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**Extra-pair paternity in a long-distance migratory songbird beyond neighbors' borders and across male age classes**

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**ABSTRACT**

Roughly 90% of socially monogamous bird species exhibit some degree of extra-pair paternity (EPP), although the extent and the underlying mechanisms vary among species. We analyzed spatial and demographic patterns of extra-pair paternity over a six-year period (2005 - 2010) as part of a long-term population study of Canada warblers (*Cardellina Canadensis* L., 1766). We identified 12 microsatellite loci used to assess paternity for 185 nestlings from 61 nests. Extra-pair young (EPY) accounted for 41.6% of all nestlings and 57.4% of nests contained at least one extra-pair young. Fewer than half of EPY were sired by males who shared territorial boundaries, and some males sired young in nests 1km from their territory. The age of social males did not differ from males who cuckolded them. The majority (83%) of EPY were sired by males in older age classes (2+ years old) while < 17% were sired by one year olds. Of the young sired by older males, 58.5% were sired by males 3 – 7 years old. Males that sired more EPY sired fewer within pair young (WPY); those without EPY sired more WPY suggesting a possible fitness tradeoff between these two strategies. Our findings suggest multiple age-based strategies within a single breeding population, and potential strategy shifts to maximize lifetime fitness as they age.

*Keywords:* Canada Warbler, *Cardellina canadensis*, within-pair paternity, lifetime fitness

## INTRODUCTION

Extra-pair paternity (EPP) is common among socially monogamous bird species with approximately 90% of socially monogamous species exhibiting some degree of EPP (Griffith et al. 2002), and this behavior has potentially strong fitness consequences (Birkhead and Møller 1998). Siring young outside a social pair bond has the ability to enhance productivity within a single breeding season and is an important component of male fitness (Griffith et al. 2002, Kaiser et al. 2015), but males within a population can differ considerably in their fitness gains from EPP (Sardell et al. 2010; Reid et al. 2014a; Kaiser et al. 2015).

Territory location, habitat quality and age have been shown to influence EPP (Kaiser et al. 2015; Sardell et al. 2010; Woolfenden et al. 2005). Older males generally rank higher in the social hierarchy and thus perform better by asserting competitive dominance (Hunt 1996; Marra and Holmes 2001; Reitsma et al. 2008). Therefore, an individual's energy allocation toward seeking EPP may be influenced by experience. Long-term studies offer some resolution on whether the proclivity toward EPP relates to an individual's changing priorities associated with age-specific benefits and constraints (Sardell et al. 2010). Tracking the cumulative fitness of individuals of known age throughout their life can add significant insight into how reproductive strategies change with age.

Long-distance migrants tend to have shorter breeding seasons, which increases nesting synchrony, thereby enhancing the opportunity for EPP (Spottiswoode and Møller 2004), although this hypothesis has mixed support (Stutchbury 1998; but see Weatherhead and Yezerinac 1998). We used a long-distance migratory songbird, the Canada warbler (*Cardellina canadensis* L., 1766), to identify how mating strategies change with age class. The Canada

warbler is a long-distance, obligate single-brooded migratory songbird with relatively high nesting synchrony. We measured reproductive output of individuals within a breeding population in New Hampshire as part of a long-term population study to test whether EPP is consistent across age classes. We performed genetic parentage analyses for nestlings studied over six consecutive years. Having documented higher nesting success among older males (Reitsma et al. 2008), we predicted they would also sire more extra-pair young (EPY) owing to their greater experience in defending territories and attracting mates (Cleasby and Nakagawa 2012). This species breeds in forested wetlands with high stem densities, and complex ground cover. Populations at landscape scales are patchily distributed in accordance with their suitable habitat comprised of ‘clusters’ of territories (hereafter, neighborhoods) that vary in size contingent upon habitat structure (Hallworth et al. 2008a). Based on the clumped dispersion documented by Hallworth et al. (2008b), we predicted greater EPY among males within the same neighborhoods, specifically among adjacent territorial males.

## METHODS

### Study Site

The study area in Canaan, New Hampshire (43°40'N, 72°03'W) encompasses ~ 450 ha with a centrally located bog separating two study sites each with distinct habitat features (Hallworth et al. 2008a). See Hallworth et al. (2008a, b) and Reitsma et al. (2008) for a detailed description of the study area. The study area south of the bog is a relatively level red maple (*Acer rubrum* L.) swamp interspersed with mixed deciduous/coniferous sections with a taller canopy and lower stem density. The study area north of the bog varies in elevation with early to mid-successional forest dominated by the same species as the plot south of the bog. This area is interspersed with

higher, drier forest and small boggy areas with mossy ground cover and persistent standing water. Both study areas have been studied without interruption since 2005 and have had consistently high annual return rates, pairing and fledging success (Hallworth et al. 2008*b*; Reitsma et al. 2008).

### **Territory Mapping**

During the 2005-2010 breeding seasons, male Canada warblers were captured and uniquely color-banded for later identification ( $n = 118$  individuals). Upon capture, each male was aged (Table 1) using plumage characteristics (distinctive molt limits, Pyle 1997). We captured fewer females ( $n = 36$ ) because they do not respond to playback and we did not attempt captures at nests. Of those males breeding for the first time in the study area, 60.5% were after second year (ASY) males, and we assigned them a conservative age of 2, the minimum age possible. All males in a given breeding season were assigned to age classes ranging from 1-7 years old. For example, returning SY individuals who bred within the population in the previous year were assigned the age class of 2. Individuals who were captured and initially aged as ASY and returned were aged as 3 years old.

From 2005 - 2007, we mapped male locations using handheld Global Positioning System (GPS) devices following the protocol reported in Hallworth et al. (2008*b*), in which color-banded males were followed and locations were marked at 5-minute intervals without influencing their behavior. During the breeding season 2008 - 2010 at least 36 ( $57.28 \pm 16.74$ ; mean  $\pm$  1 SD) locations per individual in each year were obtained opportunistically during territory visits, as opposed to the 42 minimum in prior years. Male territories were generated using kernel density estimates (KDE) which were calculated in program R 3.2.0 (R Core Team 2015). We used least-

square cross validation to estimate the bandwidth or smoothing parameter (Barg et al. 2005). We used the territory centroid, the center location of the 95% KDE, and measured distances between these centroids to determine the distance from other males within the population. We searched for nests while mapping territories, and when nests were found ( $n = 117$ ) we banded nestlings to quantify natal philopatry, obtained a blood sample, and estimated nestling age or noted hatching dates. We considered males to be social males if they were observed feeding young and/or the nest was placed within their respective territory. Boundaries are known to shift early in the season before all males arrive but thereafter remain stable until fledging (Reitsma, pers. obs.).

### **Genetic Analysis**

We collected DNA samples from Canada warbler nestlings ( $n = 185$  with confident paternity assignment) as well as breeding males and females and identified microsatellite loci useful for performing parentage analysis. Blood was stored in Queen's lysis buffer (Seutin et al. 1991) and transported to the lab where it was stored at  $-20^{\circ}\text{C}$ . DNA was extracted using the Qiagen DNeasy blood and tissue kit according to the manufacturer's instructions. Samples were eluted in buffer AE and DNA concentrations were determined using a Nanodrop ND-1000 spectrophotometer. We tested many primer sets (data not shown) and identified 15 polymorphic microsatellite loci that were used for further paternity analysis. Six of our loci were developed specifically for the Canada warbler by screening a microsatellite enriched genomic cDNA library according to the methods described by Glenn and Schable (2005). The remaining nine were developed for other avian species (supplementary Table S1)<sup>1</sup>, but amplified putatively orthologous microsatellite loci in the Canada warblers. We scored individual genotypes by amplifying genomic DNA from individual birds (100-200 ng) in a 10  $\mu\text{l}$  reaction containing 1

$\mu\text{L}$ 10x PCR buffer, 1.5 - 2.0 mM  $\text{MgCl}_2$ , 0.5 U Taq polymerase (New England Biolabs), 0.5  $\mu\text{M}$  of each primer, and 100  $\mu\text{M}$  dNTPs. PCR cycling conditions are listed in Table S1. One primer from each locus was fluorescently labeled for multiplex fragment analysis. PCR products were diluted and mixed with formamide and GeneScan™ 500 ROX™ size standards (Life Technologies). PCR fragments were sized in 10  $\mu\text{l}$  multiplexed samples on an ABI 3100 Genetic Analyzer (Applied Biosystems) at the Dartmouth College Molecular Biology Core Facility. Allele sizes of PCR fragments were calibrated with an internal size standard and scored using Genescan 3.0 software (Applied Biosystems). Data were manually checked for scoring accuracy.

The allele frequency analysis module in Cervus 3.0 (Kalinowski et al. 2007) was used to calculate heterozygosity and check loci for deviations from Hardy-Weinberg equilibrium (Table S1). Three loci, WPD4, TG0412, and CAWA 3 deviated significantly from Hardy-Weinberg equilibrium and were eliminated from further analysis.

We performed parentage analysis of microsatellite genetic data using CERVUS 3.0 (Kalinowski et al. 2007). This program analyzes genotypic data using a likelihood-based approach and generates a  $\Delta\text{LOD}$ , which is the difference in positive log likelihood scores (LOD) between the two most likely candidate parents. Within CERVUS we ran a simulation of parentage analysis to evaluate the confidence in assignment of parentage to the most likely candidate parent at > 95% confidence and > 85% confidence levels. We used a total of 10,000 offspring tests. Based on our field data we assumed that 90% of potential fathers had been sampled and 5% of potential mothers had been sampled. We examined DNA samples from a total of 338 offspring, 23 candidate mothers, and 76 candidate fathers. Individuals were excluded from the analysis if fewer than seven of the 12 loci were successfully typed (29



offspring, 1 candidate mother, 4 candidate fathers excluded). The proportion of successfully genotyped loci was estimated at 88%. This was calculated by averaging the percentage of individuals successfully genotyped at each locus used in this study. A typing error rate of 1% was incorporated into the simulation of maternity and paternity assignments. Three of our 15 original loci showed evidence of null alleles and were excluded from parentage analysis (supplementary Table S1)<sup>1</sup>. From 2005 - 2010, we assigned parentage to male parents and offspring with sufficient confidence ( $\geq 85\%$ ) to determine paternity for 52.1% of nests (61 of 117) and 54.7% of offspring (185 of 338).

### Statistical Analysis

We used a paired T-test to determine whether the age of social males differed from that of males that sired young within their nest (extra-pair males). We used chi-square to test whether social males were cuckolded by extra-pair males with adjacent territories or males from non-adjacent territories. We used a logistic regression with a logit link function to determine if distance (Euclidean distance) influenced the probability of siring extra-pair young. A Poisson linear regression, that included male identity as a random factor to account for the same individual in the dataset in multiple years, was used to test whether the number of EPY sired had an effect on the number of WPY sired. A two-sample Kolmogorov-Smirnov test was used to verify that the number of EPY followed a Poisson distribution. We randomly generated a dataset of the same length as the observed data using a Poisson distribution with a lambda value of 1.21, the mean of the observed data. The distribution of the two datasets did not differ ( $D = 0.176$ ,  $p = 0.41$ ). For the 2008 breeding season, we used Poisson regression to determine whether distance (Euclidean distance) from the genetic father's territory centroid influenced the number of young

sired in a particular nest. We selected 2008 for more detailed spatial analyses because of a high sample size of nests and high pairing of offspring with candidate fathers in that year. All analyses were performed in R 3.2.0 (R Core Team 2015).

## RESULTS

Of the 61 total nests for which sufficient confidence could be assigned, 57.4% ( $n = 35$ ) had at least one EPY within the nest. Of the 185 young confidently assigned male parentage, 58.4% ( $n = 108$ ) were sired by the social male. The paternal contribution to nests that contained EPY varied and ranged from 1 - 4 extra-pair males (EPM) (nests with 3 EPM:  $n = 5$ ; nests with 4 EPM:  $n = 5$ ). Nests in which all nestlings were sired by the social male, all within pair young constituted 42.6%, ( $n = 26$ ) of the total, followed by nests with one EPY (29.5%,  $n = 18$ ), and two EPY (13.1%,  $n = 8$ ). Nests that contained either 3 (4.6%,  $n = 3$ ), 4 (4.6%,  $n = 3$ ) or 5 (4.6%,  $n = 3$ ) EPY had equally low representation.

Roughly half (47%,  $n = 29$ ) of social males shared a territory boundary with males that cuckolded them indicating that neighbors were no more likely to cuckold than non-neighbors ( $\chi^2 = 0.184$ ,  $df = 1$ ,  $p = 0.664$ ). The probability of siring extra-pair young declined significantly with distance from a male's territory ( $\beta = -0.18 \pm 0.04$ ,  $p < 0.001$ ), noting that mean territory size = 0.97 ha, (Hallworth et al. 2008b). In addition, the number of EPY sired within a nest declined with distance between social and extra-pair males' territories ( $\beta = -0.0006 \pm 0.00027$ ,  $p = 0.03$ ; Fig. 1). However, one male sired EPY in a nest more than 2 km from his territory. Five extra-pair young were sired by males whose territory was more than 1 km from their own nest. Four males from the northern study site sired EPY in the southern study site. In these cases of longer-distanced EPP, all had pairing confidences of greater than 85% and all but one were paired at

greater than 90% confidence. The one instance of EPP at a distance greater than 2 km had the highest pairing confidence ( $\geq 95\%$ ).

We predicted that young males would be cuckolded by older individuals, however the age of extra-pair males did not differ from that of social males (mean difference: -0.24 years, 95% CI -0.69 : 0.22 ;  $t = 1.04$ ,  $df = 72$ ,  $p = 0.30$ ). Over the six years of the current study, first-year males (SYs) sired 16.9% of EPY (13 of 77); the remaining 83.1% (64 of 77) were sired by after second year males (ASYs) or males 2 years old or older. Because we have individuals of known age, we were able to assess the amount of young each age class sired. In our population, males that were 2, 3 and 4 years old sired 24.7% ( $n = 19$ ), 13.0% ( $n = 10$ ) and 31.2% ( $n = 24$ ) of the 77 EPY, respectively. Males within the oldest age classes (5 - 7 year olds) which we combined due to small sample sizes, were responsible for 14.2% ( $n = 11$  of 77).

Males that sired more EPY had fewer WPY (Fig. 2,  $\beta = -0.34 \pm 0.11$ ,  $z = -3.0$ ,  $p = 0.003$ ). The ratio of extra-pair to within-pair young differed among male age classes and the number of nests a male cuckolded, but this difference was not significant ( $df = 44$ ,  $F = 0.493$ ,  $p = 0.741$ , Fig. 3). The total number of WPY was greater for males 1-3 years old compared to those four years or older but this also was not significant ( $df = 44$ ,  $F = 0.436$ ,  $p = 0.782$ ). Males who did not sire EPY ( $n = 26$ ) sired at least 1 WPY with the exception of one male. In contrast, males that sired EPY in multiple nests within a season ( $n = 10$ ) had a lower incidence of siring WPY (Fig. 4). Males with EPY in one nest ( $N = 27$ ) were intermediate between the previous two groups. Males with the highest cumulative number of nests with EPY ( $n = 5$  nests) had the highest ratio of EPY to WPY (4:1). That ratio dropped to 1.4:1 for males that cuckolded 4 nests over the years included in this analysis. Males that sired EPY young in 3 and 2 nests had EPY to WPY ratios of

0.77:1 and 0.87:1, respectively. Males that cuckolded only one nest had a ratio of 1.18:1 and represented 41.7% of all males with EPY. The ratios reported here are conservative estimates since males were excluded from these analyses if the social nest was not found in the year where the extra-pair young he had sired were documented.

## DISCUSSION

Canada warblers, a single brooded, long-distance migratory songbird, exhibited comparatively high rates of extra-pair paternity compared with other migratory passerines. Male age class was an important, though not statistically significant, factor in determining the number of young sired outside of the social pair bond. The oldest males (4+ years old) sired more extra-pair young than younger males (< 4 years old) but at the possible cost of siring fewer within-pair young (see Cleasby and Nakagawa 2012). Our analyses of age effects are conservative. We included males assigned the age of 2 if caught as ASYs in their first breeding season on these study sites and thus the actual age of these individuals is likely to be older than the age we assigned. Males were cuckolded by individuals beyond those who shared a territory boundary. Social males were sometimes cuckolded by males with territories 1 – 2+ km from their territory, documenting extra-pair forays to territories beyond neighbors, even to other neighborhoods. Despite longer forays, EPP declined with increasing distance from male territory similar to black-throated blue warblers but on a smaller spatial scale (Kaiser et al. 2017).

The incidence of EPY (41.6%) reported here for Canada warbler is comparable to other species of migratory wood warblers breeding within the region. Black-throated blue warblers (*Setophaga caerulescens* (Gmelin, 1789)) (35.1% EPY), another Nearctic-Neotropical migrant reported from a site about 60 km northeast of our study area (Kaiser et al. 2015), and hooded

warblers (*Setophaga citrina* (Boddaert, 1783)) (34% EPY) breeding in deciduous forests of Pennsylvania (Chiver et al. 2008) migrate similar distances, about half that of the Canada warbler. As such, these species have the opportunity to double-brood while the latter is an obligate single-brooded species (Reitsma et al. 2010). In contrast, a non-migratory insular population of song sparrows (*Melospiza melodia* (A. Wilson, 1810)) had an overall EPP rate of 28% (Sardell et al. 2010).

This study may elucidate further links between EPP and life history traits, such as distance migrated, number of broods and breeding synchrony, that suggest a higher rate of EPY among longer distance migrants.

Our findings elucidate age-specific reproductive strategies that can only be identified through long-term population studies. We found that male age is important in determining which individuals sire EPY. Age has been found to be positively correlated with EPY but not WPY in other passerines as well, such as mountain bluebirds (*Sialia currucoides* (Bechstein, 1798)) (Balenger et al. 2008), reed buntings (*Emberiza schoeniclus* L. 1758) (Kleven et al. 2006), pied flycatchers (*Ficedula hypoleuco* (Pallas, 1764)) (Lehtonen et al. 2009) and splendid fairy-wrens (*Malarus splendens* (Quoy and Gaimard, 1830)) (Webster et al. 2007). Our results are similar in that we found no relationship between age and WPY but the oldest age classes had higher rates of EPY. Older males may have a greater opportunity to seek extra-pair copulations because they arrive and establish social bonds with females earlier than young males thus allowing older males to seek EPCs after their mates initiate the earliest incubation (Kaiser et al. 2017; Reitsma et al. 2008). Although males that were one or two years old were responsible for 41.6% of all EPY, the higher EPY:WPY ratio of males 4 years old or older suggests experience contributes to

the number of EPY sired within a single season. While experience likely plays a role in the number of EPY sired, the underlying mechanism for the relationship between rates of EPP and male age needs further study (Kleven et al. 2006; Webster et al. 2007; Lehtonen et al. 2009). Our results suggest reproductive strategies may shift in the oldest age classes.

Territory dispersion has been shown to contribute to paternity patterns (Norris and Stutchbury 2001; Woolfenden et al. 2005; Kaiser et al. 2015). Habitat specialists occupying isolated patches (Hallworth et al. 2008*b*), linear strips (Woolfenden et al. 2015), or fragmented landscapes (Norris and Stutchbury 2001) may be compelled to foray farther distances from territories to secure EPY. Canada warbler neighborhoods occur in suitable dense and wet habitat with interspersed lower stem density and drier forest (Hallworth et al. 2008*a*). Thus, one advantage Canada warblers may have in long-distance forays is remaining within forested habitat. EPY were not restricted to neighbors with six instances of nestlings sired by males greater than 1 km from their respective territories in 2008 alone. In this regard, they more closely resemble hooded warblers (Norris and Stutchbury 2001) and Acadian flycatchers (*Empidonax virescens* (Vieillot, 1818)) (Woolfenden et al. 2005), species that sire young across large distances due to willingness to foray among fragments or having a linearly arranged territories, respectively. EPY may, however, result from early phases of the breeding season when females are scouting and males occupy larger areas until future neighbors arrive (Reitsma, unpubl. data).

Females may select varying phenotypes among males within the population or features of the habitat associated with individual males. Female hooded warblers, for example, use song as opposed to plumage characteristics when selecting males for extra-pair copulations (Chiver et al. 2008). Canada warblers have variation in song repertoire with two distinct song modes (Demko

et al. 2013). Song-sharing within the population has also been documented where newcomers switch element structure and their frequency range to adjust to neighbors (Demko et al. 2016). However, we did not concurrently measure EPP and song characteristics in our population. EPP is thought to drive sexual selection of plumage characteristics in splendid fairy-wrens (Webster et al. 2007), pied flycatchers (Lehtonen et al. 2009) and mountain bluebirds (Balenger et al. 2009) and plumage varies among male Canada warblers even within age cohorts. However, we did not investigate whether plumage characteristics, such as the length of a male's necklace, relate to EPP success. Further research is needed to elucidate mechanisms of female choice for EPP in the Canada warbler.

Our findings suggest that there is a fitness tradeoff for siring EPY by compromising the number of WPY sired (see Fig. 2). The ratio of EPY:WPY was lower for males who cuckolded fewer nests but potentially less so for the oldest males (lowest slope in Fig. 2). Maximizing EPY may come at the expense of siring or fledging WPY in part due to lower mate guarding (Westneat et al. 1990; Kaiser et al. 2015). This tradeoff may be exacerbated for species with highly synchronized breeding attempts that do not double brood. While outside the scope of the current study, males may seek to increase fitness through EPP as they age, instead of investing at their social nest. These two behaviors have been shown to be inversely related in other studies (Tuttle 2003; Clotfelter et al. 2007). We did not compare visitation rates among males of different age classes to explicitly test this hypothesis.

The long-term nature of this study provides insights into age-related performance that can only be revealed through a more detailed examination of advanced age classes. Having a complete profile (all EPY and WPY fledged) of each male in each year would provide a more

robust measure of whether this species generally undergoes a shift in reproductive strategies with age (as in song sparrows, Sardell et al. 2010). However, we did track individuals over multiple years and our findings offer important contributions suggesting a possible shift in reproductive strategies with age in this socially monogamous species.

Canada warbler males foray across extensive forested-habitat mosaics that include patches of their preferred habitat and areas not suitable for breeding. Genetic contributions of males greater than 2 km from their own nests suggest neighborhoods in discreet habitat patches may have frequent genetic exchange. Thus, maintaining a mosaic of intact habitat may ensure occupancy and facilitate gene flow among far-ranging Canada warbler neighborhoods. These mosaics may be more likely to have diverse age classes with the requisite variation in documented reproductive strategies that likely contributes to the high reproductive success in this study area.

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**TABLE LEGEND**

Table 1

Table 1. Age composition of the male Canada warbler (*Cardellina Canadensis* L., 1766) populations in each of the four years with an adequate number of nests number of nests analyzed and beginning in the year that individuals could be in the oldest age category given when these populations were first aged. Only 9.8% ( $n = 6$ ) of males in these analyses were from 2005 and 2006 when minimum ages could not have exceeded 2 and 3, respectively.

Year	Ages (in years)			
	1	2	3	$\geq 4$
2007	10	19	8	5
2008	5	10	14	11
2009	15	6	5	12
2010	8	10	2	14

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## FIGURE LEGENDS

### Figure 1

Figure 1. The distance (m) between the social male territory centroid and the extra-pair male's territory centroid. One male Canada warbler sired EPY in a nest over 2km away. Values at distance 0 indicate the genetic father was the social mate, thus all within-pair young. Points are jittered slightly to visualize overlapping data. All these data are from the 2008 breeding season in Canaan, New Hampshire.

### Figure 2

Figure 2. The number of extra-pair young and within-pair young in each nest. Slopes for each age class are represented along with the mean of all age classes combined.

### Figure 3

Figure 3. The percentage of within-pair young (WPY) and extra-pair young (EPY) produced within the four age classes over the duration of the study, 2005-2010 (top panel). The total number of WPY and EPY within the four age classes over the duration of the study (bottom panel).

### Figure 4

Figure 4. Within-pair paternity (WPY) was verified for all but one of 26 males that had no documented extra-pair young (EPY), whereas 40.7% of males with EPY in one nest had WPY and only 20% of extra-pair males with EPY in two or more nests in a single season had documented WPY. The percentage totals are across all age classes within each category of number of nests cuckolded.

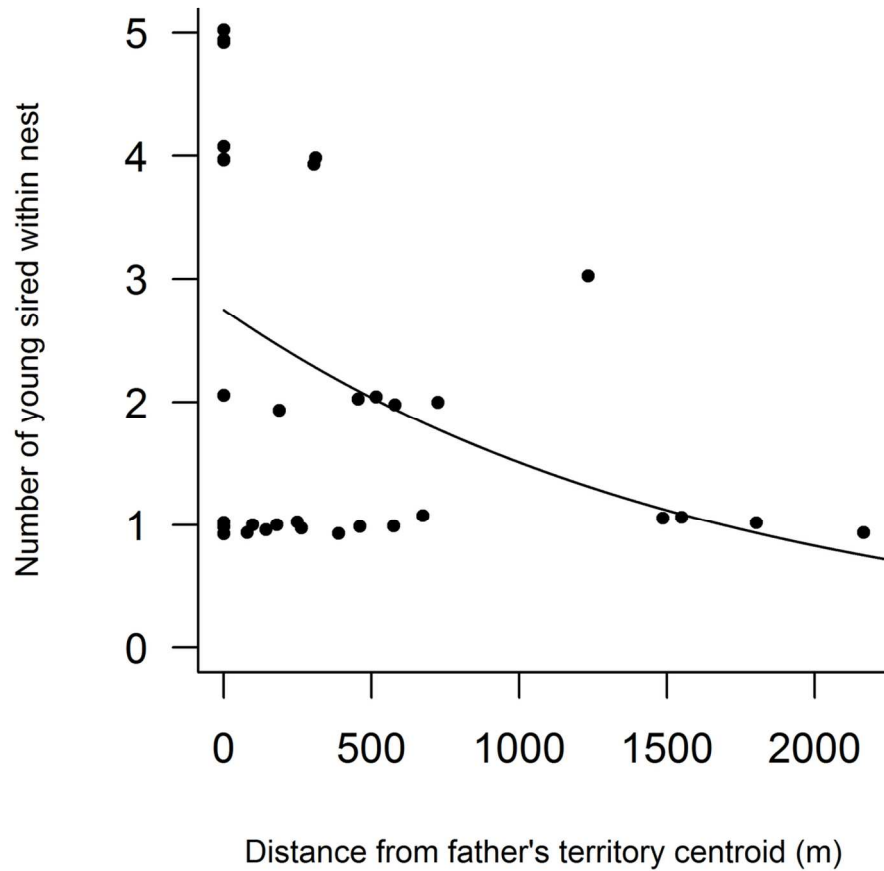


Figure 1. The distance (m) between the social male territory centroid and the extra-pair male's territory centroid. One male Canada warbler (*Cardellina canadensis*) sired EPY in a nest over 2km away. Values at distance 0 indicate the genetic father was the social mate, thus all within-pair young. Points are jittered slightly to visualize overlapping data. All these data are from the 2008 breeding season in Canaan, New Hampshire.

114x128mm (300 x 300 DPI)

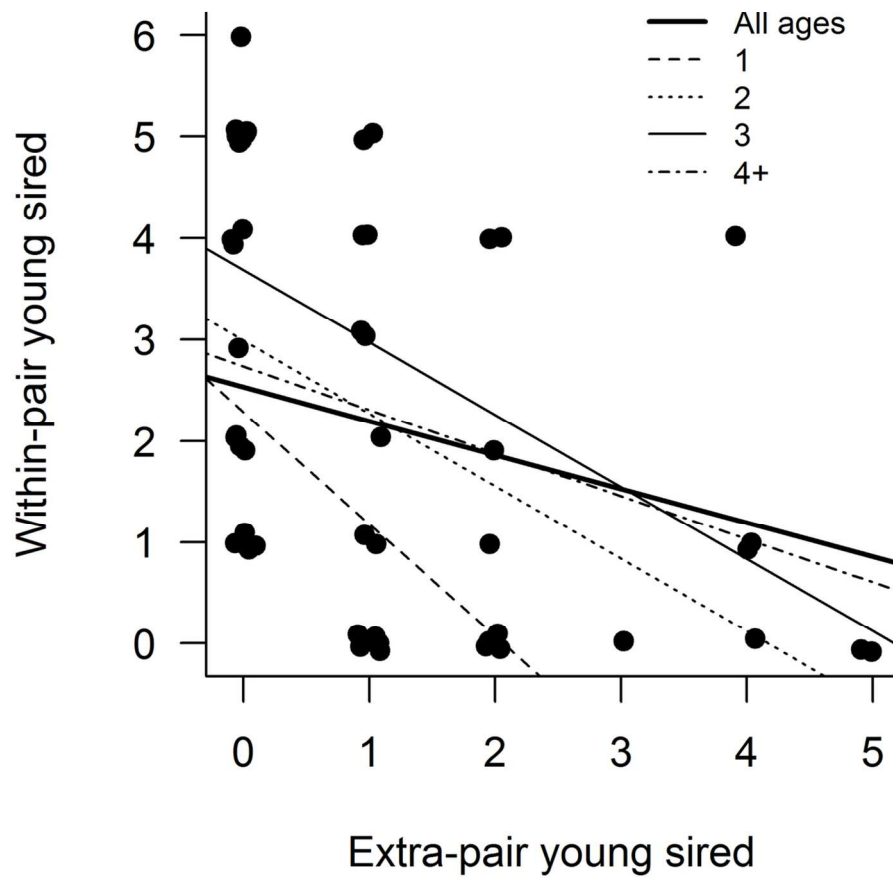


Figure 2. The number of extra-pair young and within-pair young in each nest. Slopes for each age class are represented along with the mean of all age classes combined.

114x128mm (300 x 300 DPI)

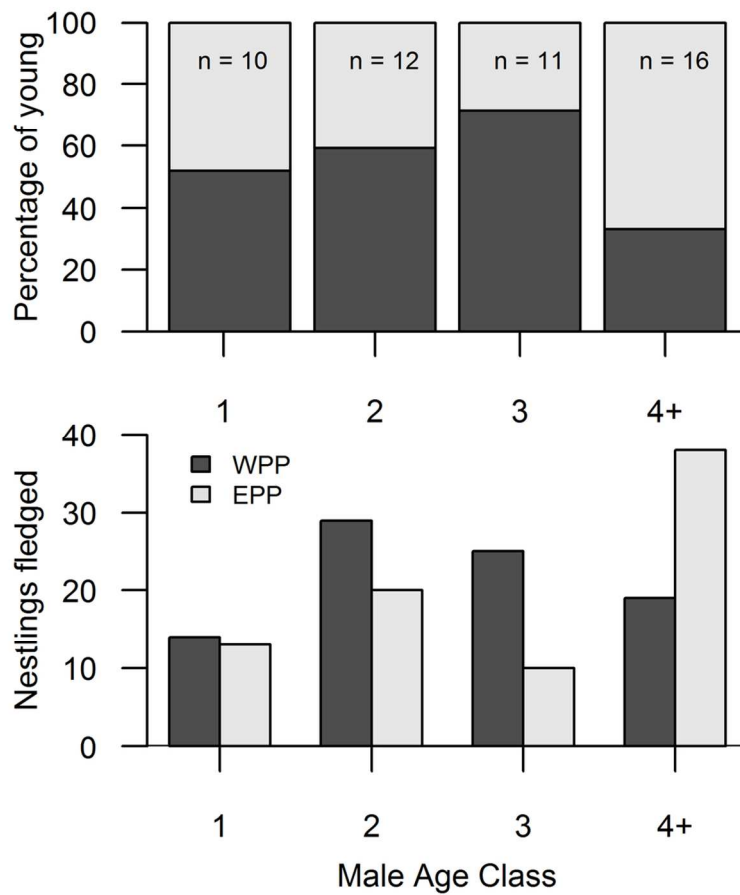


Figure 3. The percentage of within-pair young (WPP) and extra-pair young (EPP) produced within the four age classes over the duration of the study, 2005-2010 (top panel). The total number of WPP and EPP within the four age classes over the duration of the study (bottom panel).

114x128mm (300 x 300 DPI)



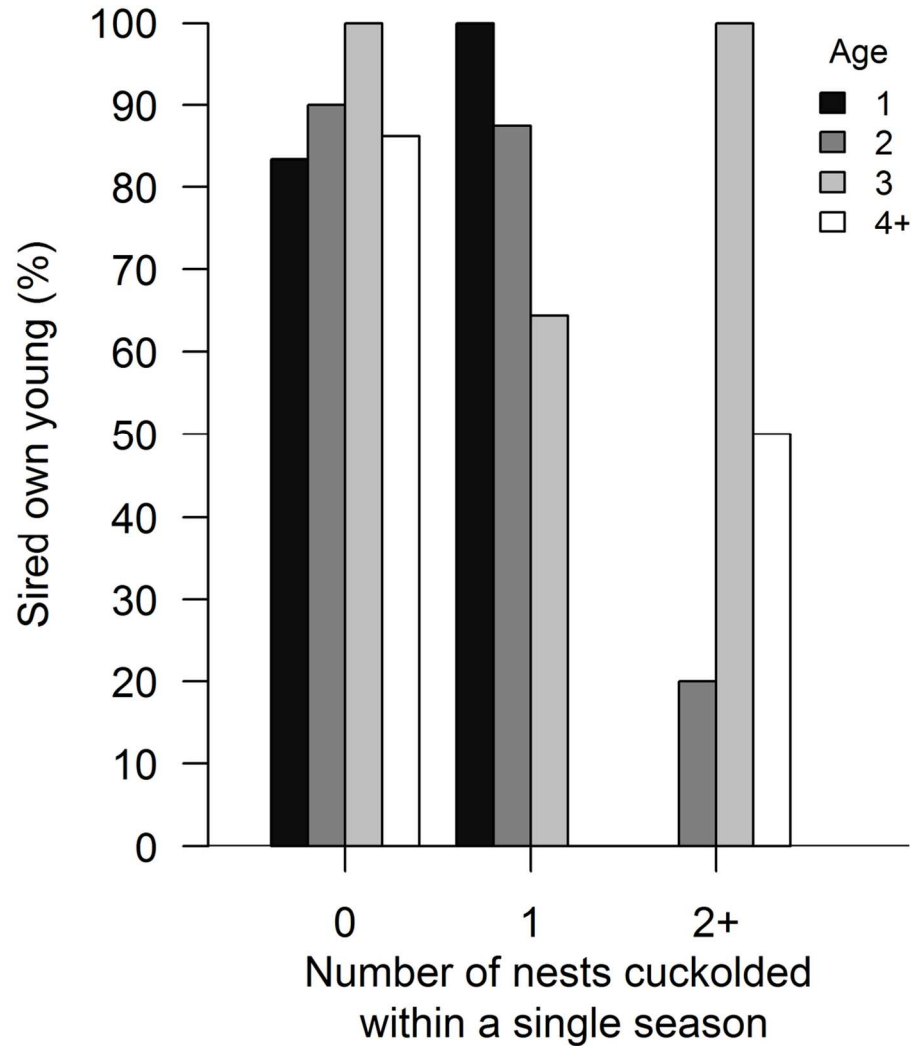


Figure 4. Within-pair paternity (WPY) was verified for all but one of 26 males that had no documented extra-pair young (EPY), whereas 40.7% of males with EPY in one nest had WPY and only 20% of extra-pair males with EPY in two or more nests in a single season had documented WPY. The percentage totals are across all age classes within each category of number of nests cuckolded.

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