	47.1
Mean bottom depth (null model)			
Individual	244.2	15.6	6.2
Trip	62.6	7.9	1.6
Residual	3612.8	60.1	92.2
Mean bottom depth (model with mass)			
Individual	150.9	12.3	4.0
Trip	62.6	7.9	1.6
Residual	3612.4	60.1	94.4
Proportion of pelagic diving (null model)			
Individual	166.4	12.9	67.5
Residual	80.1	9.0	32.5
Proportion of pelagic diving (model with mass)			
Individual	33.5	5.8	51.3
Residual	31.9	5.6	48.7

Table 7. Summary of stable isotope values for gentoo penguins *Pygoscelis papua* sampled at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) in December 2014 to January 2015; F: female, M: male, –: unsexed, NA: missing data

Bird	Sex	Blood δC^{13}	Blood δN^{15}	Feather δC^{13}	Feather δN^{15}
4	F	−18.76	11.49	−18.03	11.99
7	F	−18.25	10.93	−18.7	12.68
9	F	−17.83	12.55	−15.52	13.42
10	F	−19.05	11.38	−18.37	12.57
13	F	−20.11	8.44	−19.10	11.64
15	F	−19.16	9.95	−19.06	12.33
20	F	−20.18	9.57	−19.28	11.78
22	F	−19.9	8.83	−15.03	14.03
24	F	−16.98	10.86	−16.75	12.97
	M	−18.68	11.70	NA	NA
2	M	−16.86	13.55	−15.09	15.02
3	M	−19.00	12.33	−16.90	14.66
5	M	−19.44	12.50	−17.18	14.12
6	M	−18.57	11.90	−17.97	12.66
11	M	−19.05	11.76	−18.19	13.22
12	M	−19.46	11.02	−18.17	13.05
14	M	−18.49	11.26	−17.71	13.39
17	M	−18.63	11.83	−18.28	13.24
19	M	−18.11	12.67	−17.55	14.03
23	M	−19.98	10.29	−19.17	12.62
18	–	NA	NA	−18.72	11.09
27	F	−20.30	8.43	−18.94	12.40
29	F	−20.14	7.95	−18.59	11.86
25	M	−19.30	11.62	−17.88	12.79
30	M	−16.27	13.75	−15.69	15.47
33	M	−19.44	10.74	−18.71	12.78
26	–	NA	NA	−18.82	12.32
28	–	NA	NA	−18.03	13.39

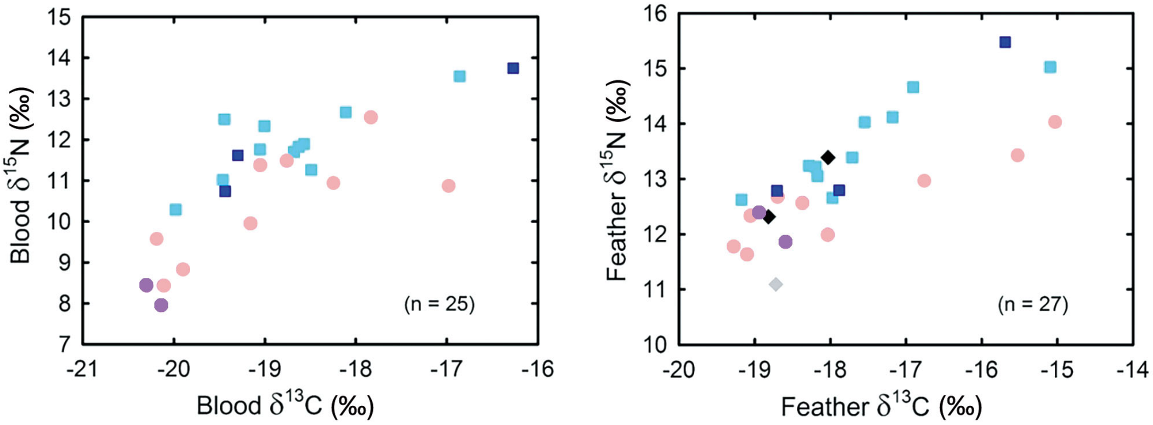

Fig. 5. Relationship between stable isotope values in carbon and nitrogen in blood and in feathers of gentoo penguins *Pygoscelis papua* sampled at Pointe Suzanne and Estacade during the crèche period in December 2014 to January 2015 (light blue squares = males from Pointe Suzanne, pink circles = females from Pointe Suzanne, dark blue squares = males from Estacade, purple circles = females from Estacade, grey diamond = 1 unsexed bird from Pointe Suzanne, black diamonds = 2 unsexed birds from Estacade)

that explained 67 and 70% of the inter-individual δ^{13}C and δ^{15}N variations, respectively (Fig. 6).

There was no relationship between maximum distances reached and blood δ^{15}N or δ^{13}C values (linear mixed effects model: $t_{18} = 0.1$, $p = 0.9$, and $t_{18} = -1.1$, $p = 0.3$). This was also the case for stable isotope values and bearings to the most distal point (linear mixed effects model: $t_{18} = -0.2$, $p = 0.9$, and $t_{18} = 0.1$, $p = 0.9$, respectively). Lastly, δ^{15}N or δ^{13}C values were not influenced by repeatability in spatial use (linear mixed effects model: $t_{10} = 1.0$, $p = 0.3$, and $t_{10} = 1.0$, $p = 0.3$, respectively) or body condition (linear mixed effects model: $t_{11} = 1.9$, $p = 0.1$, and $t_{11} = 1.8$, $p = 0.1$, respectively).

DISCUSSION

The salient findings of this study concerning an opportunistic coastal forager, the gentoo penguin, can be summarized as follows. (1) Individuals exhibited very large inter- and intra-individual variation in spatial use and diving behaviour. Heavy individuals tended to dive deeper, perform more benthic dives and travel farther. (2) Despite the large intra-individual variation in foraging, some consistency in bearing, proportion of pelagic and night diving, maximum ranges and dive depths was observed in approximately a third of individuals. Foraging behaviour and behavioural consistency were not influ-

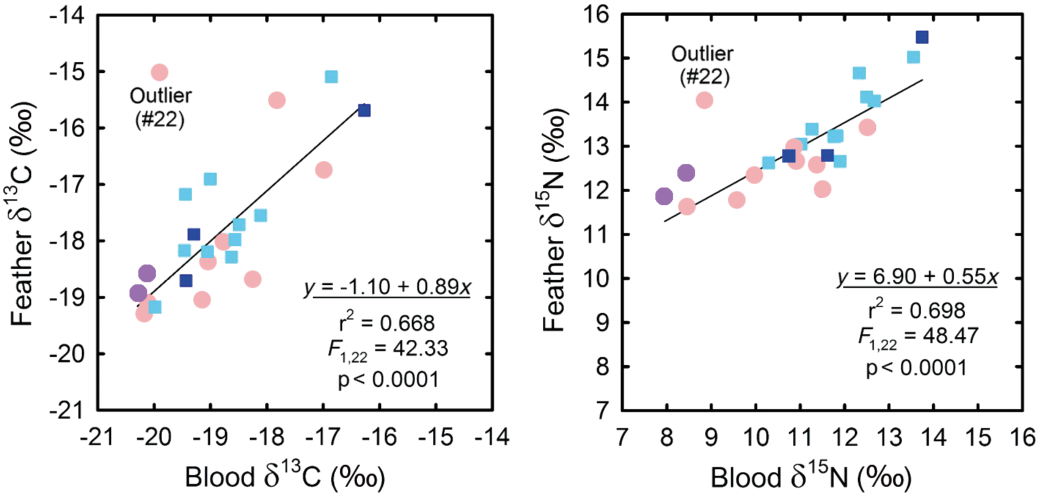

Fig. 6. Correlations between stable isotope values in blood and feather for carbon and nitrogen in gentoo penguins *Pygoscelis papua* (n = 24) sampled at Pointe Suzanne and Estacade during the crèche period in December 2014 to January 2015 (light blue squares = males from Pointe Suzanne, pink circles = females from Pointe Suzanne, dark blue squares = males from Estacade, purple circles = females from Estacade)

enced by sex and site. (3) There were large inter-individual variations in stable isotope values, and dietary specialisations were present and maintained outside of the single breeding season sampled.

As inshore foragers, gentoos are known to strongly differ in their foraging behaviour according to the local environment (Lescroël & Bost 2005). Our first prediction was that instrumented individuals would differ greatly in foraging metrics among colonies and among individuals of the same colony. In the present study, site did not seem to influence foraging metrics. However, within a single colony, birds exhibited a large inter-individual variation in foraging behaviour, with some birds conducting very short trips within 5 to 10 km of the colony while others travelled to areas 120 to 140 km away. The more pelagic individuals performed up to half of their dives at night during short trips, while more benthic foragers dived predominantly during the day and reached greater depths, regardless of colony. This is consistent with other studies reporting that this species has high behavioural flexibility over its wide range (Wilson et al. 1991, Robinson & Hindell 1996, Miller et al. 2009, Kokubun et al. 2010). Such flexible foraging habits likely provide a buffer against changes in prey availability and distribution in a limited, coastal environment (Lescroël & Bost 2005, Miller et al. 2009), as shown in other inshore foragers (Hoskins et al. 2008, Saraux et al. 2011, Camprasse et al. 2017).

In the present study, some of the individuals performed trips longer (up to 5.6 d) than previously reported during the crèche period in gentoos on Kerguelen Island (on average 1.3 d in Estacade, Lescroël et al. 2009). It is possible that some of these birds abandoned breeding during the study, as continued provisioning status could not be determined upon recapture for all birds. However, a third of birds known to still be provisioning chicks at the end of the study conducted such long trips. The large inter-individual variation in foraging behaviour observed in instrumented birds could be related to inter-individual variation in morphology (Bost & Jouventin 1990, this study). Indeed, individuals with higher body mass tended to travel farther, dive deeper and perform more benthic dives, contributing to the observed inter-individual differences in foraging. Differences in dive patterns, associated with larger oxygen stores in heavier birds, have been reported in other diving birds (Mori 1998, Cook et al. 2013).

We predicted that behavioural consistency would be detected in instrumented individuals, as numerous populations considered generalists have actually be shown to be comprised of individual specialists (Woo et al. 2008, Araújo et al. 2011, Loxdale et al. 2011, Layman & Allgeier 2012, Fodrie et al. 2015). In the present study, at the population level, individual specialisations in foraging metrics were low to moderate, with bearings to most distal locations and the proportion of pelagic diving exhibiting the highest repeatability. This suggests that gentoos stay consistent in some aspects of their foraging behaviour, which may help to reduce intra-specific competition and/or may allow individuals to catch prey they can easily handle and digest (Bolnick et al. 2003, Estes et al. 2003). This seems particularly relevant in inshore foragers, as they are restricted in their foraging range (Cook et al. 2006, Ratcliffe et al. 2013, Harris et al. 2014).

However, a significant degree of behavioural consistency at the population level does not mean that all individuals are consistent (Woo et al. 2008, Ceia et al. 2012). Indeed, we observed a large variation in the degree of individual consistency in spatial use and dive behaviour between instrumented individuals. While some birds exhibited similar foraging strategies over the course of multiple consecutive trips, others did not. For example, some individuals displayed consistency in the proportion of pelagic diving from one trip to the next while others were able to switch from being mostly benthic on one trip to being entirely pelagic. This highlights the need to sample multiple trips to obtain a more accurate description of a bird's foraging behaviour, particularly in inshore foragers which may exhibit behavioural plasticity (Saraux et al. 2011, Carpenter-Kling et al. 2017). The large inter- and intra-individual variation in foraging behaviour discussed here might contribute to gentoos having stable or expanding populations in parts of their range (e.g. Antarctic Peninsula), where sympatrically breeding penguin species, more dependent on specific resources such as Antarctic krill, experience strong population declines (Miller et al. 2009, Polito et al. 2015).

Our third prediction was that individuals displaying higher consistency in foraging behaviour would have reduced horizontal and vertical distances travelled, and higher body conditions as individual specialisations are thought to improve foraging efficiency (Watanuki 1992, Voslamber et al. 1995, Annett & Pierotti 1999, Golet et al. 2000, Votier et al. 2004). Contrary to this prediction, no difference in distance travelled (per hour) or body condition was found between consistent and non-consistent individuals in the present study. Thus, it seems that instrumented individuals adopted different strategies based on intrinsic factors (i.e. morphology, prey preferences, etc.), ultimately resulting in different repeatability indices. Indeed, the heavier, more benthic individuals performed more distant and longer trips, and such trips were less repeatable within the timeframe of the study.

Generally, it is unclear whether specialists perform better than generalists, as contradictory results have been reported in the literature (Golet et al. 2000, Votier et al. 2004, Ceia et al. 2012, Dehnhard et al. 2016). Our findings are in agreement with results on a long-distance forager, the wandering albatross *Diomedea exulans*, demonstrating that specialist and generalist individuals had similar levels of body condition (Ceia et al. 2012). No effect of specialisation on reproductive outcomes has been detected in other bird species (Votier et al. 2004, Katzner et al. 2005, Dehnhard et al. 2016). Indeed, even though generalists may deliver somewhat less energy per day, specialisation may not have an impact on measures of evolutionary fitness (Woo et al. 2008). In contrast, other studies on gulls, cormorants, guillemots and skuas have shown specialists to have higher reproductive success, food delivery rates, chick condition or adult survival (Watanuki 1992, Voslamber et al. 1995, Annett & Pierotti 1999, Golet et al. 2000, Votier et al. 2004). In gentoos, individual specialisations in foraging behaviour may be linked with intrinsic factors, and may be more or less advantageous depending on prey availability, with generalists performing better when food availability is low.

Lastly, in agreement with our second prediction, long-term dietary consistency was detected in the birds sampled. Stable isotope values in blood and feathers in breeding gentoos were positively correlated, indicating that dietary specialisations are maintained outside of the breeding season. This is consistent with recent stomach contents and stable isotope analysis studies on the diet of gentoos, indicating that they may not be as opportunistic as previously thought (Clausen et al. 2005, Polito et al. 2015). Within generalist populations, 2 types can be found: type 'A' generalists, when individuals all take a wide range of food types; and type 'B' generalists, when individuals each specialise on a different range of food types (Bearhop et al. 2004). The results from our study, documenting a large inter-individual variation in diet, matching the high inter-individual variation in foraging behaviour, and documenting the fact that instrumented birds tend to display a similar feeding ecology in the breeding and inter-breeding seasons, seem to indicate that gentoos at the studied site are type 'B' generalists.

The results of the present study should be interpreted with caution for two main reasons: the large difference in sample sizes between colonies where deployments were performed, and the potentially poor environmental conditions the instrumented birds experienced, seemingly leading to low prey availability as judged by the low number of chicks raised by gentoos and sympatrically breeding shags (E. C. M. Camprasse pers. obs.). More data are needed from Estacade to confirm the lack of a site effect on the gentoos' foraging behaviour and feeding ecology. Factors including a high incidence of night diving and long trip durations could reflect poor environmental conditions in the 2014/2015 breeding season, forcing penguins to forage in suboptimal conditions. This is consistent with poor breeding success on Kerguelen Islands during deployments compared with normal years, with brooders losing chicks at the crèche stage (E. C. M. Camprasse pers. obs.). In the present study, shallow nighttime dives were observed in the more pelagic individuals, probably to allow them to take advantage of pelagic prey distributed near the surface at night during their diurnal vertical migration. Night/twilight diving has been recorded in pygoscelid penguins including gentoos (Croxall et al. 1988, Williams & Rodwell 1992, Robinson & Hindell 1996) and other penguin species (Schiavini & Rey 2004, Rey et al. 2012), but was thought to be uncommon in such visual predators (Williams 1995, Bost et al. 2002). Lastly, low prey availability, linked with the seemingly poor environmental conditions experienced by the birds instrumented in the present study, could increase the degree of individual specialisation, as individuals are forced to add different alternative prey not consumed by conspecifics to their diet (Svanbäck & Bolnick 2007, Tinker et al. 2008).

In summary, we showed that gentoo penguins on Kerguelen Island exhibited large inter- and intra-individual variations in foraging behaviour. These may provide gentoos greater resilience to buffer against changes in prey availability and fast changing environmental conditions, especially as their foraging range is usually limited (Lescroël & Bost 2005, Polito et al. 2015). However, within this context, gentoos still exhibit individual specialisation, helping them reduce intra-specific competition and/or increasing their foraging efficiency (dit Durell 2000, Masello et al. 2013). Dietary specialisations outside of a single breeding season were also highlighted, suggesting that gentoo penguins are type 'B' generalists. The next step to understand the consequences of individual specialisations would be to look at the link between behavioural consistency and reproductive output, which could not be done in this study due to logistical constraints. In order to fully understand the effects of individual consistency of parents on their offspring, researchers should also aim at obtaining information on both partners of breeding pairs (Polito et al. 2015). In the future, repetitive sampling of the same individuals across stages of the same breeding season and across years will help to characterize the persistence of dietary specialisations at different temporal scales in seabirds.

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Contribution to the Theme Section 'Individual variability in seabird foraging and migration'

Shifting individual habitat specialization of a successful predator living in anthropogenic landscapes

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ABSTRACT: Population expansions of successful species have gained importance as a major conservation and management concern. The success of these 'winners' is widely attributed to their high adaptability and behavioural plasticity, which allow them to efficiently use opportunities provided by human-modified habitats. However, most of these studies consider conspecifics as ecological equivalents, without considering the individual components within populations. This is critical for a better understanding of the main ecological mechanisms related to the success of winning species. Here, we investigated the spatial ecology of the opportunistic yellow-legged gull *Larus michahellis*, a clear example of a winning species in southern Europe, to examine its degree of individual specialization in habitat use. To test for such individual strategies, we applied specialization metrics to spatial data obtained from 18 yellow-legged gulls that were GPS-tracked simultaneously during the breeding season. The results revealed that population-level generalism in habitat use in the yellow-legged gull arises through varying levels of individual specialization, and individual spatial segregation within each habitat. Importantly, we found that the combination of individual specialization and individual spatial segregation may reduce intra-specific competition, with these 2 important mechanisms driving the success of this winning species.

KEY WORDS: Foraging strategies · Gulls · GPS · Habitat use · Individual specialization · Movement ecology · Opportunistic seabirds · Seabird · Spatial ecology · Winning species

INTRODUCTION

Human activities are globally impacting ecosystems, with important effects on biodiversity, including extinction processes (McKinney 2006, Worm et al. 2006). Species vary in their responses to human perturbations; while most seem unable to cope with drastic changes, others may persist, or even flourish within human-transformed ecosystems (McKinney & Lockwood 1999). The general pattern of expansion of some widespread non-native and native species, so-called 'winners', and the contraction of rare and often endemic native species, so-called 'losers', leads to a biotic homogenization process. This has led to biological impoverishment worldwide (Olden et al. 2004).

Population expansions of winning species have gained importance as a major conservation and management concern (Cardador et al. 2011, Sih et al. 2011, Newsome et al. 2015). The success of these winners is widely attributed to their high adaptability and behavioural plasticity, which allow them to efficiently exploit opportunities provided by novel,

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human-modified environments (Shultz et al. 2005, Clavel et al. 2011). Among marine predators, it is well-known that some gull species are particularly successful. They efficiently adapt to exploiting a wide suite of novel resources that provide direct biotic and abiotic benefits, including food, shelter and refuge from predation (Ramírez et al. 2012, Alonso et al. 2015, Osterback et al. 2015). These winning seabirds are often perceived as pests because of their impacts on urban areas, water reservoirs and threatened species (Vidal et al. 1998, Skórka et al. 2014, Rock et al. 2016). As a consequence, abundant research has been conducted on these opportunistic predators, mainly focused on their population dynamics, feeding ecology, pollution levels and pathogen load (e.g. Ramos et al. 2011, Payo-Payo et al. 2015). However, most of these studies consider conspecifics as ecological equivalents. Although this simplification can be useful to provide an overview of population-level feeding preferences or population dynamics (Ramos et al. 2011, Payo-Payo et al. 2015), taking into account the individual component within populations is essential for a better understanding of the main ecological mechanisms related to the success of winning species (Grémillet et al. 1999, Cardador et al. 2012, Chapple et al. 2012, Liebl & Martin 2014, Ceia & Ramos 2015, Potier et al. 2015)

Individual specialization occurs when some individuals within a population utilize only a subset of the resources that the population uses as a whole. This may be expressed via an animal's diet, patterns of movement or other specific behaviour (Bolnick et al. 2003, Matich et al. 2011, Ceia & Ramos 2015). Individual specialization may vary between populations and across species, which may further enhance ecological consequences at the individual level (Bolnick et al. 2003, Araújo et al. 2011). Variation in individual specialization directly affects the population dynamics of winning species, by facilitating their adaptability to a large suite of environmental conditions, while reducing competition among conspecifics (Bolnick et al. 2003, Tinker et al. 2007, Dall et al. 2012, Liebl & Martin 2014). Thus, taking into account the individual component should allow for a better understanding of ecological processes. In addition, knowing the degree of individual specialization in winning species that negatively affect human or wildlife health may help to implement more effective management actions (Sanz-Aguilar et al. 2009, Bowen & Lidgard 2013, Ceia et al. 2014).

In the present study, we investigated the spatial ecology of the opportunistic yellow-legged gull *Larus michahellis* in a breeding population of southeastern Spain, to examine its degree of individual specialization in habitat use. This species is a clear example of a winning predator in southern Europe, as a result of its ability to efficiently exploit a diverse suite of novel resources (e.g. Alonso et al. 2015, Payo-Payo et al. 2015, Martínez-Abraín & Jiménez 2016). This gull is also considered a pest within urban, agricultural and coastal areas (Vidal et al. 1998). Based on previous information (Ceia et al. 2014, Tyson et al. 2015, Ceia & Ramos 2015), we hypothesized that yellow-legged gulls present a significant level of individual differences in habitat use. Specifically, we predicted that individuals within the population would show niche segregation with respect to habitat use. To test for such individual strategies, we applied metrics previously used to identify diet specialization (Bolnick et al. 2002, Fodrie et al. 2015). These metrics were applied to spatial data obtained from 18 yellow-legged gulls that were GPS-tracked simultaneously during 4 wk of the breeding season (Bouten et al. 2013). This is one of the first studies to investigate the spatial movements of this gull species continuously across several weeks (see Ceia et al. 2014).

MATERIALS AND METHODS

Fieldwork procedures

Fieldwork was carried out at the natural protected Biosphere Reserve of Marismas del Odiel (37° 13′ N, 6° 59′ W, Gulf of Cadiz, SW Iberian Peninsula; Fig. 1) in a colony of 250 to 300 breeding pairs. To investigate spatial movements during the breeding period (May 2015), we deployed high-resolution GPS-trackers recording the positions of individuals at 5 min intervals (www.UvA-BiTS.nl; Bouten et al. 2013) on 18 breeding adult gulls >4 yr old. Age was determined from plumage characteristics. Incubating birds were caught at the nest using a walk-in wire mesh trap and devices were attached using a wing harness fixed with a reef knot in the tracheal pit, an attachment method recommended for large gulls (see Thaxter et al. 2014, 2016). The GPS logger and harness weighed less than 1.8% of the body mass of the birds (19 g for the GPS versus 1062 ± 120 g [mean ± SD] for the tracked gulls), less than the 3 to 5% threshold suggested for seabirds (Phillips et al. 2003, Passos et al. 2010). GPS data were downloaded remotely through a local base station and automatically uploaded to the central database (Bouten et al. 2013). To avoid potential biases associated with differences between individuals in the number of days with GPS

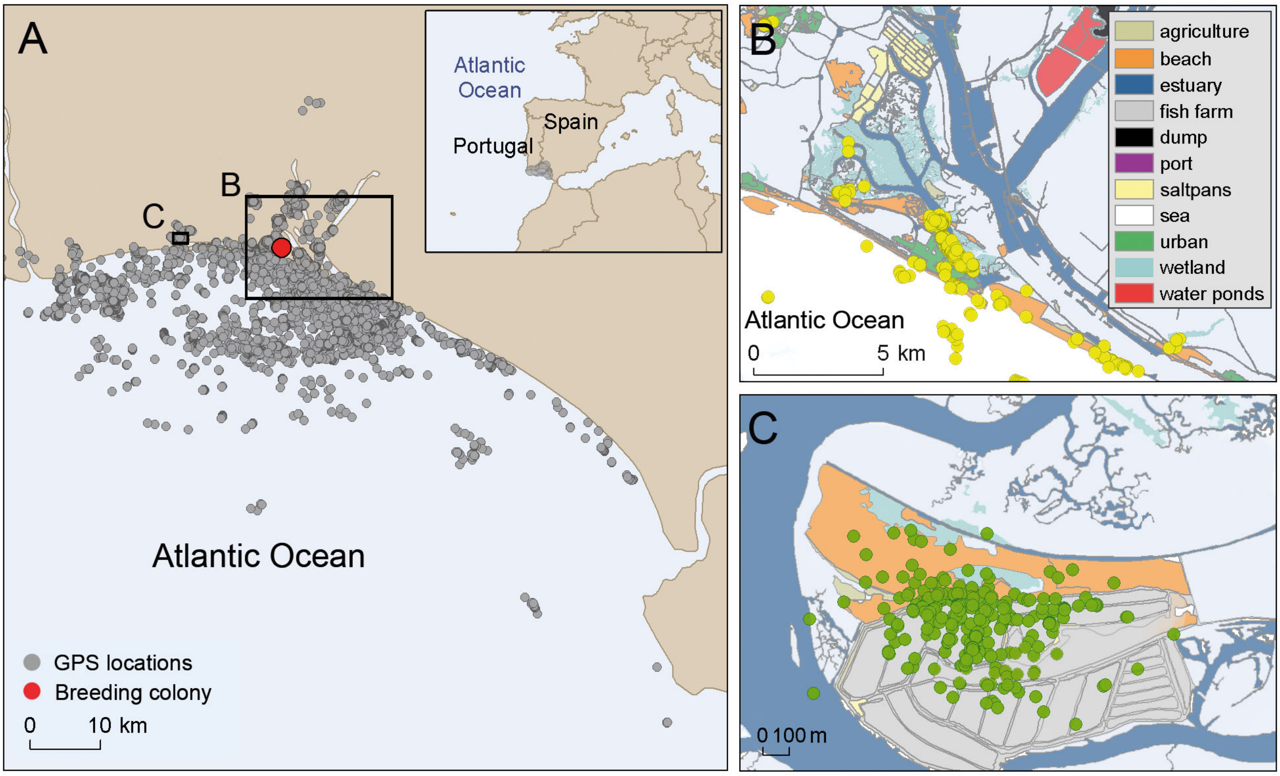

Fig. 1. (A) Study area showing the filtered GPS locations of the 18 tracked yellow-legged gulls *Larus michahellis* during the 2015 breeding season; (B) example of the habitats exploited by a generalist individual; and (C) example of an individual that specializes in the use of fish farm habitats

data and the potential differential spatial behaviour during the breeding period, we focused our analyses on the time period from 14 May to 15 June 2015 (incubation period). We considered only locations recorded outside the colony (using a radius of 500 m around each nest) and we removed all travelling locations (speed >4 km h^{-1}; Navarro et al. 2016). The total number of GPS locations ranged from a mean of 8200 to 9129, with a mean of 8644 ± 495 locations $ind.^{-1}$.

Individual specialization and individual spatial segregation

Individual specialization in habitat use by each tracked yellow-legged gull was quantified following Bolnick et al. (2002) and Fodrie et al. (2015). Specifically, we calculated the proportional habitat use by each yellow-legged gull as the number of habitat-specific positions divided by the total number of GPS positions recorded during the entire tracking period for a particular individual. Habitat was determined by merging all filtered foraging GPS locations with high-resolution land cover information (SIOSE, Soil Information System of Spain, Junta de Andalucía; scale was 1:2500; last update 2011). Using this information, we calculated the proportional similarity index (PSi) following Schoener (1968). PSi is a measure of individual specialization based on habitat-by-habitat deviations in an individual's habitat use relative to population level, average habitat use (0 = more specialized; 1 = more generalist). PSi is based on the average pairwise overlap of the niche distribution of individuals and the population (Bolnick et al. 2002). Mean PSi among individuals was used to determine the average amount or prevalence of individual specialization in habitat use in the population (IS). We ran Monte Carlo permutations to test whether observed PSi values differed significantly from a random distribution of values subsampled from the population. We randomly reassigned habitat use for each yellow-legged gull in equal proportion to our observed data, and then calculated individual and population-level metrics for the random population. We generated random habitat use data for 10 000 populations, thereby creating a null distribution of PSi values. We concluded that individuals were not sampling from a shared distribution of habitat use if our observed PSi values were <95% of all randomly generated values (Araújo et al. 2007).

All of these analyses were performed using the RInSp package (Zaccarelli et al. 2013) in the software package R (R Core Team 2015). Pearson correlation tests indicated that no significant relationship exists between the number of GPS positions and the PSi values at the individual level ($p = 0.71$). We did not consider a sex effect because no significant differences in PSi values were found between sexes (ANOVA tests: $F_{1,17} = 1.92$, $p = 0.19$).

In addition to the PSi values, we quantified the degree of individual spatial segregation within each habitat using Schoener's overlap index *D*-metric (Schoener 1968), indicating the relative use of particular microhabitats (Friedlaender et al. 2011). For this, we overlaid all filtered locations onto a grid of 100 m^2 (corresponding to the minimum area used by the tracking gulls in the present study) to estimate the proportion of locations in any grid cell. The cell size was based on the minimum area encompassing a single habitat. *D*-metric values of 1 indicate a complete spatial overlap between 2 yellow-legged gulls in a pair, whereas values of 0 indicate complete spatial segregation. ANOVA and post hoc tests were applied to test differences in the *D*-metric index between individuals.

Table 1. Habitat type and the main potential behaviours of the yellow-legged gull *Larus michahellis*

Habitat type	Main potential behaviours
Sea	Foraging (marine resources and fishery discards)
Estuary	Foraging (estuarine fish and crustaceans) Resting and socializing
Wetland	Foraging (fish and other resources such as bird chicks or eggs) Resting (safe places)
Beach	Scavenging (dead cetaceans/fish and human food)
Fishing port	Scavenging (fishery discards)
Fish farm	Foraging (farm fish)
Saltpans	Foraging (fish and crustaceans) Resting (safe places)
Water pond	Foraging (fish) Cleaning (freshwater) Resting (safe place)
Agriculture area	Foraging (olives, insects and other terrestrial prey)
Urban	Scavenging (human food) Foraging (urban birds and other prey) Cleaning (freshwater ponds in urban parks)
Garbage dump	Scavenging (human food) Preying (small mammals and insects)

RESULTS

Based on the 28 917 filtered locations recorded during 1 mo of the 2015 breeding season from the 18 tracked yellow-legged gulls, we detected the use of 11 different habitats (Table 1, Figs. 1 & 2). At the population level, the relative use of each habitat (percentage of total locations) ranged from 28.4% for fishing ports and estuaries (22.3%) to ~1.0% for garbage dumps, agricultural lands and fish farms (Fig. 2).

Individual specialization in habitat use

At the individual level, we found PSi values ranging from 0.37 to 0.78, with specialized individuals (low PSi values) mainly exploiting habitats such as fish farms, sea or estuarine areas, and less specialized individuals (high PSi values) using a higher diversity of habitats (Fig. 2). Monte Carlo analyses of individual-versus-population niche variation indicated that specialized individuals were significantly prevalent within the population (IS = 0.52, $p < 0.001$; Fig. 2).

Individual spatial segregation within each habitat

Based on *D*-metric values (spatial segregation between individuals within the same habitats), we found marked differences between habitats ($F_{10,1710} = 136.69$, $p < 0.001$; Fig. 3). Post hoc tests indicated that spatial overlap between individuals was significantly higher in garbage dumps (*D*-metric = 0.78 ± 0.06), followed by water ponds, fish farms and fishing ports (*D*-metric ranging from 0.36 to 0.41), and estuaries (*D*-metric = 0.24 ± 0.15). The lowest spatial overlap values were found for urban, wetland, saltpans, beach, sea and agricultural areas (*D*-metric ranging from 0 to 0.16) (Fig. 3).

DISCUSSION

We examined the spatial ecology of yellow-legged gulls to test the degree of individual specialization in their habitat use, by tracking 18 individuals simultaneously over 1 mo during the breeding period. Our results support the hypothesis about winning spe-

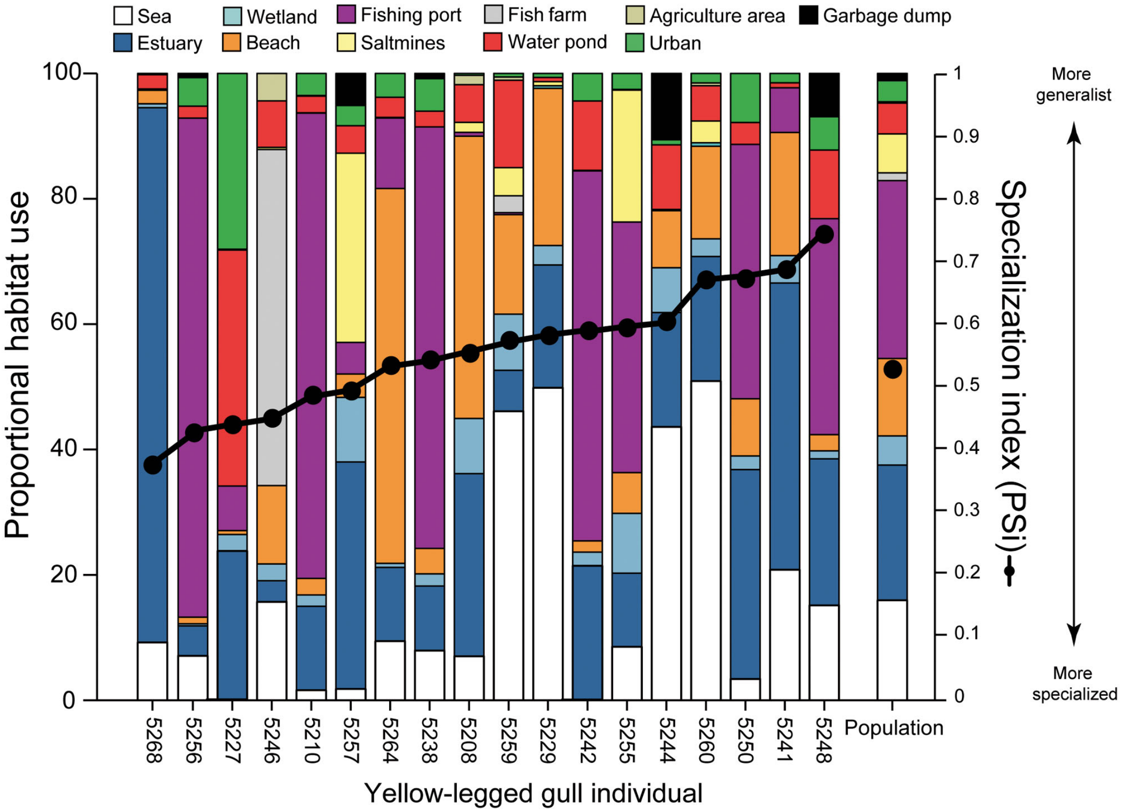

Fig. 2. Individual variation in habitat use between the 18 GPS-tracked yellow-legged gull *Larus michahellis* individuals during one month of the 2015 breeding season. Each individual (*x*-axis) is represented by a vertical bar, subdivided by the proportion of locations in each habitat in relation to the total GPS locations and the specialization index PSi (black dots; 0 = more specialized; 1 = more generalist). Mean habitat use and the prevalence of individual specialization in habitat use in the population (IS; black dot in the population bar) are also represented (right bar)

cies, as they revealed a high diversity of habitats used by the yellow-legged gulls. Moreover, in accordance with ecological theory related to generalist species (Bolnick et al. 2003, Araújo et al. 2011), we also showed that variation within the population predominately derives from individual specialization in habitat use. Importantly, we found that the degree of spatial segregation between individuals differed markedly between habitats.

At the population level, yellow-legged gulls were able to use up to 11 main habitats present both in marine and terrestrial domains, including natural and human-made habitats. This high plasticity reflects the pronounced ability and behavioural flexibility of the yellow-legged gull to exploit a diverse suite of trophic resources, some of which are novel resources provided by humans, or use them for other activities such as resting, bathing or socializing. For example, it has been reported that in the marine environment or in fishing ports the yellow-legged gull exploits marine resources by foraging on natural prey in the open sea, or opportunistically forages on fishery discards (Duhem et al. 2003, Ramos et al. 2009). In the saltpans, estuaries and wetlands, birds exploit different resources such as fish, crustaceans and bivalves, predate on eggs and chicks of other birds, or use undisturbed areas to rest or socialize with conspecifics (Bosch 1996, Munilla 1997, Vidal et al. 1998, Buechley & Şekercioğlu 2016). In beaches or urban areas, individuals scavenge on organic matter present in human waste or dead marine organisms, predate on urban vertebrates such as pigeons, or use the ponds present in the urban parks to bath or drink freshwater (Britton & Morton 1994, Buechley & Şekercioğlu 2016, Huig et al. 2016). In some specific habitats such as water ponds, in addition to preying on amphibians or freshwater fish, the gulls wash their feathers or rest (Sebastián-González et al. 2012). Most published studies indicate the high importance of trophic resources present in garbage dumps for the yellow-legged gull (Duhem et al. 2003, Ramos et al. 2009). Surprisingly, in our study, the importance of this habitat was very low. This result may be related to the low availability of urban dumps in the area

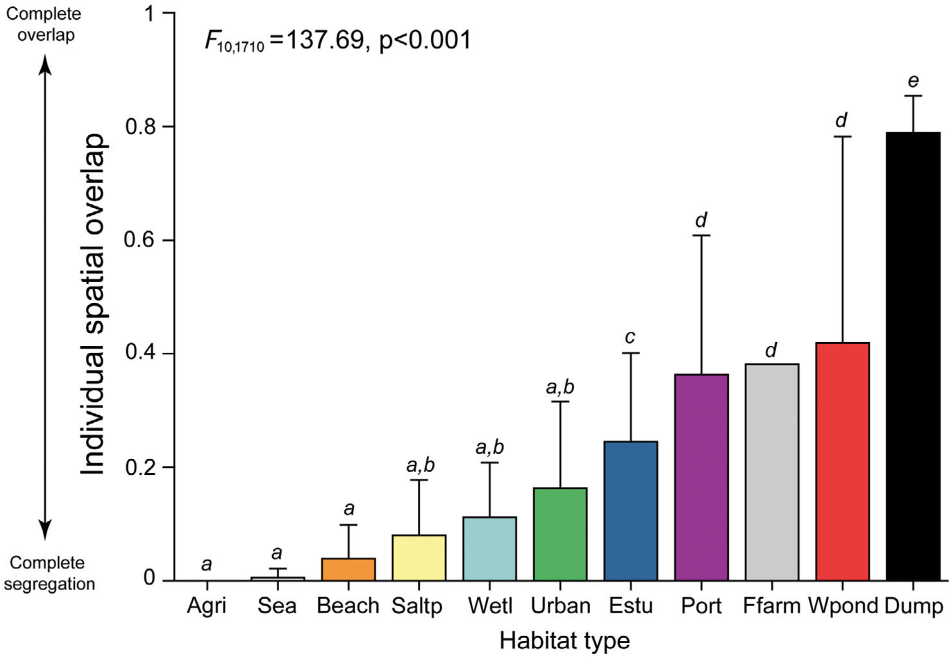

Fig. 3. Spatial overlap (mean and SD) between yellow-legged gull *Larus michahellis* individuals within each habitat (Agri = agriculture area, Saltp = saltpans, Wetl = wetlands, Estu = estuaries, Port = fishing ports, Ffarm = fish farms, Wpond = water ponds, Dump = garbage dumps) based on Schoener's spatial overlap metric (0 = more segregation; 1 = more overlap). The results of post-hoc Tukey HSD tests are shown by the lowercase letters above each bar: for individual spatial overlap, the means of habitats with the same letter were not significantly different

covered by GPS-tracked individuals (Navarro et al. 2016).

Although all GPS-tracked yellow-legged gulls could potentially exploit all available habitats, based on PSi values—a metric to test individual specialization (Bolnick et al. 2002, Fodrie et al. 2015)—we found clear differences in habitat use among individuals within the population. These results are coherent with the prediction that some generalist or opportunistic species are composed of ecologically heterogeneous individuals that repeatedly differ in behaviour and use of different subsets of available resources (Bolnick et al. 2002, Bearhop et al. 2004, Bell et al. 2009). Individual specialization is known to be widespread across a diverse set of taxa (Bolnick et al. 2003, Bell et al. 2009, Ceia & Ramos 2015), including different seabird species and other marine predators (e.g. Vander Zanden et al. 2010, Votier et al. 2010, Masello et al. 2013, Ceia & Ramos 2015, Tyson et al. 2015, Towner et al. 2016, Yurkowski et al. 2016). In general, individual specialization may have a strong impact on ecological processes and population dynamics, and there is evidence that this mechanism may reduce intra-specific competition among individuals, increase individual foraging efficiency and improve breeding success (Pierotti & Annett 1991, Bolnick et al. 2003, Woo et al. 2008, Araújo et al. 2011). For this reason, the existence of individual specialization within populations of winning species could partially explain their success (Grémillet et al. 1999, Cardador et al. 2012, Chapple et al. 2012, Liebl & Martin 2014, Ceia & Ramos 2015, Potier et al. 2015). Specifically, individual specialization could help opportunistic species to exploit the wide range of ecological opportunities provided by human activities (food or shelter, among others) in heterogeneous landscapes, thereby becoming more competitive than losing species (Carrete et al. 2010, Cardador et al. 2011, Layman et al. 2015, Newsome et al. 2015, Robertson et al. 2015).

The high degree of specialization across yellow-legged gulls of southern Spain has management and conservation implications related to the implementation of effective actions to reduce specific impacts on human or conservation interests (Sanz-Aguilar et al. 2009, Bowen & Lidgard 2013). For example, if the owners of fish farms wish to reduce the potential impact of yellow-legged gulls on their installations, one tractable management option is to remove gulls that specialize in this resource. One piece of clear evidence of the efficacy of such targeted measures is the reduction of the predation of the European storm petrel *Hydrobates pelagicus* by yellow-legged gulls, through the removal of specific petrel predators within the gull population (Sanz-Aguilar et al. 2009). However, it is important to point out that although these management measures could be efficient in the short term, other individuals can occupy the empty niche over longer periods.

Interestingly, we also found that the degree of spatial segregation between yellow-legged gulls differed between habitats. Based on the principle of competitive exclusion, competing individuals exploiting similar habitats are expected to segregate, especially when particular resources are limited (Gause 1973, Pianka 2000). Although we did not measure the availability of trophic resources or other types of resource related to other particular behaviours in each habitat, some of these observed differences may be explained by inter-habitat differences. For example, in garbage dumps or fish farms, high availability of resources and limited profitable surface area could allow some degree of spatial overlap between individuals exploiting similar trophic resources (Cortés-Avizanda et al. 2012, Arizaga et al. 2014). In contrast, in other habitats with prey resources for gulls, such as fishery discards at sea, individuals probably need to segregate in space to find food, or to reduce competition between conspecifics or with other bird species (Navarro et al. 2013, Patrick et al. 2014, Tyson et al. 2015). For this reason, the different degrees of individual spatial segregation between habitats may be viewed as a consequence of the distribution or availability of the resources used by gulls, or as a potential mechanism to reduce intra-specific competition (Bolnick et al. 2007, Matich et al. 2011, Robertson et al. 2015).

CONCLUSIONS

Our findings revealed that population-level generalism in habitat use in the yellow-legged gull arises through varying levels of individual specialization in habitat use and individual spatial segregation within each habitat, rather than all individuals being broad generalists. This combination of individual specialization and individual spatial segregation may reduce intra-specific competition, serving as 2 important mechanisms related to the success of these winning species in comparison to other, less successful species. Further multispecific investigations involving long-term GPS-tracking data covering the annual cycle of different colonies located in different environmental contexts would be useful to confirm that individual specialization in habitat use is a common phenomenon in winning and successful predators.

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Contribution to the Theme Section 'Individual variability in seabird foraging and migration'

Relationship between telomere dynamics and movement and behavior during winter in the thick-billed murre

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ABSTRACT: Connecting the life history stages of the annual cycle via carry-over effects crucially informs estimates of mortality and reproduction. This study explores variables linking the breeding and wintering seasons in a pursuit-diving seabird, the thick-billed murre *Uria lomvia*. We deployed global location sensing loggers on chick-rearing murres breeding in the southeastern Bering Sea to examine subsequent overwinter locations and foraging behavior. In the tracked individuals, we measured individual telomere length and longitudinal telomere length changes in blood and used feathers molted during fall and early spring to assess trophic niche (via stable isotopes) and stress levels (as reflected in feather corticosterone levels). Longitudinal changes in telomere length were better predicted by winter diving parameters than by geographic distribution and movement variables, such that birds that foraged more intensely (more time diving, more dive bouts) also experienced higher telomere loss. This indicates that in a pursuit-diving species with high flight costs, patterns of water-column use through diving may be more important than horizontal spatial movement for predicting physiological changes underlying carry-over effects. We conclude that telomere dynamics might be used as an indicator connecting behavior and physiological stress from season to season.

KEY WORDS: Telomeres · Carry-over effects · Feather corticosterone · Stable isotope analysis · Migration · Thick-billed murre · *Uria lomvia* · Wintering grounds · Geolocator

INTRODUCTION

Carry-over effects are often important drivers of population processes, including individual reproductive success, especially in migratory animals (Norris & Taylor 2006, Holmes 2007, Morrissette et al. 2010). These effects describe situations in which fitness-related outcomes in one season are affected by success or state in a previous season (O'Connor et al. 2014). Many carry-over effect studies describe how quality of winter habitat and diet affect phenology and reproductive success of subsequent breeding seasons (Reudink et al. 2009, Sorensen et al. 2009, Drake et al. 2013), while others describe effects of the breeding season on the non-breeding period (Stutchbury et al. 2011, Schultner et al. 2014b). However, the proximate physiological changes that accompany these effects are not as well studied.

One of the strongest components of carry-over effects is quality of the winter environment. Winter habitat choice (Reudink et al. 2009, Inger et al. 2010, Angelier et al. 2013, González-Prieto & Hobson 2013) and diet (Sorensen et al. 2009) can strongly influence performance and condition during subsequent breeding seasons. At the same time, quality and dominance status may influence access to wintering habi-

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tat (Rockwell et al. 2012, Angelier et al. 2013), so that these effects may be a combination of extrinsic (environmental) or intrinsic (reflecting individual quality through habitat access) factors. Some studies indicate that these carry-over effects are mediated interseasonally by glucocorticoid stress hormones (Sanderson et al. 2014), levels of which elevate in response to poor environment or low food availability. For example, elevated corticosterone in blood plasma indicates nutritional stress in common murres *Uria aalge* (Kitaysky et al. 2007).

In this study, we use physiological measures and biologging to explore the relationship between variables associated with the non-breeding period (wintering variables) and inter-annual telomere dynamics in the thick-billed murre *U. lomvia* (hereafter murre). We deployed geolocation and depth loggers to track murre location and diving behavior during migration and wintering in the North Pacific (Orben et al. 2015). As habitat use may change within the wintering period (e.g. Takahashi et al. 2015), we also compare diet and stress variables measured in plumage molted during fall and spring. Stable isotope values in feathers reflect diet during the molt in which they were grown (Becker et al. 2007, Bourgeon et al. 2014). Specifically, stable isotope values for nitrogen (ratios of $^{15}N/^{14}N$ as compared to an international standard; $\delta^{15}N$) provide a proxy for the trophic level of foraging (Karnovsky et al. 2012), which may influence reproductive parameters via carry-over effects (Sorensen et al. 2009). During the breeding season, murres at our study colonies eat a mixture of prey including invertebrates (squid and euphausiids) and fish (especially juvenile pollock *Gadus chalcogrammus*) (Harding et al. 2013). In general, higher trophic-level prey (i.e. fish) are a higher-quality food source, since they have high protein and fat content and do not require energy expenditure to excrete excess salt (Nehls 1996). Thus, a diet of high-quality, high trophic-level prey may contribute to recovery from the breeding season. Fish and squid may also require more skill to catch, since they are active swimmers which must be pursued (Kokubun et al. 2016). Therefore, access to this high-quality prey may be more dependent on diving skills than patterns in spatial use.

Telomeres are non-coding DNA repeats which cap eukaryotic chromosomes and function to protect DNA (Monaghan & Haussmann 2006). Degradation of telomeres occurs when cells divide, and loss rates are accelerated by oxidative damage (von Zglinicki 2002). Telomere length (TL) is considered a potential indicator of individual state or quality and is increasingly used in ecology as an indicator of biological age (Monaghan & Haussmann 2006, Barrett et al. 2013). Short TL and loss of TL may be related to variation in migration distance (Plot et al. 2012), elevated breeding stress (Schultner et al. 2014a), lower survival (Salomons et al. 2009, Barrett et al. 2013), or poor-quality wintering habitat (Angelier et al. 2013), making telomere dynamics a good candidate for reflecting patterns in carry-over effects. TL loss has also been used as a cost of reproduction in avian systems (Bauch et al. 2013, Sudyka et al. 2014). However, there are still many links to be made between telomere dynamics, individual quality, and survival (Monaghan 2010). Some studies, especially of long-lived species, have not found relationships with longevity (Pauliny et al. 2006) or changes in body mass and survival (Pauliny et al. 2012). In thick-billed murres, TL is related to physiological stress (baseline corticosterone) (Young et al. 2016) and interacts with habitat quality to predict patterns in foraging behavior during the breeding season (Young et al. 2015). Links to other phases of the annual cycle, however, have not been tested.

The stress hormone corticosterone is passively deposited into feathers as they are grown; thus, the concentration of corticosterone in feathers acts as an integrated measure of stress experienced during feather growth (Bortolotti et al. 2008, Lattin et al. 2011). Feather corticosterone (fCORT) is linked to use of high-quality wintering grounds during migration in great skuas *Stercorarius skua* (Bourgeon et al. 2014), overwinter survival in house sparrows *Passer domesticus* (Koren et al. 2012), and nutritional stress in rhinoceros auklets *Cerorhinca monocerata* (Will et al. 2015). Our use of feathers from 2 parts of the body allows evaluation of stress levels in fall and in spring.

This study addresses the relationship between TL and change and wintering variables. Wintering variables included diving variables (average dive depth, dive bouts per day, and a measure of foraging intensity), spatial variables (winter home range area and maximum distance from colony), fall and spring fCORT, and fall and spring $\delta^{15}N$ values. We test (1) the effect of TL (in year 1) on wintering variables; (2) the effect of wintering variables on the annual change in TL (ΔTL); and (3) the possible effects of TL, ΔTL, and wintering variables on subsequent breeding probability. We predict that TL will explain variation in wintering variables, indicating more effort (e.g. high fCORT, large winter home range, high foraging intensity) or lower foraging ability (lower $\delta^{15}N$ values) in birds with short TL (Prediction 1). TL may act as an integrative measure of individual state

(Monaghan & Haussmann 2006, Barrett et al. 2013), so this prediction describes a carry-over effect by which accumulated life history may affect behavior in the upcoming winter. Second, we test the relationships between wintering behaviors and ΔTL. Murres have some of the most energetically expensive avian flight (Elliott et al. 2013), but their wing-propelled pursuit-diving behavior allows them to exploit the oceanic environment in a third dimension, diving to depths of over 200 m (Orben et al. 2015). We predict that diving behaviors will be more important predictors of telomere changes than spatial variables (e.g. winter home range area, maximum distance from colony) (Prediction 2). Third, we test for a relationship between wintering variables and subsequent breeding. If telomeres mediate carry-over effects, then wintering variables associated with TL will be associated with subsequent breeding (Prediction 3). We also directly test the effect of TL in deployment year and TL change between years on breeding probability.

MATERIALS AND METHODS

Field sampling

Geolocation loggers and time-depth recorders (LAT2500 and LAT1500, Lotek Wireless) were deployed on breeding thick-billed murres during July and August of 2008 and 2009 at 2 of the Pribilof Islands (St. Paul Island: 57° 10′ N, 170° 17′ W; and St. George Island: 56° 34′ N, 169° 36′ W) and at Bogoslof Island in 2008 only (53° 55′ N, 168° 02′ W) (Orben et al. 2015). The colonies are located in the southeastern Bering Sea, Alaska, and murres at all 3 colonies conduct short-distance migrations, either in the vicinity of the colonies or nearby in the western Bering Sea, Gulf of Alaska, or North Pacific (Orben et al. 2015). Loggers were retrieved 1 to 2 yr after deployment (n = 49), also in July and August, and blood samples and measurements were taken again. Most birds (n = 39) were blood sampled in both years, allowing calculation of ΔTL. Of the remaining 10 birds, 9 were only sampled in the year of device deployment, and 1 was only sampled in the year of retrieval. Blood samples (<0.5 ml) were taken from the wing vein, preserved in a 2% EDTA buffer, and stored at the University of Alaska Fairbanks in a glycerol storage buffer at −80°C. Body size was calculated as a principal component of wing, tarsus, and culmen measurements. Principal component 1 (PC1) explained 51% of the variation, and all 3 variables were negatively correlated with PC1 (mean: −0.72 ± 0.01), so the inverse PC1 score was used as body size.

Geolocation and diving data

Geolocator data were analyzed as in Orben et al. (2015). After filtering erroneous locations, we used a generalized additive model to smooth latitude and longitude over time. Winter home range area was calculated as the minimum convex hull area of high residency time based on a radius of 60 km. High residency locations were identified as the upper quartile of residence time for each murre (Orben et al. 2015). Loggers recorded pressure conditionally every minute below 5 dbar (5 m). Using maximum likelihood estimates, dive bout end criteria were calculated for each murre (DIVEMOVE 1.3.4; Luque & Guinet 2007), and dives were separated into bouts when 25.7 min occurred between dives (Orben et al. 2015). Migration and diving were analyzed at either the annual level (e.g. maximum distance from the colony) or the seasonal level (e.g. fCORT levels in fall or spring). Seasonal divisions were as follows: fall = September, October, November; winter = December, January, February; and spring = March, April, May. Diving variables of interest were the percent of the day spent diving, bout duration, dives per bout, and percent of the bout diving. These variables were all positively correlated (mean correlation = 0.53, mean variance inflation factor = 17.9), so they were collapsed into 1 foraging intensity variable using a principal component analysis. The variance explained by PC1 was 65%, and all factors had strong positive loadings (Table 1).

Laboratory techniques

Telomeres were measured using the telomere restriction fragment assay following Young et al. (2015). Briefly, 5 µl of packed red blood cells were extracted

Table 1. Measures of thick-billed murre foraging intensity. Variable loadings and correlations from the first principal component of a principal component analysis

Variable	Loading	Correlation
Percent of 24 h diving	1.38	0.768
Bout duration	1.47	0.819
Dives per bout	1.73	0.963
Percent of the bout diving	1.16	0.646

into agarose plugs using the Chef Genomic DNA Plug Kit (Bio-Rad). DNA was separated on a 0.8% agarose gel using pulsed field gel electrophoresis. TL values were calculated from gel images following Salomons et al. (2009) and Young et al. (2015). Longitudinal samples from the same individual were analyzed in adjacent lanes, and gels included 2 control samples per gel to determine intra-assay variability (CV = range/mean; mean CV = 4.7 ± 1.4%). TL values were standardized to these control samples to reduce the potential effects of inter-assay variability.

For $\delta^{15}N$ and fCORT analyses, we sampled breast feathers grown in the autumn and throat feathers from breeding plumage grown in February and March (Gaston & Jones 1998). Stable isotope values were analyzed using a Carlo-Erba elemental analyzer interfaced with a Finnigan Delta Plus XP mass spectrometer (Light Stable Isotope Lab, University of California Santa Cruz [UCSC]). Measurement precision (standard deviation), based on within-run replicates of the laboratory standard (pugel), was 0.14%. Fall and spring $\delta^{15}N$ values were not correlated (correlation = 0.261, 95% CI = –0.028 to 0.51). For fCORT assays, throat (3 feathers) and breast (1 feather) feathers were weighed to the nearest mg and measured to the nearest 0.5 mm. Throat feathers were measured separately but were weighed together (Lattin et al. 2011). We followed methods outlined in Bortolotti et al. (2008) but did not mince feathers. Feathers were extracted in 5 ml of HPLC-grade methanol (Fisher Scientific), sonicated for 60 min at 50°C, and incubated overnight in a 50°C water bath. Whole feathers were analyzed in a single radioimmunoassay (Wingfield & Farner 1975) using a Sigma-Aldrich antibody (C8784) with an intra-assay CV < 1%. Samples were combined with 2000 cpm of tritium-labeled corticosterone (NET399, Perkin Elmer) to control for loss of hormone during analysis. Final fCORT titers were adjusted for percent recovery (mean 95%). Results were converted to pg mm^{-1} (Bortolotti et al. 2008). Fall and spring fCORT values were correlated (correlation = 0.50, 95% CI = 0.19–0.71), indicating that a murre stressed in the fall is also likely to incur high stress in the spring.

Analysis

Analysis was conducted in program R (R Development Core Team 2011). Prediction 1 was addressed using MANOVA, in which TL was the independent variable, and dependent variables were a subset of the wintering variables (foraging intensity, maximum distance from the colony, winter home range area, fall $\delta^{15}N$ values, spring $\delta^{15}N$ values, fall fCORT levels, and spring fCORT levels). Only 29 birds had data for each of these variables and could be included in the MANOVA. As fall fCORT demonstrated an effect in the larger analysis, a follow-up univariate ANOVA with a larger sample size (n = 34) was also run for this variable. For Predictions 2 and 3, models used the 'lm' function in R and were compared using Akaike's information criterion corrected for small sample size (AICc). For Prediction 2, the models were $\Delta TL \sim X$, where ΔTL was the percent change in TL from deployment to recapture, and X was wintering variables. ΔTL was usually calculated from 1 yr to the following year, but in 4 cases telomeres were re-sampled after 2 yr; in these cases, ΔTL was divided by 2 to indicate mean annual change. In addition to wintering variables, we include other measures likely to affect migration and TL: year (of global location sensing deployment, first capture), sex (Young et al. 2013, 2015), colony (Young et al. 2015), body size (Barrett et al. 2013, Orben et al. 2015), body mass, and the annual change in body mass. Twenty-three birds had complete data and could be used in this analysis. The variables which most strongly limited sample size were the fall and spring $\delta^{15}N$ values, so a secondary analysis was done which excluded these variables but increased the sample size (n = 31).

We addressed Prediction 3, the effect of wintering variables on breeding in the following year, using logistic regression. Wintering variables included maximum distance from the colony, winter home range area, fall and spring $\delta^{15}N$ values, fall and spring fCORT, and foraging intensity. Telomere variables were deployment TL and ΔTL. We also tested the effect of deployment year, sex, colony, change in body mass from year 1 to year 2, and body size. Twenty-one birds had complete data and could be used in this analysis. Birds were recaptured at breeding sites, so birds recaptured as 'not breeding' were likely birds that failed very early in breeding or were attending nest sites but deferred reproduction. Thus, non-breeding recaptures represented birds that survived the winter but were unable or unwilling to successfully breed. We could not distinguish between birds that were not breeding due to high stress levels or poor condition and those that may have failed for extrinsic reasons; however, even in years with a high reproductive failure due to extrinsic causes, poor parental condition may still play a large role in determining which nests fail.

RESULTS

Effect of deployment TL on wintering variables (Prediction 1)

A MANOVA in which TL was tested against foraging intensity, maximum distance from the colony, winter home range area, fall $\delta^{15}N$ values, spring $\delta^{15}N$ values, fall fCORT, and spring fCORT was not significant (Pillai = 0.31, $F_{7,21}$ = 1.33, p = 0.28). However, the univariate ANOVAs indicated that fall fCORT may be positively related to TL ($F_{1,27}$ = 6.0, p = 0.021). A follow-up univariate ANOVA, which used a larger sample size to test the relationship between fall fCORT and TL (n = 34), also demonstrated the positive relationship (Fig. 1; $\beta = 4.35 \times 10^{-4} \pm 1.82 \times 10^{-4}$).

Annual and seasonal predictors of telomere change (Prediction 2)

We tested the effects of wintering variables on longitudinal ΔTL. Models making up 95% of AICc weight are presented in Table 2. Parameter estimates were model-averaged using these models (Table 3). The only parameter with an estimate that did not overlap zero was foraging intensity. Foraging intensity showed a negative relationship with ΔTL (Fig. 2), such that birds that foraged more intensively (more time spent diving, more dive bouts) lost more TL.

In the larger analysis, without stable isotope values, models making up 95% of AIC weight were foraging intensity, year, null, maximum distance from colony, sex, and body size. Foraging intensity remained the best model (ΔAICc = 0), with the second model having a higher ΔAICc (year, ΔAICc = 4.02). Foraging intensity also remained the only parameter with a weighted estimate that did not overlap zero (weighted β = –3.61 ± 2.35).

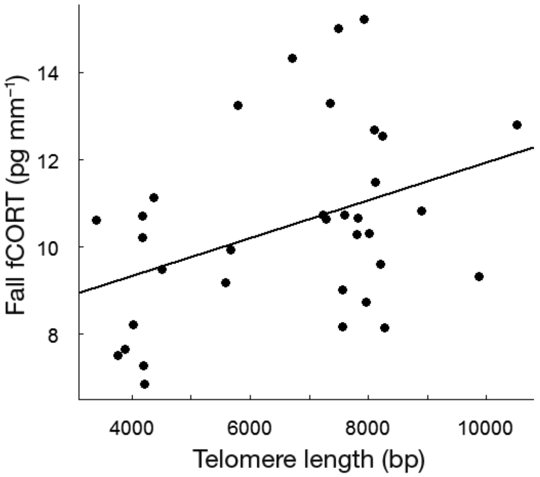

Fig. 1. Deployment (breeding season) telomere length predicting feather corticosterone (fCORT) levels in thick-billed murres, as measured in feathers grown during the fall

Table 2. Akaike's information criterion corrected for sample size (AICc) output for models of wintering variables (as predictors) and change in telomere length (response variable in the thick-billed murre). Presented are the model, the ΔAICc value (difference between model AICc and the lowest AICc), the AIC weight of the model (w, which indicates the proportional support for this model), and a column summing those weights to 95% of total weight. fCORT: feather corticosterone value

Model	ΔAICc	w	Sum w
Foraging intensity	0	0.379	0.379
Null	2.56	0.105	0.484
Year	2.64	0.101	0.585
Fall $\delta^{15}N$ value	3.15	0.0785	0.664
Body size	4.35	0.0430	0.707
Sex	4.42	0.0416	0.748
Mean depth	4.54	0.0391	0.787
Home range area	4.65	0.0370	0.824
Spring $\delta^{15}N$ value	4.76	0.0350	0.859
Maximum distance from colony	4.83	0.0338	0.893
Fall fCORT level	4.91	0.0324	0.926
Spring fCORT level	4.95	0.0319	0.958

Table 3. Weighted parameter estimates for models of wintering variables and change in telomere length in the thick-billed murre. Presented are the parameter, the weighted estimate (based on models making up 95% of Akaike's information criterion weight), and the weighted standard deviation (SD). Parameter estimates that do not overlap zero, indicating good predictive strength, are in **bold**

Parameter	Weighted estimate	SD
Intercept	3.77	6.05
Foraging intensity	**–4.37**	**3.41**
Year (2009)	–1.12	1.44
Fall $\delta^{15}N$ value	0.408	0.551
Body size	0.244	0.387
Sex (male)	0.217	0.351
Mean depth	0.00922	0.0155
Home range area	0.000	0.000
Spring $\delta^{15}N$ value	0.0491	0.0952
Maximum distance from colony	–0.00123	0.00263
Fall fCORT level	0.0122	0.0338
Spring fCORT level	0.0122	0.0457

Telomere change, wintering variables, and subsequent breeding (Prediction 3)

Models with the lowest ΔAICc for predicting breeding status in the recapture year (0 = non-breeding; 1 = breeding) were foraging intensity, body size,

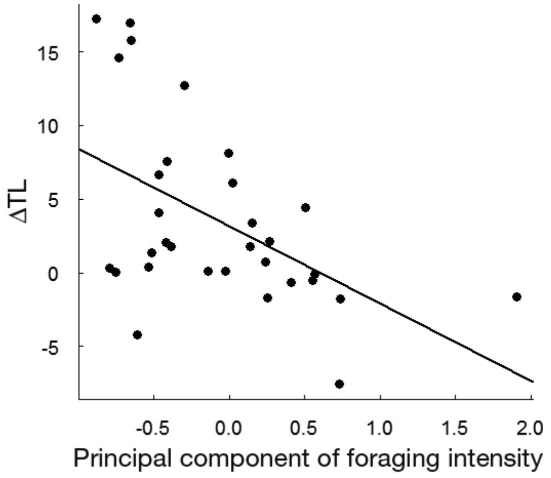

Fig. 2. Percent change in telomere length (ΔTL) from one breeding season to the next predicted by foraging intensity in the thick-billed murre. See Table 1 for details of the foraging intensity principal component

Table 4. AICc output for models predicting successful breeding in the thick-billed murre. See Table 2 for details

Model	ΔAICc	w	Sum w
Foraging intensity	0	0.375	0.375
Body size	1.83	0.150	0.525
Change in body mass	2.57	0.104	0.629
Null	3.39	0.0688	0.698
Year	4.25	0.0448	0.742
Fall fCORT level	4.49	0.0397	0.782
TL	4.90	0.0323	0.814
Maximum distance from colony	4.94	0.0317	0.846
Spring δ^{15}N value	5.11	0.0291	0.875
Spring fCORT level	5.26	0.0270	0.902
Home range area	5.43	0.0248	0.927
Sex	5.58	0.0231	0.950

and the change in mass (Table 4). However, all model-averaged parameter estimates overlapped zero (Table 5), indicating little influence of these variables on successful reproduction. Eliminating variables that did not perform well and limited the sample size allowed an increase to n = 35 but did not change the results (not shown).

DISCUSSION

TL and wintering variables

We found that deployment TL did not predict spatial wintering variables or foraging intensity but may be related to winter fCORT levels. Birds with longer TL had higher fCORT in the autumn (Fig. 1). Long TL may indicate high-quality individuals (Le Vaillant et al. 2015) that may have invested heavily in offspring, behaviorally or energetically. TL in murres is associated with breeding season foraging patterns, especially depth and choice of water masses (Young et al. 2015). Behavioral changes such as increased depth and trip duration led to higher post-breeding stress in rhinoceros auklets (Will et al. 2015), and similar patterns may drive post-breeding stress in murre fCORT as well. TL did not predict the location of wintering but may indicate individuals suffering carry-over effects from the breeding season, potentially due to lack of experience or high reproductive effort, although we cannot demonstrate a causal role for TL affecting fCORT.

Table 5. Weighted parameter estimates for models predicting successful breeding in the thick-billed murre. Presented are the parameter, the weighted estimate (based on models making up 95% of Akaike's information criterion weight), and the weighted standard deviation (SD). All parameter estimates overlap zero, indicating low predictive strength. fCORT: feather corticosterone value; TL: telomere length

Parameter	Weighted estimate	SD
Intercept	0.229	1.25
Foraging intensity	−0.843	1.18
Body size	0.356	0.664
Change in body mass	−0.000932	0.00184
Year (2009)	−0.0568	0.125
Fall fCORT level	−0.0104	0.0236
TL	0.00000790	0.0000189
Maximum distance from colony	0.000534	0.00129
Spring δ^{15}N value	0.0104	0.0262
Spring fCORT level	−0.00713	0.0186
Home range area	−0.000000124	0.000000350
Sex (male)	0.0114	0.0358

Overwinter behaviors and ΔTL

Our second prediction was supported by the wintering data; foraging intensity, a principal component made up of diving-related behaviors, was a good predictor of ΔTL (Tables 2 & 3). Murres with high foraging intensity scores (long bout duration, high percentage of time spent diving) lost more TL than those with lower scores. Birds with high foraging intensity may be inefficient foragers, recovering from stressful breeding seasons, or of lower quality, but their intense foraging is reflected in physiological changes to telomeres. However, spatial wintering variables (winter home range area and maximum distance from the colony) did not perform well as predictors of telomere change. Murres have extremely high wing-loading and flight costs but are adept wing-propelled pursuit-diving foragers, specializing in catching agile, fast-moving prey underwater. Species-specific parameters related to the ability to extract energy from the environment should drive quality indicators, and telomeres were sensitive to these qualities, related to diving, in murres. Our findings support the idea that in a specialist diver, variation in water column use is more associated with TL maintenance than are flight patterns.

Although TL (and rates of change) have previously been shown to differ by sex and breeding colony in many species (reviewed in Barrett & Richardson 2011) including the thick-billed murre (Young et al. 2013), such differences were not found in this study. However, male murres spend the first weeks after colony departure with the fledgling, diving intensely to supply both chick and self (Elliott & Gaston 2014). Thus, telomere loss associated with intense foraging may contribute to the sex differences found in other studies. It should also be noted that, although many of our ΔTL values were positive, a positive value is unlikely to be a true telomere lengthening (Steenstrup et al. 2013). Lengthening is likely due to short follow-up time (1 yr instead of many years in a long-lived species) and also to methodological constraints. Therefore, we avoid interpreting a positive ΔTL as an increase in TL but rather as TL maintenance or a reflection of relative differences in food availability or other conditions affecting those birds.

ΔTL and subsequent breeding

TL and ΔTL were not associated with the probability of breeding in year 2. No parameter had an estimate that was different from zero, but models of foraging intensity and body size had ΔAICc < 2. These models indicated that deployment year body mass was higher in birds that were breeding at recapture, and their overwinter foraging intensity was lower. This may indicate that the better condition of these birds carried over into the next year, although the results are not strong enough to make a definitive conclusion and certainly not strong enough to infer causation. We did find a relationship between ΔTL and winter foraging intensity (previous subsection), but this did not carry over to breeding probability. Investigating longer time series of changes in foraging and breeding parameters, in relation to changes in body mass and ΔTL, would be a good subject for future research on drivers of carry-over effects.

There are 2 likely explanations for the lack of relationship between TL variables and subsequent breeding. It is possible that the birds which were not recaptured had extremely high TL loss, but variation in ΔTL among recaptured birds was minimal, regardless of breeding status. Alternatively, as non-breeding status may be due to parental quality or extrinsic causes, perhaps the murres recaptured as non-breeders are not the lowest-quality individuals, so their status is not associated with a quality indicator. It would be useful to assess fledging probability and adult survival in relation to TL and ΔTL. Perhaps on a scale of several years, the cumulative effect of winter stress and low trophic level diet will lead to fitness outcomes.

CONCLUSION

TL did not predict the spatial wintering patterns but may indicate individuals suffering high stress due to carry-over effects from the breeding season. Our findings also support the idea that telomeres, a physiological quality indicator, were sensitive to a species-specific parameter related to the ability to extract energy from the environment, in this case diving behaviors rather than spatial use. Winter foraging intensity was related to the maintenance of TL from year to year, although causation cannot be inferred. In this pursuit diver, variation in water column use was more important for maintaining TL than the size of the wintering area and distances travelled.

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