

**NUTRITIONAL AND GENETIC
ADAPTATION OF GALLIFORM
BIRDS: IMPLICATIONS FOR
HAND-REARING AND
RESTOCKING**

**TUIJA
LIUKKONEN-ANTTILA**

Department of Biology,
University of Oulu

OULU 2001



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Academic Dissertation to be presented with the assent of the Faculty of Science, University of Oulu, for public discussion in Kajaaninsali (Auditorium L6), Linnanmaa, on June 9th, 2001, at 12 noon.

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Abstract

The impact of hand-rearing on the morphology and physiology of captive and wild grey partridges (*Perdix perdix*) and capercaillies (*Tetrao urogallus*) was studied in three feeding trials conducted under laboratory conditions, and two comparative studies between wild and captive birds. Finally, wild and hand-reared grey partridges from several localities in Europe were sampled and the control region 1 of mitochondrial DNA was sequenced to reveal genetic variation between populations, as well as to compare wild and captive stocks.

Wild capercaillies had heavier pectoral muscles, hearts, livers and gizzards, longer small intestines than hand-reared ones, and a higher cytochrome-c oxidase activity in muscle and heart. Invertebrates were essential to the growth, primary and temperature regulation development in grey partridge chicks. Fish was not sufficient to replace invertebrates in the diet. A change in diet from commercial to natural decreased the assimilation efficiency in the grey partridge. It also increased the mass of gizzard reflecting the need for greater grinding ability. Of hepatic P450 enzymes used in this study 7-ethoxyresorufin-0-deethylase and 7-pentoxyresorufin-0-deethylase differed between wild and hand-reared birds. Coumarin-7-hydroxylase activity was higher in grey partridges than capercaillies. Diet differences may have caused these differences. Quebracho tannin added to the diet lowered nitrogen concentration in caecal feces, and elevated the level of excreted tannin. Otherwise its effects were slight.

Mitochondrial control region revealed 14 variable sites between two main lineages detected. Nucleotide and haplotype diversities varied greatly between populations. The markedly deep divergence between the two lineages indicated most probably post-glacial recolonisations from geographically isolated refuges. In Finland, wild birds represented the eastern lineage, while the farmstock represented the western lineage. Surprisingly little trace, contrary to expectations, from the large-scale releasing of imported partridges could be seen in the European populations.

Keywords: mitochondrial control region, capercaillie, grey partridge, nutrition, *Perdix perdix*, *Tetrao urogallus*

The grey partridge



Photo: Jouni Klinga



Photo: Lassi Kujala

The capercaillie



Photo: Timo Yli-Viikari



Photo: Hannu Hautala

To my family

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Oulu, May 2001

Tuija Liukkonen-Anttila

Abbreviations

| | |
|----------------|---|
| asl | above sea level |
| BP | before present |
| COH | coumarin-7-hydroxylase |
| COX | cytochrome-c oxidase |
| CRI | control region 1 |
| CYP | cytochrome P450 enzyme superfamily (CYP1A, CYP2B etc.) |
| EE | excretory energy |
| EROD | 7-ethoxyresorufin-0-deethylase |
| FG | fast-glycolytic fibres |
| FOG | fast-oxidative-glycolytic fibres |
| GE | gross energy |
| GI | gastrointestinal |
| Hb | haemoglobin |
| Hcr | haematocrit |
| ME | metabolisable energy |
| MEC | metabolisable energy coefficient (or assimilation efficiency) |
| mtDNA | mitochondrial DNA |
| Myr | million years |
| P1–P10 | primary wing feathers |
| PCR | polymerase chain reaction |
| PROD | 7-pentoxoresorufin-0-deethylase |
| tRNA | transfer ribonucleic acid |
| T ₃ | triiodothyronine |
| T ₄ | thyroxine |

List of original papers

This thesis is based on the following publications, which are referred to in the text by their Roman numerals.

- I Liukkonen-Anttila T, Saartoala R & Hissa R (2000) Impact of hand-rearing on morphology and physiology of the capercaillie (*Tetrao urogallus*). *Comp Biochem Physiol* 125A: 211-221.
- II Liukkonen-Anttila T, Putaala A & Hissa R (2001) Feeding of hand-reared grey partridge *Perdix perdix* chicks – importance of invertebrates. *Wildl Biol* 7 (in press)
- III Liukkonen-Anttila T, Putaala A & Hissa R (1999) Does shifting from a commercial to a natural diet affect the nutritional status of hand-reared grey partridges *Perdix perdix*? *Wildl Biol* 5: 147-156.
- IV Liukkonen-Anttila T, Peltokangas P, Raunio H, Pelkonen O & Hissa R (2001) Liver cytochrome P450 enzyme activity of hand-reared and wild grey partridges *Perdix perdix* and capercaillies *Tetrao urogallus*: an exploratory analysis. Manuscript (submitted).
- V Liukkonen-Anttila T, Kentala A & Hissa R (2001) Tannins – a dietary problem for hand-reared grey partridges *Perdix perdix* after release? *Comp Biochem Physiol* (accepted)
- VI Liukkonen-Anttila T, Uimaniemi L, Orell M & Lumme J (2001) Mitochondrial DNA variation and the phylogeography of the grey partridge (*Perdix perdix*) in Europe: from Pleistocene history to implications of introductions. Manuscript (submitted).

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1 Introduction: Gamebird management

1.1 Hand-rearing of gamebirds for release

Hand-rearing of gamebirds has long traditions; as early as ancient Romans and Greeks hand-reared pheasants *Phasianus colchicus* “for table” (Robertson 1997). Hand-rearing of gamebirds is traditionally carried out for game management purposes, and the main aim of stocking and releasing gamebirds has been increasing the size of the game bag. Of the 132 species of partridges, quails and francolins 66 are maintained in captivity, either for quarry or domestic use (Robbins 1992). Despite their economic value, gamebirds have both socially and culturally important status as well.

Besides hunting purposes, hand-rearing and releasing of animals can be used as tools for conservation of endangered species or biodiversity (Nesbitt & Carpenter 1993, Kleiman *et al.* 1994, Cade & Temple 1995). Sixty-eight galliform species out of 256 (27 %) are globally endangered. This includes 42 Phasianidae species (Rands 1992). The proportion of galliform birds from all hand-reared and released animal species is about 39 % (Griffith *et al.* 1989). Many hand-rearing and releasing programmes have been carried out, not for hunting, but to strengthen natural populations or reintroduce species (Angelstam & Sandegren 1981, Paolo & Piodi 1988, Schroth 1991, Starling 1991, Kavanagh 1998). The popularity of hand-rearing and releasing of gamebirds is undisputable: about 20 million pheasants, two million red-legged partridges (redlegs) *Alectoris rufa* (Tapper 1999), and about 50 000 grey partridges *Perdix perdix* (D. Potts, pers. comm.) are annually released solely in the United Kingdom.

Methods for rearing birds in captivity are many, and they can be tested with closely relative, non-endangered, species (Nesbitt & Carpenter 1993). Birds may be machine-reared, parent-reared or reared by a surrogate parent. They may be fostered or cross-fostered as eggs or nestlings into the nest of wild birds. Birds may be released into the wild as juveniles or adults. In “hard” release birds are released immediately after arrival at the releasing site, whereas in “soft” release birds are preconditioned to the releasing site. Released birds may be captive for the first or more generations (Scott & Carpenter 1987). All techniques have an impact on the success of the release.

Captive-rearing is more expensive and also more problematical than translocation (Starling 1991), or “trap and transfer” (Dowell 1992), where animals are moved from areas of high population density to areas with low or zero densities (Griffith *et al.* 1989). There have been some successful translocations, for example those conducted to Perthshire, Scotland, in 1836–1838. The historical translocations of 64 capercaillies *Tetrao urogallus* from Sweden formed the base to a population of about 2 000 birds (Starling 1991). The grey partridge population in the mid-western states of the USA is another result of successful translocations (Potts 1986), whereas every attempt to introduce grey partridge to New Zealand has failed (Westerskov 1958, Potts 1986).

Results obtained from releasing projects of hand-reared grey partridges, pheasants, and capercaillies have not been encouraging. Several studies conducted on these species have clearly shown that the survival of hand-reared individuals is poor after the release into the wild (Angelstam & Sandegren 1981, Hill & Robertson 1988, Panek 1988, Paolo & Piodi 1988, Dowell 1990, Schroth 1991, Brittas *et al.* 1992, Putaala & Hissa 1993, 1998, Leif 1994, Kavanagh 1998). Similar results are also obtained from species other than galliforms, e.g. the lesser white-fronted goose *Anser erythropus* (Lorentsen *et al.* 1999, Markkola *et al.* 1999).

1.2 Factors affecting the survival of hand-reared birds after release

The poor survival of hand-reared birds after release into the wild has been widely observed. The main reason for the high mortality is predation (Angelstam & Sandegren 1981, Robertson 1988, Carroll 1990, Brittas *et al.* 1992, Putaala & Hissa 1993, 1998), but starvation has also been reported as a cause of death (Brittas *et al.* 1992, Putaala & Hissa 1993, Putaala *et al.* 2001).

The quality of hand-reared birds may vary enormously depending on rearing methods. The birds may be vulnerable to predation because of their poorly developed anti-predator behaviour (Dowell 1989, 1990, Anttila *et al.* 1995). Wild-caught spruce grouse *Dendragapus canadensis* are reported to accommodate quickly to captive conditions and they are tame and fearless for human presence (Pendergast & Boag 1971a). The artificial environment of hand-rearing aviaries multiplies the risk for hand-reared birds to get infected by numerous parasites or diseases (Beer 1988, Hielm & Nyberg 1991, Anon. 1994). Further, parasitism may increase the risk for predation, since predators may selectively prey upon birds which carry heavy parasite burdens. This is the case with the red grouse *Lagopus lagopus scoticus* (Hudson *et al.* 1992) and the pheasant (Tompkins *et al.* 2000), the capercaillie, the black grouse *Tetrao tetrix* and the hazel grouse *Bonasa bonasia* (Rätti *et al.* 1999).

Starvation may cause death directly because of a bird's inability to find, recognize and/or process proper food items. Indirectly, foraging of hand-reared birds may take longer and birds may be visible for longer periods, thus predisposing them for predation.

1.2.1 Nutritive constraints

Most galliform chicks feed on invertebrates during their first weeks of life (Rajala 1959, Potts 1986, Dahlgren 1987, Johnson & Boyce 1990, Panek 1992, Itämies *et al.* 1996), from which they usually change their diet gradually to plant food (Ford *et al.* 1938, Dahlgren 1987, Itämies *et al.* 1996, Picozzi *et al.* 1999). Invertebrates are supposed to be essential for the survival and growth of the grey partridge chicks (Southwood & Cross 1969, Potts 1980, 1986, Green 1984, Dahlgren 1987, Panek 1992) and for the development of the plumage (Bagliacca *et al.* 1985). Many of the vegetable proteins may not be available to the chicks even if they were consumed. In comparison to the grey partridge, the redleg chicks are able to grind grass seeds in their gizzards only a couple of days after hatching, a “skill” which in grey partridges takes about ten days to develop (Green *et al.* 1987).

The food amino acids, especially the sulphur-rich methionine and cysteine play an important role in the development of the feathers (Murphy & King 1982, 1984, Bagliacca *et al.* 1985, Murphy *et al.* 1990). Furthermore, abnormal feather growth or raggedness may express a shortage of amino acids and proteins (National Research Council 1984). The feather proteins include relatively more cysteine than other tissues or food proteins (Lucas & Stettenheim 1972, Murphy & King 1982, Murphy *et al.* 1990). The amount of cysteine may affect the feather quality and its tolerance to rubbing or twisting (Murphy & King 1982). Because methionine and cysteine affect the growth, plumage development and growth of the wing feathers, it is reasonable to assume that they have an indirect impact on the flight ability and temperature regulation of a chick as well. Methionine and cysteine concentrations are normally higher in the proteins of insects or fish relative to plant proteins (F.A.O. 1970).

”Animal – Plant Warfare” –theory (Gonzalez & Nebert 1990) assumes that plants synthesise toxic ingredients to avoid herbivory (Levin 1971, Freeland & Janzen 1974), and conversely, animals evolve detoxication mechanisms against plant toxins (Freeland & Janzen 1974, Palo 1987). The most common plant secondary compounds are the phenolics, such as tannins (Levin 1971, Swain 1977). The bitter repellent taste of tannins (Palo *et al.* 1983) may be sufficient to protect plants from herbivory, but the most important physiological property of tannins is their ability to form bonds with protein-containing material. Thus, they may bind with food proteins, which inhibits protein absorption, or they may inactivate digestive enzymes (Mould & Robbins 1981, Robbins *et al.* 1987, Feeny 1992). In general, wild animals avoid eating tannin-containing plants if other plants are available (Bryant & Kuropat 1980, Schwartz *et al.* 1980, Smallwood & Peters 1986, Suomela & Ayres 1994, Ramos 1996).

Hand-reared galliform chicks are usually fed with commercial chicken foods to save time and effort, and to ensure a sufficient supply of nutrients and energy. To gather or raise natural food may be time-consuming and troublesome. Adult hand-reared birds are also usually fed with high-digestible commercial poultry foods, with high energy and low fibre content. However, after being released birds have to cope with a totally different kind of diet – natural food which is coarse, low in nutrients, rich in fibre, and contains plant secondary compounds. Natural food is considered ”low-quality” food, since the utilisation of nutrients may be more difficult than from ”high-quality” commercial poultry food (Miller 1975, Geluso & Hayes 1999). The composition and structure of poultry

foods make it easily digested and very rich in energy. In contrast, the low digestibility of high-fibre diet requires birds to consume large quantities of it in order to obtain sufficient energy (Pendergast & Boag 1971b, Robel & Arruda 1986, Giuliano *et al.* 1996). Daily food consumption is assumed to be lower in commercial low-fibre diet relative to natural high-fibre diet (Moss 1972, Gasaway 1976b).

In previous studies it has been shown that the nutritional status of a bird, especially starvation, affects several blood parameters (Klandorf *et al.* 1981, Jeffrey *et al.* 1985, Ferrer *et al.* 1987, Robin *et al.* 1987). Nutritional status may be a result of hand-rearing and feeding on a commercial diet. Blood composition of wild individuals of several bird species have been studied, and may help in determining "normal" levels of blood parameters for other species (Balasch *et al.* 1976, Alonso *et al.* 1990, González & Hiraldo 1991, Abelenda *et al.* 1993) or even for captive conspecifics (Burke *et al.* 1977b, deGraw *et al.* 1979).

1.2.2 Gastrointestinal tract adjustments to variable diets

The morphology of the gastrointestinal (GI) tract (Fig. 1) varies substantially among birds. The relationship between the structure of the GI tract and diet is widely studied, both across and within taxa.

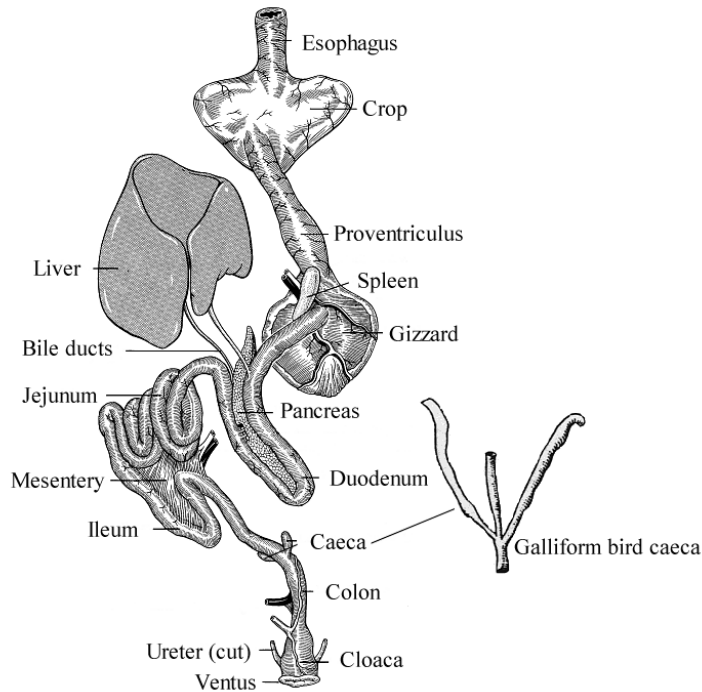


Fig. 1. Gastrointestinal tract of the rock dove *Columba livia* (modified from Proctor & Lynch 1993) and long paired caeca typical for galliform birds.

The development of the caeca and systematic position usually has no correlation, with one exception. In grouse (Tetraonidae) the long caeca are believed to be related to the high fibre content of their diet (McLelland 1989). The seasonal variation in the length of the small intestine and caeca of the Tetraonid birds is known to reflect changes in their diets (Leopold 1953, Pendergast & Boag 1973, Gasaway 1976a, Pulliainen & Tunkkari 1983).

Diet composition, at least increased fibre content in food, is assumed to increase the gut and gizzard size in some galliform species (Moss 1972, 1974, Savory & Gentle 1976a,b, Paganin & Meneguz 1992, Starck & Kloss 1995) and also in some waterfowl (Miller 1975, Kehoe & Ankney 1985). The most spectacular example of the impact of hand-rearing on the gut, is the disparity between wild and hand-reared birds of the same species. Hand-reared birds have lighter gizzards and shorter caeca and small intestine than their wild counterparts at least in the red grouse (Moss 1972), the willow grouse *Lagopus lagopus lagopus* (Hanssen 1979a), the pheasant (Majewska *et al.* 1979), the mottled duck *Anas fulvigula* (Moorman *et al.* 1992), and the grey partridge (Putala & Hissa 1995). Feeding of captive willow grouse with commercial chicken food is known to generate a gut microflora similar to the one in domestic fowl *Gallus domesticus*, and unlike the one in wild willow grouse (Hanssen 1979b). The adjustment time of the GI to new feeding conditions may range from weeks to months (Hanssen 1979b, Moss 1989, Redig 1989).

1.2.3 Temperature regulation in chicks

Chicks of precocial birds, such as galliforms, are downy at hatching. They are able to follow their parents and find their food shortly after hatching. However, their body temperature follows the ambient temperature, and they respond to cold mostly behaviourally (by getting under a parent, or huddled together). Chicks are still dependent on parental warming weeks after hatching (Spiers *et al.* 1974, Marjoniemi *et al.* 1995), but this dependence decreases gradually when the temperature regulation develops (Aulie 1976, Boggs *et al.* 1977, Pedersen & Steen 1979). The impact of weather on chick survival may be direct or indirect. Cold and rainy weather shortens the time chicks may spend on feeding (Potts 1986), or it may decrease the amount of insects available (Green 1984, Potts 1986).

In several galliform species a chick's body temperature is on average 4–5 °C lower than that of adult birds (Spiers *et al.* 1974, Aulie 1976, Myhre & Steen 1979, Hissa *et al.* 1983b, Jurkschat *et al.* 1989, Modrey & Nichelmann 1992, Marjoniemi *et al.* 1995), which may be considered a strategy for reducing the thermal gradient between the chick and its environment (Hissa *et al.* 1983b, Pedersen & Steen 1979). Body temperature control is poorly developed in newly hatched chicks, resulting partly from incomplete plumage and subsequent insulation development (Ricklefs 1979, Hissa *et al.* 1983b, Marjoniemi *et al.* 1995). Wetting of the plumage increases the cooling rate sharply. The plumage is fully water-resistant later than its thermal insulation has developed (Marjoniemi *et al.* 1995).

Chicks of precocial birds need muscles for both locomotive and thermogenic purposes soon after hatching (Ricklefs 1979, Hohtola & Visser 1998). In the beginning, the most important heat producing tissues are the leg muscles (Whittow & Tazawa 1991, Marjoniemi & Hohtola 1999). Pectoral muscles grow faster than leg muscles, and they are activated for shivering thermogenesis already in chicks only a few days old (Aulie & Moen 1975, Aulie 1976, Marjoniemi *et al.* 1995). Grey partridge (Marjoniemi *et al.* 1995) and pheasant (Gdowska *et al.* 1993) chicks are assumed to reach adult-like cold resistance at the age of 30 days.

1.2.4 Plumage and primary growth

The plumage of a bird at a certain point in time is only one in a series of plumages it has during its lifetime. However, some feathers are sometimes left unmoulted, and the plumage may contain feathers representing two or even three different developmental stages (Dwight 1900). The downy plumage starts developing in a 15-day-old embryo. This plumage does not contain any structural feathers, although the development of primaries (Fig. 2) starts before hatching (Lucas & Stettenheim 1972).

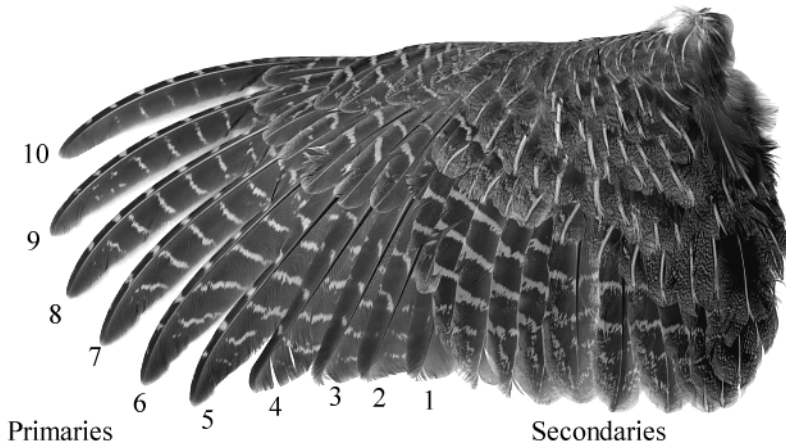


Fig. 2. The wing feathers (primaries and secondaries) of the grey partridge. Numbering of primaries starts from the innermost feather, i.e. closest to body is the P1 primary.

Galliform chicks usually moult twice in their first summer. In the first, postnatal moult, most of the downs are replaced by feathers. The first plumage, which contains feathers, is called the juvenile plumage, and its development starts from the outermost wing feathers at the age of ca. one week (Dwight 1900, McCabe & Hawkins 1946, Lucas & Stettenheim 1972). Also insulation increases as a result of this moult (McNabb & McNabb 1977). In the postjuvenile moult the juvenile plumage is replaced by the postjuvenile plumage. This moult is incomplete, because as typical of galliform birds, the two outermost primaries are not changed (Dwight 1900, McCabe & Hawkins 1946, Thompson & Taber 1948, Lucas & Stettenheim 1972, Stenman & Helminen 1974).

The postjuvenile plumage is kept over the first winter. Before the breeding season a partial, prenuptial moult, occurs. This moult keeps to the neck and head. After the chicks have hatched a complete postnuptial moult of breeders occurs, where the tail and wing feathers are renewed. In this moult the two outermost primaries are also moulted (Dwight 1900, Lucas & Stettenheim 1972). Because galliform birds do not attain in complete adult plumage before their second winter, this characteristic have been widely used in the age determination of these birds (Leopold 1939, McCabe & Hawkins 1946, Pulliainen 1974, Stenman & Helminen 1974, Malinen 1998).

Galliform birds usually have ten primaries (Fig. 2), which are named P1–P10 beginning from the innermost primary (P1), the one closest to body (Thompson & Taber 1948, Stenman & Helminen 1974, but see Malinen 1998 for opposite naming). The growth and renewal of the primaries occur outwards from P1 to P10, but P1 grows and is lost before the outermost primary is completed (Dwight 1900, Stenman & Helminen 1974). The moulting process is assumed to be faster in wild birds relative to hand-reared birds (McCabe & Hawkins 1946).

1.2.5 Energy reserves and flight ability

Flight ability, both take-off and sustained flight, of hand-reared birds may be reduced (Robertson *et al.* 1991, Robertson *et al.* 1993, Putaala *et al.* 1997) compared to wild birds, as a result of reduction of certain morphological and physiological characteristics connected with the flight. Rearing aviaries are usually of relatively small size, which is not encouraging to flight exercise. In fact, flight may not be desirable, since it increases the risks of injuries to the birds if they fly into the cage wires. Limited exercise, however, is known to cause pectoral muscle atrophy in birds (Majewska *et al.* 1979, Piersma 1988, Gaunt *et al.* 1990, Chaplin *et al.* 1997).

Disparities in muscle fibre composition (Parker & George 1975, Viscor *et al.* 1992) and metabolism (Pagés & Planas 1983, Chaplin *et al.* 1997) are reported to occur between birds exercised or restrained. In hand-reared birds the oxidative capacity of muscle may be reduced (Putaala & Hissa 1995), as well as the capacity of muscle to reserve energy in the form of glycogen (Majewska *et al.* 1979, Putaala & Hissa 1995). Species differences in muscle size are well known: good flyers are known to have bigger hearts (Viscor *et al.* 1985) and pectoral muscles (Hartman 1961) than moderate flyers. Some blood parameters may also reveal flight activity of wild birds. In homing pigeons *Columba livia f. dom.*, haematocrit, plasma protein and triglyceride levels are all known to decrease (Bordel & Haase 1993), and uric acid level to increase (George & John 1993) in flown birds when compared with unexercised birds. Reduction in thyroxine (T₄) and triiodothyronine (T₃) levels in blood is reported in flown homing pigeons (George & John 1992).

1.2.6 Genetic adaptation

According to O'Brien and Mayr (1991) subspecies include "individual populations that share a unique geographic range or habitat, a group of phylogenetically concordant phenotypic characters, and a unique natural history relative to other subdivisions of the species". Subspecies interbreed when in contact, but they should be conserved separately as they represent an important component of the genetic diversity of a species.

Species may be divided into subspecies based on one single or a limited number of morphological characteristics (Potts 1986, Shields & Wilson 1987b, Van Wagner & Baker 1990, Questiau *et al.* 1998, Bensch *et al.* 1999, Holder *et al.* 2000). According to O'Brien (1994a) subspecies may also be distinguished by genetic variation, but the morphological classification and genetic differentiation may not be strictly comparable.

Many species consist of geographically and genetically distinct populations. Separate populations often meet in narrow hybrid zones where they may mate (Barton & Hewitt 1985, Hewitt 1988). Cross-breeding, either occurring between species or subspecies, produces hybrids (Hewitt 1988). In rare species the tendency to hybridise may increase when conspecific mates are lacking (Short 1969). Species differ in their propensity to hybridise, for example, ducks and geese are known for their tendency to hybridise (Grant & Grant 1992). According to Haldane's rule (Haldane 1922) hybrid offspring may suffer from reduced viability or fertility, but over 10 % of recognized avian species have been estimated to have produced viable offspring (Grant & Grant 1992). Hybridisation may lead to decreased fitness due to disruption of adaptive gene complexes and even a short-term reduction in fitness may emphasise the extinction risk in a small population (Templeton 1986). Gene flow prevents, and genetic drift enhances, local adaptation and speciation. Under natural conditions maladaptive traits in marginal (sink) areas can be explained by immigrants from central populations, living in more favourable (source) areas (e.g. Dhondt *et al.* 1990, Dias 1996). In artificial situation maladaptive traits may be introduced into natural populations when hand-reared birds are released into the wild.

In 1957 Professor Lauri Siivonen (1957) discussed the reasons for the grey partridge population crash in Finland. He considered the possibility that imported birds of southern origin might have weakened the genetic adaptation of native partridges to the hard Finnish winter conditions.

1.3 The gamebird species studied

1.3.1 The grey partridge

The grey partridge is divided into eight subspecies, based mainly on the plumage colour (VI, Table 1, after Potts 1986): *P. p. hispaniensis*, *P. p. italica*, *P. p. armoricana*, *P. p. sphagnetorum*, *P. p. perdix*, *P. p. lucida*, *P. p. canescens*, and *P. p. robusta*. The existence of additional three subspecies *P. p. belesiae*, *P. p. galliae* (France) and *P. p. hilgerti* (Germany) is discussed (Birkan & Jacob 1988). The species has its origin in steppes, but has taken advantage of cultivated farmland in the temperate zone. Its distributional range

covers most of Europe, Asia Minor, and Caucasus from the northern parts of the Caspian Sea to Central Asia. In Europe its distribution covers the continent excluding Iceland and the northernmost parts of Fennoscandia and Russia (Potts 1986).

In Finland, the grey partridge lives at its northernmost distribution range, the northern border of which crosses Finland from the Oulu region to the southeastern part of the country (Väisänen *et al.* 1998). Its highest numbers can be found in South Ostrobothnia, where in the winter of 1999/00 about 9 200 birds were counted (J. Bisi, pers. comm.). In Finland, the grey partridge is classified as a near-threatened species (Rassi 2000).

The grey partridge is believed to have arrived in Finland in the beginning of the 1800's from the east via the Karelian isthmus (Kivirikko 1948), but entry may have occurred as early as in 1690 (Merikallio 1958). The first introduced birds in 1750 (Merikallio 1958) were probably of Swedish origin. According to early Finnish ornithological literature and handbooks, and categorisation by morphological characteristics, the Finnish population represents subspecies *P. p. lucida*, while the nominate *P. p. perdix* is a more southern and western subspecies (Westerskov 1964, Cramp & Simmons 1980, Potts 1986).

The number of the grey partridges in Finland has dramatically decreased during past decades. In the 1950's the population size was estimated to be 15 000 pairs (Merikallio 1958), but in the early 1990's there were only 4 000 pairs (Koskimies 1992). The population decline in the whole distributional area is estimated to be about 80 % since the 1950's. Additionally, the distribution area has become patchy (Potts 1986).

The worldwide decline in the numbers of the grey partridge is extremely well documented (for review, see Potts 1986). The main reason for the worldwide population crash is considered to be the changes in agriculture practices (Rands 1985, Potts 1980, 1986, Fog 1988, Matteucci 1988, Olech 1988, Panek 1992). The grey partridge uses open ditch banks to find cover and nesting sites, as well as plant material for adults and invertebrates for chicks (Pulliainen 1965, Potts 1986, Panek 1992, Sotherton 1992). Adult birds feed mainly on weed seeds (hemp-nettle *Galeopsis* spp., pale persicaria *Persicaria lapathifolia*, knotgrass *Polygonum aviculare*, black-bindweed *Fallopia convolvulus*, fat-hen *Chenopodium album*), grains, and shoots (oats *Avena sativa*, barley *Hordeum vulgare*, rye *Secale cereale*, wheat *Triticum aestivum*) (Potts 1970, Pulliainen 1965, 1984). Chicks feed on a variety of invertebrates (Ford *et al.* 1938, Potts 1986, Itämies *et al.* 1996); most preferred are leaf-hoppers (Delphacidae) and beetles (Coleoptera) (Itämies *et al.* 1996). Intensive farming with large monotonous, subsurface drained fields, hard machinery and use of pesticides have reduced the survival and breeding success of the grey partridge (Potts 1980, 1986, Panek 1992, Sotherton 1992) by reducing the quantity and diversity of invertebrates. Indirectly, the use of pesticides has reduced the quality and quantity of weeds, which in turn has decreased the numbers of invertebrates feeding on these plants (Potts 1986, Panek 1992, Sotherton 1992). In addition to this modern farming has changed the habitat more unsuitable for partridges – and to some extent more suitable for predators (Potts 1986).

1.3.2 *The capercaillie*

The capercaillie breeds in Eurasian coniferous taiga forests from Scandinavia to Central Siberia (Cramp & Simmons 1980). In Finland it is absent only in the northernmost parts of the country. Its distribution follows the distribution of the Scots pine *Pinus sylvestris*, from the southern coast to Kittilä and Inari. The lowest densities can be found in the Åland Islands, on the archipelago, and in Southern Lapland. The highest densities are found in Ostrobothnia and in Kainuu near lake Oulujärvi (Väisänen *et al.* 1998). The population size of the capercaillie in Finland is about 750 000 adult birds (Lindén 1996).

The capercaillie is often taken as an indicator for old and mature forests (Storch 1993, but see Helle & Helle 1991, Picozzi *et al.* 1992), preferring mature spruce *Picea abies* or pine forests, mires or bogs. It also prefers mixed to monotypic forests. The optimal area is mosaic-like diverse, providing the capercaillie with proper environment throughout the year (Helle *et al.* 1990, 1994, but see Helle & Helle 1991). The diet of the capercaillie consists almost entirely of berries and leaves of cowberry *Vaccinium vitis-idaea*, bog bilberry *V. uliginosum*, bilberry *V. myrtillus*, crowberry *Empetrum nigrum* and cloudberry *Rubus chamaemorus* in the autumn. In September, it starts to feed on pine needles, and becomes monophagous by December (Pulliainen 1978, 1981). Mostly browsed pines are often injured by fire (Lindroth & Lindgren 1950). Chicks feed mainly on invertebrates (Rajala 1959, Picozzi *et al.* 1999), and young birds may feed on insects in the autumn, although their proportion of the diet is only about 0.1–0.3 % (Pulliainen 1979).

The declining number of capercaillie is a general phenomenon in Europe (Angelstam & Sandegren 1981, Rolstad & Wegge 1989, Helle & Helle 1991, Schroth 1991). The population in Finland has decreased by about 70 % during the last three decades and the distribution area has become patchy. The main reason for this decline is considered to be forest fragmentation, and decreasing number of large old-growth forests (Lindén & Rajala 1981, Lindén & Pasanen 1987, Storch 1991, Lindén *et al.* 2000). Effective predation (Helle *et al.* 1999), and also effective hunting of adult birds, especially hens, may have severely influenced the population size (Lindén 1981).

2 Aims of the study

Grey partridge research has a long history at the University of Oulu. Former professors in Zoology, Lauri Siivonen, Seppo Sulkava and Erkki Pulliainen published several papers on the ecology of this species (Siivonen 1957, Sulkava 1964, Pulliainen 1965, 1968a,b,c, 1984). Since 1990 the wide field of grey partridge research, directed by Professor Raimo Hissa, has included studies on thermoregulation (Hohtola *et al.* 1991, Marjoniemi *et al.* 1995, Putaala *et al.* 1995, Marjoniemi & Hohtola 1999), feeding of broods in the wild (Itämies *et al.* 1996), morphological, physiological and behavioural disparities between wild and hand-reared birds (Putaala *et al.* 1993, Anttila *et al.* 1995, Putaala & Hissa 1995, Pyörmilä *et al.* 1998), and the survival and breeding success of hand-reared grey partridges after release (Putaala & Hissa 1993, 1998).

The capercaillie is also a well-studied species at the University of Oulu. Professor Pulliainen conducted several studies on the ecology of the capercaillie (Pulliainen 1978, 1979, 1981, Pulliainen & Tunkkari 1991). Professor Hissa and his collaborators have widely studied the temperature regulation and hormonal cycle of the capercaillie (Hissa *et al.* 1983a,b, 1990, Marjakangas *et al.* 1984, Rintamäki *et al.* 1984, Saarela *et al.* 1990).

The poor survival of hand-reared gamebirds after release into the wild is assumed to be at least partly a result of the "poor quality" of released birds. In the ecophysiological part of this study, wild and hand-reared birds were compared with each other to find possible morphological and physiological disparities between them (I, IV). Feeding trials were conducted to examine the effects of the animal food on chick development (II), effects of an abrupt change in diet (III), and effects of a certain plant secondary compound – tannin – (V), on the nutritional status of the grey partridge. Finally, grey partridge populations throughout Europe were examined using mitochondrial DNA as a tool to find possible genetic explanation for the poor success of introductions (VI).

3 Material and methods

3.1 The birds studied

This study was conducted on both wild and hand-reared birds of two different galliform species (for numbers of birds and their origins, see Table 1). Among galliforms the grey partridge is a good study species, since hand-rearing and releasing of this species has long traditions. The capercaillie has arised a great deal of interest among scientists and hunters, since it is the largest galliform gamebird in Europe and occupies both an economic (game) and conservation (biodiversity) value. Hunters in Finland respect the capercaillie most of the grouse, and the grey partridge of the field quarry (Leinonen & Ermala 1995). The capercaillie is no longer permitted to be hand-reared in Finland.

Table 1. Origins and numbers of birds used in this study.

| Work/birds | Origin | N |
|---------------------|-------------------|--------|
| I: Capercaillie | Hand-reared/ Wild | 20/11 |
| II: Grey partridge | Hand-reared/Wild | 60/7 |
| III: Grey partridge | Hand-reared | 54 |
| IV: Grey partridge | Hand-reared/ Wild | 5/4 |
| Capercaillie | Hand-reared/ Wild | 3/8 |
| IV: Grey partridge | Hand-reared | 22 |
| VI: Grey partridge | Hand-reared/ Wild | 68/159 |

Hand-reared grey partridges were raised at the Zoological Gardens (University of Oulu, Department of Biology), and the hand-reared capercaillies were either from the Zoological Gardens or from the Meltaus Research Station of the Finnish Game and Fisheries Research Institute. A more detailed description of the rearing methods is given by Putaala (1997). This work was reviewed and approved by the Committee of Animal Experimentation at the University of Oulu (licences 32/93 and 1/96).

3.2 Morphological features

Morphological measurements were taken to reveal the differences between wild and hand-reared capercaillies (I), as well as between grey partridges fed with different diets (II, III, V). Body mass of birds, mass of gizzards and livers and lengths of small intestine and caeca were measured. The gizzard was weighed without its inner cuticle. Small intestine and caeca were measured straightened but not stretched on a flat surface.

To be able to study the potential flight capacity disparities between wild and hand-reared capercaillies, heart, and pectoral muscle were weighed (I). As an indicator of growth and capability to fly, the lengths of primary feathers were measured from grey partridge chicks given different diets (II).

3.3 Blood sampling

Blood samples (1–1.5 ml) were taken from the *vena brachialis* of grey partridge using needles (23 G) and syringes containing either 20.8 % EDTA (III) or heparin (V) as an anticoagulant. From the capercaillies, blood was drained into heparinised tubes after decapitation (I).

Blood parameters, which may reflect starvation or differences in the diet were chosen in works I and III (Halliwell 1981, Lewandowski *et al.* 1986). Haemoglobin (Hb) and haematocrit (Hcr) were analysed from whole blood, glucose, triglycerides, total protein, uric acid, T₃ and T₄ from plasma using commercial kits.

Total protein was analysed to reveal protein degradation as a result of tannin in the diet (V). Effects of tannin on plasma amino acids were estimated by analysing concentrations of alanine, glycine, methionine, ornithine and proline, and on some other nitrogenous compounds by analysing amino adipic acid, ammonia, urea and 3-methylhistidine concentrations. Total protein concentration was assayed with a commercial kit, and amino acids and nitrogen containing compounds with the ion-exchange chromatography method.

3.4 Temperature regulation

A thermocouple (32 gauge) was inserted through the cloaca into the rectum of the grey partridge chicks, whereafter the chicks were transferred into a chamber of 0 °C. The cooling speed of the chicks was measured at the age of 1, 7, 11, 15, 18 and 21 days. The body temperature was monitored for 20 minutes or until it dropped to +25 °C in 1-day-old chicks, to +30 °C in 7- and 11-day-old chicks, to 33 °C in 15-day-old chicks, and to +35 °C in 18-day-old chicks. At the age of 21 days the body temperature was expected to remain above +35 °C for 20 minutes in every chick. Also wild chicks were exposed to cold at the age of 7 days.

3.5 Nutritional status

To study the nutritional status of grey partridges, assimilation efficiency (metabolisable energy coefficient = MEC) was estimated, which in turn required close monitoring of food consumption and excretion (III). Daily gross energy (GE) intake and excretory energy (EE) were determined using a bomb calorimeter, and the metabolised energy (ME) amount was calculated ($ME = GE - EE$). The assimilation efficiency was then obtained from $MEC = ME/GE$ (Lindén 1984a, Nikiforov 1992).

Food consumption and excretion were monitored in the study of the effects of quebracho tannin on the grey partridge (V). In this work the nitrogen and tannin contents of the excreta were studied assuming that they might indicate increased protein excretion. Tannin content of the excreta was estimated using the acid butanol method of Porter *et al.* (1986), and nitrogen content with Elemental Analyzer EA 1110 CHN.

Disparities in diets may be expressed in the chemical composition (water, protein, fat, ash) and glycogen content of certain tissues. The chemical composition of the pectoral muscle (*musculus pectoralis major*), leg muscle (*m. iliotibialis cranialis*), heart and liver of hand-reared and wild capercaillies (I) was estimated by the method described by Hissa *et al.* (1990). Glycogen content was analysed using the method of Lo *et al.* (1970) and the protein content of the mitochondrial fractions with the method of Lowry *et al.* (1951).

3.6 Power production

Of the earlier mentioned parameters, the mass of heart and pectoral muscle, as well as the chemical composition, glycogen, and protein contents of the tissues may be of value in estimating the birds' ability for power production and flight. In addition to these, the cytochrome-c oxidase (COX) activities of pectoral muscle and heart (from both the homogenate and the mitochondrial fraction) were analysed from wild and hand-reared capercaillies (I), because cytochrome-c oxidase activity can be considered an indicator of the aerobic capacity of a tissue. The method originally described by Rafael *et al.* (1970) and later modified by Saarela *et al.* (1989) was used.

3.7 Detoxication mechanisms

Wild and hand-reared grey partridges and capercaillies were used to study both inter- and intraspecific differences in the hepatic detoxication ability (IV). Connected with this work, the effect of time spent in sampling on the hepatic enzyme activity was examined. The activities of three different easily induced cytochrome P450 (CYP) enzymes, 7-ethoxyresorufin-0-deethylase (EROD), 7-pentoxyresorufin-0-deethylase (PROD), and coumarin-7-hydroxylase (COH) were analysed. EROD and PROD activities were analysed using the method of Burke *et al.* (1977a), and COH activity using the method of Aitio (1978). The activities of these monooxygenases in mammalian liver are catalysed by CYP1A, CYP2B and CYP2A enzymes, respectively (Mattson *et al.* 1998). The same

enzymes were used to examine the detoxication mechanisms in grey partridges after a change in the diet from commercial to either natural or tannin-containing commercial food (V).

3.8 Mitochondrial DNA

Maternally inherited, haploid mitochondrial DNA (mtDNA) control region 1 (CR 1) was used to study the genetic background of grey partridge populations in Europe (VI). Fresh or museum samples (feathers, tissue, blood, eggs) were collected from several locations. Finnish wild populations were sampled from four separate areas: eastern Uusimaa, southern Häme, South and North Ostrobothnia (Oulu region). Finnish hand-reared birds were sampled from two different private farmstocks; Lars Ahlström (the Jokiniemi Mansion, Ruotsinpyhtää), and Veijo Mikkilä (Lapua). Samples from wild populations were received from Austria, Bulgaria, England, Estonia, France, Germany, Greece, Ireland, Italy, Kazakhstan (Fig. 3), Poland, Russia and Sweden. Gamefarm samples were received from Hungary, Italy, and Sweden, and museum samples from Estonia and Latvia.



Fig. 3. Feather samples could be received like these from Kazakhstan – fastened in a notebook.

Total DNA was extracted using separate methods for feathers (modified Chelex-method, Walsh *et al.* 1991), blood and other tissues (standard phenol-chloroform method, Sambrook *et al.* 1989, and PureGene procedure). MtDNA was extracted from the embryonic plates in eggs using the method of Tamura and Aotsuka (1988), modified by

Kvist *et al.* (1998). Even though hardened feather quills seem relatively poor source of DNA, they are less problematic than blood with respect to nuclear contamination (Sorenson & Quinn 1998).

DNA-extraction was followed by the PCR. Amplified PCR product was purified from 1 % agarose gel using polyester plug spin inserts (Glenn & Glenn 1994). Sequencing was carried out using the automatic ABI377 DNA sequencer.

The primers for whole CR were designed based on the conserved regions located in the tRNA^{Glu} and tRNA^{Phe} genes of the chicken *Gallus gallus* (Desjardins & Morais 1990) and the quail *Coturnix coturnix* (Desjardins & Morais 1991) available in GeneBank. After sequencing of CR, more specific primers were designed. The forward primer for the first 410 nucleotides of the control region 1 (downstream from tRNA^{Glu}) was LPPGLU (5'CACTGTTGTTCTCAACTACAGG) and the reverse primer was H414 (5'GGTGTAGGGGGAAAGAATGGG).

4 Results

4.1 Body mass and morphological characteristics of organs

Wild capercaillies tended to be heavier than hand-reared birds, but the difference was not significant (I, Table 2). Grey partridges fed with natural food lost body mass dramatically after the change in diet (III, Fig. 1; V, Fig. 1b). In work III they could regain mass 7–10 days after the change in diet, but not in work V. Tannin added to food had no significant effect on body mass (V, Fig. 1b).

The mean body mass of newly hatched grey partridge chicks was 9.2 ± 0.1 (SE) grams (II, Fig. 1, Table 2). Chicks fed an insect-rich diet were significantly heavier than chicks fed a low-insect diet, from the age of three days until the age of 21 days. Further, they were significantly heavier than the chicks fed a fish diet, from the age of six days until the age of 18 days (II, Fig. 1). No difference was found in body mass between low-insect diet and fish-fed chicks. At the age of one week, wild chicks seemed heavier than chicks fed a low-insect diet, but their body mass was similar to those fed an insect-rich or a fish-diet. At the age of eight weeks chicks fed an insect-rich diet were still heavier than chicks fed a fish diet, but at the age of thirteen week chicks did not differ from each other any more in body mass (II, Table 2).

The gut dimensions of wild capercaillies differed from those of hand-reared birds. Wild birds had heavier gizzards and livers and longer small intestines and caeca (I, Table 2). Hand-reared grey partridges fed natural food had heavier gizzards than birds fed either control or tannin-laced food (III, Table 7; V, Table 1). Tannin-fed grey partridges had longer small intestines than birds fed either control or natural food (V, Table 1).

The hearts of wild capercaillies were heavier than those of the hand-reared birds (I, Table 2). Hand-reared capercaillie males had heavier pectoral muscles than wild males, but in females the result was the opposite.

4.2 Primaries

Primary development varied among diet groups. At the age of one week, wild chicks had longer primaries than hand-reared chicks in general (II, Table 3). Only two chicks in the insect-rich diet group had primary P8 measurable. Primaries were longest in chicks fed an insect-rich diet (II, Tables 3, 4) until the age of 21 days. Fully developed primaries could be found earlier in the chicks that were fed insect-rich diet than other chicks. Chicks fed an insect-rich diet had at least five completely developed juvenile primaries at the age of 28 days, while chicks fed a low-insect diet or a fish diet had only three. At the age of 13 weeks every chick had fully developed P10 primaries, and no difference in their length was found among diet groups.

4.3 Plasma analysis

Hand-reared capercaillies had a higher uric acid and T_4 concentration in plasma (I, Table 3). No differences were found between birds fed natural and control food in work III (Table 6). No effects of tannin were seen in amino acid or nitrogenous compound concentrations (V, Fig. 2). However, birds fed natural food had elevated alanine concentration in plasma in comparison to control or tannin food fed birds (V, Fig. 2).

4.4 Cooling rate

During the first day of life the cooling rate of chicks in different diet groups did not differ from each other (II, Fig. 2). On the seventh and eleventh day, chicks fed an insect-rich diet had a lower cooling rate than chicks fed a low-insect diet or a fish diet. Chicks fed a low-insect or a fish diet did not differ from each other. The response of wild chicks to cold was similar to that of chicks fed an insect-rich diet at the age of seven days. At the fifteenth day the cooling rate was similar in each diet group the first eight minutes, but the chicks fed an insect-rich diet could stay longer in the experiment. At the eighteenth day the cooling rate varied substantially, and differences among groups were not unambiguous. However, the chicks fed a fish diet seemed to cool faster than other chicks (II, Fig. 2). At the age of 21 days chicks fed an insect-rich diet could keep their body temperature relatively constant. The chicks fed a fish diet had significantly lower initial body temperature and they seemed to cool faster than other chicks.

4.5 Food consumption, excretion, and assimilation efficiency

Birds fed natural food ate more than control birds during the feeding trial excluding the first week in work III (Table 5), but there was no difference between groups in work V (Fig. 1a). Tannin had no effect on the amount of food eaten (V, Fig. 1a).

In work III the diet groups differed in the amount of produced excreta during the feeding trial, although the results were not unambiguous (Table 5). The amount of food was calculated based on fresh weight, and MEC based on the dry weight of food. Based on the dry weight of the food, the test group consumed less food than the control group (III, Table 5), depending on the high water content of the shoots of barley (III, Table 1). The change in diet decreased the GE, ME and MEC, and increased the EE in the test group (III, Table 5).

The nitrogen content of intestinal excreta was higher in natural than in control or tannin groups, but in caecal excreta the control group showed the highest nitrogen content (V, Figs. 3a, 4a). The tannin content of both intestinal and caecal excreta was highest in the tannin group (V, Figs. 3b, 4b).

4.6 Biochemical tissue analysis

Hand-reared and wild capercaillies differed from each other in liver composition. The difference was significant, showing higher water content and lower fat, protein and ash content in wild birds compared with hand-reared birds (I, Table 5). No difference was found in the chemical composition of pectoral, leg and heart muscle between wild and hand-reared birds (I, Table 5).

Cytochrome-c oxidase activities of the homogenate and mitochondrial fraction of pectoral muscle and heart were lower in hand-reared birds compared with wild birds. In hand-reared birds the mitochondrial fraction of pectoral muscle showed a lower oxidative enzyme activity than in wild birds but in heart the difference was not significant (I, Figs. 1a, 1b). The protein content of the mitochondrial fraction of pectoral muscle and heart was higher in wild capercaillie compared with the hand-reared birds. Glycogen content was not different between wild and hand-reared birds (I, Table 4).

4.7 Hepatic enzyme activity

Wild capercaillies had lower EROD activity than hand-reared capercaillies, but no interspecific difference could be detected in the activity of this enzyme. Both capercaillies and grey partridges had similar PROD activity, but hand-reared birds had higher enzyme activity than wild birds of either of the species. Capercaillies had lower COH activity than grey partridges (IV, Table 1), but the enzyme activity was similar in both wild and hand-reared individuals of either of these species.

The quebracho tannin added in the food of hand-reared grey partridges did not affect the hepatic enzyme activity (V, Table 2). Postmortal decrease in the hepatic enzyme activity in grey partridges was obvious (IV, Fig. 1). After 30 minutes the enzyme activity had lowered by about 34–69 % depending on the substrate used.

4.8 Variation in the CR1 sequence

The CR of the mtDNA of the grey partridge consisted of 1151 nucleotides (VI). Two basic mtDNA lineages were detected, hereafter named “eastern, E” and “western, W”, with a disparity of 25 nucleotides (2.2 %). There was a difference of 14 nucleotides (3.6 %) in the CR1 between the lineages. The read 390 nucleotides of the sequences included 49 (12.6 %) variable sites, of which 24 (49.0 %) were phylogenetically informative. One insertion/deletion was found in position 77 (VI, Appendix). From the 227 analysed grey partridges 45 CR1 haplotypes were identified (VI, Table 3, Fig. 2, Appendix). Both lineages included one basic haplotype (VI, Table 3, Fig. 2).

In both lineages the haplotype diversity (h) among populations varied greatly, from 0.00000 (GE1) to 0.90000 (GE2) (VI, Table 4). The lowest nucleotide diversity (π) was 0.00000 (GE1) and highest 0.01902 (BUL and IRE). θ_s values estimated from the number of polymorphic nucleotide sites per nucleotide, were in concordance with the values of π (VI, Table 4). Within the western lineage, the maximum Jukes-Cantor (1969) pairwise genetic distance was found between W19 from England and W21 from an Italian farm. Within the eastern lineage the maximum distance was found between E9 from Sweden and E14 from Bulgaria, and from E6, Southern Finland, as well as between E14 and E6. For the whole data the maximum distance was found between W17 from England and E13 from Bulgaria.

4.9 Population structuring and gene flow

According to Excoffier *et al.* (1992) the analysis of molecular variance (AMOVA) produces estimates reflecting the correlation of haplotypic diversity at different levels of hierarchical subdivision. Thus, AMOVA was conducted based on subspecies, lineages, and populations with or without the subspecies as a structural variable (VI, Table 5). Based on this, the genetic variation depended rather on these qualifiers than on the individual variation. Pairwise ϕ_{ST} values between populations (VI, Table 6) showed, that most populations were significantly differentiated from each other. A surprising result was that the Irish population did not differ from geographically distant Finnish (FI1), Greek or Bulgarian populations. Pairwise ϕ_{ST} values between subspecies showed that birds from the expected areas of subspecies *P. p. sphagnetorum* and *P. p. perdix* did not differ from each other (Table 2).

Population pairwise ϕ_{ST} values were also reflected in gene flow estimates (VI, Tables 6, 7). In most cases the gene flow estimates were less than one individual per generation between populations. Estimated gene flow tended to be high for populations, which were not significantly differentiated from each other. The geographical distance and gene flow between populations were significantly and negatively correlated.

Table 2. Pairwise Φ_{ST} values between expected subspecies in grey partridge. NS = non-significant, otherwise $P < 0.001$.

| Subspecies | <i>P. p.</i> <i>lucida</i> | <i>P. p.</i> <i>perdix</i> | <i>P. p.</i> <i>armoricana</i> | <i>P. p.</i> <i>hispaniensis</i> | <i>P. p.</i> <i>italica</i> |
|---------------------------|-------------------------------|-------------------------------|-----------------------------------|-------------------------------------|--------------------------------|
| <i>P. p. perdix</i> | 0.81427 | | | | |
| <i>P. p. armoricana</i> | 0.79596 | 0.49237 | | | |
| <i>P. p. hispaniensis</i> | 0.80674 | 0.42195 | 0.71187 | | |
| <i>P. p. italica</i> | 0.78507 | 0.51526 | 0.60850 | 0.39514 | |
| <i>P. p. sphagnetorum</i> | 0.82264 | -0.01444 NS | 0.95720 | 0.73818 | 0.74076 |

4.10 Changes in the population size

In the eastern lineage of the grey partridge the observed distribution of pairwise genetic distances followed that of an expected distribution under population expansion (VI, Fig. 3). This model was also supported by the star-like minimum-spanning network (VI, Fig. 2), with one basic and several closely related haplotypes. Also Tajima's D , which in addition to assessing neutrality of the used marker reflects demographic changes in the past in relation to the population size (Tajima 1989), was significantly negative. On the other hand, the significantly positive D found in Finland (F11) may express the finding of both lineages in this population (VI).

The western lineage did not follow the models for either expansion or equilibrium (VI, Fig. 3). However, the minimum-spanning network of the western lineage was star-like as in the eastern lineage, and Tajima's D was significantly negative. The significantly negative D found in England (EN2) may have resulted from a past population bottleneck and expansion (VI, Table 4).

4.11 Patterns of phylogeography

The main western (MW) haplotype of the grey partridge was widely found in Europe (VI, Table 3, Fig. 1). The rarer haplotypes were mainly found in a single population each, except for the W17 haplotype. This haplotype was found from Finland and Germany (wild), from Hungary and Italy (farm), and from the Latvian Museum of Natural History, Riga. The Pyrenean population contained one main type (W9) and five other haplotypes, and the Italian wild population two deviant haplotypes (W2, W3). The main eastern (ME) haplotype (VI, Table 3, Fig 1) was found in Bulgaria, Finland (F11), Greece, and Ireland. Eastern haplotypes were found in Estonia, Kazakhstan, Russia, and on the Island of Öland, Sweden.

Among the western populations, π slightly declined in continental Europe northwards from the Pyrenees to Poland (VI, Table 4), showing a phylogeographic pattern. A similar trend could not be found in the eastern lineage. Haplotype diversity h did not show any south-north clinal pattern. The mutation rate used for the whole CR was 2 %/Myr (Brown

et al. 1982, Shields & Wilson 1987a, Randi 1996, Klicka & Zink 1997, Kvist *et al.* 1999a,b). This led to a divergence time of ca. 1.1 Myr between the lineages. The mean pairwise genetic distance of 0.008886 in the eastern haplotypes led to a divergence time of ca. 440 000 years, and a distance of 0.006576 in the western haplotypes led to ca. 330 000 years. When the mutation rate of 20.8 % was used (Quinn 1992, Wenink *et al.* 1993), the divergence time was ca. 170 000 years between lineages, and the coalescence time 43 000 and 32 000 years, respectively, between western and eastern haplotypes.

5 Discussion

5.1 Body mass reflected the diet and changes in it

Body mass is generally used as an indicator of the nutritional status of birds (Brittas & Marcström 1982, Barton & Houston 1993, but see van der Meer & Piersma 1994). Bone marrow fat is considered an accurate index of the nutritional status in the barn owl *Tyto alba* (Thouzeau *et al.* 1997), but this method demands killing the birds.

Because of low locomotive activity and *ad libitum* feeding with high-energy commercial food, hand-reared grey partridges (Putala & Hissa 1995), pheasants (Robertson *et al.* 1991, 1993) and spruce grouse (Pendergast & Boag 1971a) are heavier than their wild counterparts. Results obtained from hand-reared and wild capercaillies (I) were not in agreement with these results. This finding may be a result of the small sample size, or high variation in the data resulting from the wide age-class. Capercaillies grow slowly and reach their adult mass in the second year (Lindén 1984a).

Grey partridge chicks that received insect-rich diet were heavier than other chicks, and low-insect diet produced the lightest chicks. This result was consistent with the observations by Dahlgren (1987). Wild chicks had similar body mass to chicks fed an insect-rich or a fish diet. Chicks that received insect-rich diet were still heavier than chicks fed fish at the age of eight weeks. However, the body mass of chicks fed low-insect and fish diet increased rapidly after receiving commercial food. According to Dahlgren (1987) the effects of an insufficient diet during growth may last until the first breeding season. Both Moss *et al.* (1993) and Marjoniemi *et al.* (1995) found that chicks fed commercial food grew fast. Heavier wild chicks are assumed to fly earlier than the lighter ones, thus facilitating their survival (Potts 1986).

Grey partridges fed natural food (III, V) lost body mass soon after the change in diet, but began to regain mass in about one week (III). Mass loss and the period of very low body mass coincides with the period of high mortality rate among released birds. In 1996 fifteen of twenty released female grey partridges died during the first week (unpublished data). Birds fed natural food remained lighter in weight than other chicks. The birds were still growing in both studies and probably did not get energy enough from the natural food for growth. The mass loss later during the feeding trial may have been a response to the experimental conditions and the stress experienced.

Tannin was not seen to lower body mass, in contrast to the results of Elkin and Rogler (1991), Voltura and Wunder (1994), Helsper *et al.* (1996), and Hewitt *et al.* (1997). As a matter of fact, tannin fed birds were heavier than other birds during the feeding trial. Birds may have met their protein requirements in spite of the added tannin because of *ad libitum* feeding (Helsper *et al.* 1996), or the pelleting of food may have decreased the effects of tannin, as assumed by Elkin and Rogler (1991). The excess protein from commercial food may have been used for binding tannins. It is also possible that tannins partly denature proteins, and this could further make them easier to digest (Butler 1989). In prairie voles *Microtus ochrogaster* quebracho tannin was reported to be lethal at all levels of protein, because of inhibited feeding (Lindroth & Batzli 1984).

5.2 Gut dimensions may reflect the diet

The most significant difference between the "browsing" Tetraonidae and the "seed-eating" Phasianidae birds is in the relative size of their caeca. The caeca of the browsers may be over twice as long (per unit body mass) as those of the seed eaters. Grouse in the 500-gram weight class (ruffed grouse *Bonasa umbellus*, spruce grouse, ptarmigans) have a mean caecal length of 44 cm, whereas in partridges of same size (the grey partridge, the chukar partridge *Alectoris chukar*) the caecal length is less than 20 cm (Leopold 1953). The length of the caeca seems to reflect the selection of coarse, fibre-rich food (McLelland 1989) and also digestive efficiency (Barton & Houston 1993).

Natural food is fibre-rich compared with commercial poultry food (III). Increased fibre content in food increases the length of the intestine and the weight of the gizzard in hand-reared red grouse (Moss 1972), mallard *Anas platyrhynchos* (Miller 1975), Japanese quail *Coturnix coturnix japonica* (Savory & Gentle 1976a, Starck & Kloss 1995), rock partridge *Alectoris graeca* (Paganin & Meneguz 1992), and also in some diving ducks *Aythya* spp. (Kehoe & Ankney 1985). Similar results on European starlings *Sturnus vulgaris* were reported by Geluso and Hayes (1999). The weight of the gizzard increased as a result from changing the diet to coarse, fibre rich natural food (III, V). Further, the gizzards were heavier in wild than in captive capercaillies (I). This probably reflected the need for a more effective grinding ability when feeding on fibre-rich diet. Tannin had no effect on the gizzard mass (V).

There was no difference in the length of small intestine and caeca between grey partridges fed natural or commercial foods (III, V). However, wild capercaillies had longer intestines and caeca than captive birds (I), which was in agreement with the studies of Pendergast and Boag (1973), Hanssen (1979a), Majewska *et al.* (1979), Paganin and Meneguz (1992), and Putaala and Hissa (1995). It was noticeable that grey partridges (III, V) had shorter intestines and lighter gizzards, as well as livers, than wild grey partridges or birds that were of wild origin and had spent only 1–2 generations in captivity (Putaala & Hissa 1995). Moss (1972) showed that the caeca shortened in the red grouse in captivity from generation to generation.

The length of the GI tract is known to vary seasonally (Pendergast & Boag 1973, Pulliainen & Tunkkari 1983). The adjustment time to changed food varies from a couple of weeks in the Japanese quail (Starck & Kloss 1995) to 4–6 weeks in the red grouse

(Moss & Trenholm 1987) or it may take even longer (Duke *et al.* 1984). Since no differences in the length of small intestine and caeca in the grey partridge were found, this may reflect their feeding habits; grey partridges have a similar diet throughout the year. Therefore, it is possible that they do not have a similar need for adaptation to changing diets as do Tetraonid birds. It is also possible that feeding four (V) or six (III) weeks on natural diet was insufficient to cause any visible changes in the gut length of grey partridges. However, the effect of tannin on the length of the small intestines of the grey partridge was obvious even though the feeding trial lasted only for four weeks (V). Tannin-fed birds had longer small intestines than control birds, which may reflect the increased enzyme activity or increased need for absorptive surface in the gut. Short-term fasting or food restriction, as well as switching to a totally different diet may cause partial atrophy of the gut, which may limit utilisation of ingested food energy and nutrients (McWilliams & Karasov 2001).

Caeca play an important role in the digestion of cellulose (Suomalainen & Arhimo 1945, Fenna & Boag 1974, Thompson & Boag 1975, Moss 1989, but see Andreev 1988, Remington 1989), and water absorption (Gasaway *et al.* 1976, Chaplin 1989, Thomas & Skadhauge 1988, 1989, Williams & Braun 1996) in galliform birds. Therefore, watery composition of the excreta of the birds fed natural food after the change in the diet may indicate disturbed caecal function (III, V). The excreta became dry ("normal") by the time a bird's body mass reached the initial level (III). The caeca take part in balancing nitrogen levels (Gasaway *et al.* 1976, Mortensen & Tindall 1981, Björnhag 1989, Karasawa 1989, Karasawa *et al.* 1997), since galliform birds are able to recycle uric acid through caeca by microbial activity (Mortensen & Tindall 1981, Karasawa 1989, Karasawa *et al.* 1997). If hand-rearing shortens the caeca, this may reduce effective decomposition and absorption activities in them. Also tannin-fed birds had high water content in their excreta, which may reflect the need to keep tannin concentration low, or to facilitate the removal of tannins dissolved in water.

Wild capercaillies had heavier livers than hand-reared birds (I). The liver's capacity to store glycogen may partly affect its size. The assumption was, that heavier livers would partly reflect the quantity of detoxication enzyme activity. However, the results obtained in grey partridges (V) did not support this, because tannin fed birds did not have significantly larger livers than the control birds. The liver fat, protein, and ash content was higher and the water content lower in hand-reared than in wild capercaillies (I). This result is in agreement with the results of Putaala and Hissa (1995) on grey partridges. Because in the willow grouse the size of the liver shows diet-dependent seasonal variation (Pulliainen & Tunkkari 1984), the difference in the liver composition found in this study may result from the different food of wild and captive capercaillies. The effect of food on liver composition has also been reported in geese *Anser* sp. (Benard & Labie 1992).

5.3 Nutritional status affected the blood parameters only slightly

Certain blood parameters were used to describe the nutritional status of birds (I, III, V). Grey partridges did not show any response in analysed blood parameters to the change in diet from commercial to natural (III). Perhaps the analysed parameters were not

sufficiently sensitive to indicate nutritional stress in grey partridges, although some of them have been successfully used in the study of starvation (Jeffrey *et al.* 1985, Robin *et al.* 1987, Totzke *et al.* 1999). Plasma total protein and thyroid hormones are shown to decrease as a response to food deprivation in herring gulls *Larus argentatus* (Totzke *et al.* 1999). However, birds fed natural food had higher alanine concentration (V) in plasma in comparison to control birds. This may have been a sign of catabolism of nutrient reserves, because the birds fed natural food were lighter in weight (III, V) than birds on other diets.

Hand-reared grey partridges had lower Hb and Hcr than hand-reared or wild capercaillies, but the values varied in a range of flight-restrained birds of several other species (Balasch *et al.* 1974). Flight – or in this case flightlessness as a result of limited exercise ability in test cages, may have had an impact on plasma composition.

Glycine takes part in some detoxication reactions (Stevens 1996), which may explain the somewhat elevated glycine (V) level in the birds fed natural food. Tannin had no significant effects on the blood parameters, but methionine should be mentioned. Methionine level seemed to be somewhat elevated in the tannin group. Added methionine in the diet is known to decrease the effects of tannin (Elkin & Rogler 1991). In birds, phenolic compounds may be conjugated with ornithine (Jakubas *et al.* 1993), but no elevated ornithine levels were observed. The last sampling was conducted simultaneously with decapitation, which affected plasma consistency.

Hand-reared capercaillies had higher uric acid and T_4 levels than wild birds (I). Results obtained from grey partridges (III) were in agreement with this, but the difference between test and control groups was not significant. High uric acid levels may have resulted from the high protein concentration in the commercial poultry food, or from the reduced ability of the caecum to recycle uric acid (Karasawa 1989). Plasma uric acid is assumed to indicate protein breakdown in starving Svalbard ptarmigan *Lagopus mutus hyperboreus* (Lindgård *et al.* 1992).

Hand-reared grey partridges (Putala *et al.* 1993) and turkeys *Meleagris gallopavo* (Burke *et al.* 1977b) have significantly higher T_3 concentration in plasma than wild birds. This may reflect a higher metabolic rate in hand-reared birds when compared with the wild birds (Warkentin & West 1990). According to Bishop *et al.* (1995) T_4 may be important in birds in affecting the aerobic capacity of certain muscles, as T_4 -treated tufted ducks (*Aythya fuligula*) have higher cytochrome oxidase activity in the pectoral muscle than control birds. The high plasma T_4 level of hand-reared birds (I) may reflect a lower level of metabolism in comparison to wild birds, expressing the unnecessary of the hormone in low level activity. This may be linked to the flightlessness of birds in aviaries.

Serum total protein is known to be higher in adult than in juvenile hand-reared capercaillies (Cuenca *et al.* 1995). The somewhat higher total protein level of captive birds (I) may be explained by the higher number of adult birds among them. In general, the results of the blood characteristics in captive capercaillies were in agreement with those obtained from a wide sampling of captive birds of several species (Polo *et al.* 1994). Birds are generally able to maintain a high and relatively constant plasma glucose level, even during fasting (Langslow 1978, Groscolas & Rodriguez 1981).

No statistically significant effects could be seen in the nitrogenous compounds of plasma in the grey partridges fed tannin or natural food. However, potential short-term effects, that the change in diet had, coincide with the period of body mass loss, and also with the high mortality rate after release into the wild.

5.4 Food consumption and MEC responded to the change in diet

The change in diet lowered the food consumption immediately in grey partridges fed natural food (III). This may have reflected the natural suspiciousness of birds to new situations. During the feeding trial the food consumption in test group (III) was somewhat higher than in the control group based on the fresh weight of food. A similar response to natural food was found in the red grouse (Moss 1972), the mallard (Miller 1975) and the rock ptarmigan *Lagopus mutus* (Gasaway 1976b). Japanese quails adapted to the use of more fibrous food in about one week, and decreased food intake back to initial levels (Savory & Gentle 1976b), even though they initially increased food intake as a response to an increased fibre content in the food (Savory & Gentle 1976a).

The birds fed natural food ate more than the control birds by fresh weight, but the result was opposite when based on analyses of dry weight. This depended on the birds' preference for barley shoots. The water content of shoots was about 90 %. Shoots might have been favoured because of the forthcoming breeding season, when they are very important for the breeding condition of female grey partridges (Siivonen 1957). However, it was of no interest to calculate food consumption on the basis of dry matter, because of the nature of the natural food in comparison to pelleted commercial food. Much information about the amounts of the consumed food would have been lost in that case.

Excreta production varied from week to week, which also affected assimilation efficiency, MEC (III). In the test group assimilation efficiency varied between 49–67 % and in the control group between 61–88 %. These values were within the normal range of the galliforms (30–86 %, for review, see Castro *et al.* 1989). The daily energy (GE) requirement of the rock ptarmigan (Gasaway 1976b), or the daily metabolised energy (ME) of the red grouse and the Japanese quail (Moss & Trenholm 1987, Starck & Kloss 1995) were not affected by the fibre content of food (but see Savory & Gentle 1976a). According to Duke *et al.* (1984) the preconditioning of turkeys to fibre-rich food quadrupled their ability to utilise food cellulose. In this study both GE and ME decreased when the diet was changed from commercial to natural. This was presumed to result to some extent from the high plant secondary compound concentration in the food (see Servello *et al.* 1987, Koenig 1991).

Tannin (6 %) added to the food did not lower food intake, which was in contrast to previous studies on chickens (Elkin & Rogler 1991, Helsper *et al.* 1996) and ruffed grouse (Hewitt *et al.* 1997). In the Canada geese (Buchsbaum *et al.* 1984) and the ruffed grouse, 8 % quebracho tannin (Hewitt *et al.* 1997) is known to decrease food intake, but this was not supported by our study. The commercial quebracho product used in this study included 73 % of condensed tannins, which means that the effective tannin content

of this product was ca. 4.4 % (Robbins *et al.* 1991). On the other hand, it was reported by Chung-MacCoubrey *et al.* (1997) that quebracho had no dose-dependent effects on the captive eastern grey squirrels *Sciurus carolinensis*.

5.5 Added dietary tannin expressed in excreted nitrogen and tannin content

Galliform birds produce two different kinds of excreta, or "droppings". Intestinal droppings are fibrous and cylindrical, and they are excreted regularly throughout the day. Caecal droppings, in turn, are soft, shapeless and semi-liquid, and they are usually excreted once a day.

The wet composition of both caecal and intestinal excreta was obvious in grey partridges fed natural food (III, V) or tannin (V). The appearance was different in other ways as well. In the natural food group, fibre strands from shoots and grain were visible (III, V). The quebracho-tannin powder tainted the excreta of birds fed tannin dark reddish-brownish. It is noteworthy, that the tannin-fed birds emptied their caeca several times per day. Increased water elimination may indicate a decreased capacity to concentrate urine (i. e. nephrotoxic effect). It may also indicate a disruption in gastrointestinal absorption. A larger volume of water may also be needed to void the high concentration of secondary compounds (Jakubas *et al.* 1993).

Ingested phenolics are reported to significantly increase fecal nitrogen excretion in the American elk *Cervus elaphus nelsoni* (Mould & Robbins 1981), thus reflecting the amount of tannin-protein complexes in excreta (Mould & Robbins 1981, Bernays *et al.* 1989, Hewitt & Kirkpatrick 1997). In contrary to this, in this study birds fed natural food had the highest nitrogen content of intestinal excreta (V), not the birds fed tannin. The high nitrogen concentration immediately after the change in diet may have resulted from the inhibiting effect of the high fibre content on the assimilation of nitrogen. Nitrogen assimilation improved during the feeding trial, and nitrogen content of intestinal excreta decreased to the initial level.

The nitrogen content of caecal droppings lowered in both tannin and natural food groups (V). It is possible that more material was actively transported to the caeca in natural and tannin groups, which could then be seen in decreased nitrogen content in the excreta. The excreta were not weighed, so only the relative amount of nitrogen in the excreta is known. Since tannin did not increase the caecal excreta nitrogen level, it may be assumed that the food was sufficient to inhibit the effects of tannin. In the western scrub-jay (*Aphelocoma californica*) effects of tannins were eliminated in high-protein (30 %) diets (Fleck & Tomback 1996). According to Blytt *et al.* (1988) the antinutritional effects of dietary tannins did not result from the direct inhibition or binding of digestive enzymes with tannins, but other membrane-associated processes, such as absorption, may have been slightly affected.

Highly water-soluble tannins, like quebracho, probably have low bonding capacity to gut proteins (Haslam 1989), and are difficult to degrade to low molecular weight phenolics (McArthur *et al.* 1991). The high tannin concentration of caecal excreta (V) also supported the idea that more material was transported to caeca for processing. The

low nitrogen concentration of caecal excreta could then be explained by the high tannin concentration. According to Hewitt *et al.* (1997) northern bobwhites *Colinus virginianus* excreted 56 % of dietary tannins in caecal excreta.

In ruffed grouse, tannins had the highest impact on caecal function (Hewitt *et al.* 1997). Transportation of tannin to the caeca could have explained the increased proportion of caecal excreta of total excreta. Although in the northern bobwhite increased filling of caeca could not be explained only by the effects of tannin, caecal volume may also have increased because of abnormal amounts of digested food received. In addition, more uric acid may be transported to the caeca for nitrogen recycling (Karasawa 1989, Karasawa *et al.* 1997, Stevens 1996). Symbiotic micro-organisms of the caeca (Suomalainen & Arhimo 1945, Barnes 1977, Hanssen 1979b) may metabolise proteins and tannins of tannin-protein-complexes, which may be facilitated by an effective filling of the caeca. The excreta were not weighed, but the caeca of the birds fed tannin were full of material in contrast to other birds. The frequent emptying of the caeca may have been a reflection of rapid filling.

5.6 Energy reserves and power production vs. morphology and biochemistry of tissues

Hand-reared capercaillie males had somewhat heavier pectoral muscles than wild males, whereas the result obtained from females showed the opposite (I). This probably resulted from the different growth strategies of males and females (Lindén *et al.* 1984): males usually gain mass already during autumn and winter in preparation for the breeding season and *ad libitum* feeding of hand-reared birds could have facilitated the mass gain of pectoral muscle. Low locomotive activity was reported to cause pectoral muscle atrophy in pheasants (Majewska *et al.* 1979), pigeons (Chaplin *et al.* 1997), great crested grebes *Podiceps cristatus* (Piersma 1988) and black-necked grebes *Podiceps nigricollis* (Gaunt *et al.* 1990). In contrast, Lindström *et al.* (2000) suggested that avian muscles do not need power-training as do mammalian muscles, and that in their windtunnel experiment, repeatedly flown red knots (*Calidris canutus*) did not have any thicker pectoral muscles than their unflown counterparts.

The size of the heart is positively correlating with flying ability (Thomas 1985, Viscor *et al.* 1985); good flyers tend to have bigger hearts than moderate flyers. Hand-reared capercaillies had smaller hearts than wild ones (Hissa *et al.* 1990, I), which probably was a result of limited flying possibilities in rearing aviaries. Domingo *et al.* (1991) reported heart burst in capercaillies as a consequence of handling stress. In Nappée's study (1982) heart failure caused death in released capercaillies. Thus, untrained heart may be more vulnerable to the impact of sudden stress effects.

The oxidative capacity of a muscle may be expressed in cytochrome-c oxidase activity. Enzyme activity in the pectoral muscle of the wild capercaillies was over three times that of the hand-reared birds. Also, the heart enzyme activity was higher in the wild birds compared with the hand-reared birds (I). The concentrations of mitochondrial protein in the pectoral muscle and the heart were higher in wild capercaillies compared with the hand-reared birds, which most probably was connected to the higher cytochrome-c

oxidase activity in the wild birds. The low tissue enzyme activity indicated a poor ability for long-term flight performance in hand-reared birds. Additionally, it may have indicated an adaptation to low energy demands of living in captivity (I). However, Warkentin and West (1990) suggested that the basal metabolic rate (BMR) is significantly higher in captive than in wild, freshly caught merlins *Falco columbarius*.

In short term power production (take-off), hand-reared grey partridges are weaker than wild birds (Putala *et al.* 1997). Cytochrome-c oxidase activity plays an important role in long-term power production (flight), which in hand-reared grey partridges (Putala & Hissa 1995) and capercaillies (I) is lower than in their wild counterparts. Wild grey partridges (Pyörnilä *et al.* 1998) and capercaillies (Mäkinen *et al.* 1997) have more muscle cells, which are needed in long-term exercise (red, fast-oxidative-glycolytic fibres = FOG) than hand-reared bird. In contrast, captive birds have more muscle cells for short-term exercise or short spurts (white, fast-glycolytic fibres = FG). This could at least partly explain the difference in the COX activity. According to Kaiser and George (1973) and Rosser and George (1986) FG fibres are rich in glycolytic enzymes, and adapted to anaerobic metabolism using glycogen as their main fuel. FOG fibres are rich in oxidative enzymes, adapted to aerobic metabolism, and mainly use fat as fuel for long-lasting activities. In relatively poor flyers, like the chicken or the pheasant, the pectoral muscle comprises mainly FG fibres, whereas in good flyers like the pigeon, FOG fibres dominate (see Hissa 1988 and references therein). According to Rome *et al.* (1988) FG cells are needed for maximal movement, because FOG cells do not shorten fast enough.

Glycogen is metabolised anaerobically and used predominantly during take-off and landing (Parker & George 1975). The glycogen content of a tissue is a labile parameter, depending on the bird's previous activity. This probably affected the results. No difference was found in the glycogen content of tissues between wild and hand-reared birds, although the glycogen content in the liver of wild birds was somewhat higher than that in hand-reared birds (I). According to Hissa *et al.* (1990), wild capercaillies stored more glycogen in the pectoral muscles than hand-reared birds. Putala and Hissa (1995) reported for wild grey partridges that the glycogen content of the pectoral muscle was almost ten times that of hand-reared birds. Wild pheasants had higher glycogen content in both pectoral muscle and liver in comparison to captive birds (Majewska *et al.* 1979), and seasonal variation in the glycogen content of the liver was also reported (Pulliainen & Tunkkari 1984).

5.7 Primary growth and temperature regulation

Primary length and development may be considered as indicators of a chick's ability to fly and avoid predation. These parameters may also be used as indicators of plumage quality and insulation. It is probable that wild birds moult more rapidly than hand-reared birds, as a response to a more hazardous life in the wild (McCabe & Hawkins 1946). Handling of the chicks may not have disturbed the mode of moult (Holmberg 1992) in the present study. When wild and hand-reared grey partridge chicks were compared

according to the primary length at the age of one week, it was obvious that the wild chicks had longer primary feathers than other chicks. However, chicks fed an insect-rich diet had longer primaries than chicks fed a low-insect or a fish diet (II).

There was a difference between diet groups in the speed and mode of the development of the primaries. Chicks fed an insect-rich diet had fully grown feathers and moulted earlier than other chicks. According to McCabe and Hawkins (1946), and Thompson and Taber (1948) the P1 primary is moulted at the age of 3.5 weeks. This was the case in the chicks fed an insect-rich diet, whereas the chicks fed a fish or a low-insect diet started to moult later than at the age of four weeks. In the chicks fed an insect-rich diet, moulting speed and stage at the age of seven weeks was in agreement with Thompson and Taber (1948) (Fig. 4).

Moult always includes synthesis of epidermal proteins, mostly sulphur-rich keratin, which in turn includes a high amount of cysteine. The feather proteins include more cysteine than other tissues or food (Murphy & King 1982, Murphy *et al.* 1990). The process, in which a feather gets a hard form, is called keratinisation. Amino acids methionine and cysteine are known to positively affect plumage development (Murphy & King 1982, Bagliacca *et al.* 1985, Potts 1986, Murphy *et al.* 1990).

In the wild, birds usually get enough protein and proper amino acids from their usual nutrition, even during the moult (Ankney 1979, Murphy & King 1984). However, an effect of food quality on the feather development was reported in pheasant chicks (Woodard *et al.* 1977), where high protein content of food during the first five weeks of life facilitated the growth of tail feathers. Food protein content had an impact on body mass and feather growth in captive European quail *Coturnix coturnix coturnix* (Combreau & Guyomarc'h 1992). Insect food was essential for the survival and growth of sage grouse *Centrocercus urophasianus* chicks until the age of three weeks, and even after that it was important for optimal growth (Johnson & Boyce 1990). According to Hermes *et al.* (1984), the rock partridge chicks were not dependent on animal matter during the first weeks, if nutrients like vitamins and minerals were available. On the other hand, animal matter was an important source of phosphorous, B₁₂-vitamin (Savory 1974) and nitrogen (Dahlgren 1987). Although fish is rich in protein (Almqvist 1952) and methionine and cysteine (F.A.O. 1970), in comparison to many other foods, its negative rather than positive effect on the plumage growth of the grey partridge chicks revealed its inability to replace invertebrates in the diet of hand-reared chicks.

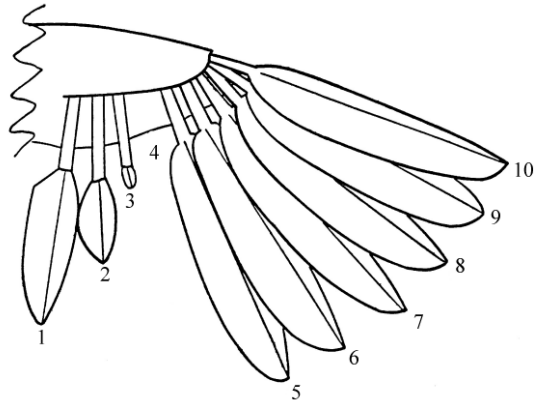


Fig. 4. The primaries of a seven-week-old grey partridge. P1-P3 are postjuvenile primaries, P4 has been moulted, and P5-P10 are juvenile primaries (Thompson & Taber 1948).

Seven-day-old wild chicks and chicks fed an insect-rich diet displayed superior temperature regulation in comparison to chicks fed a low-insect or a fish diet. The chicks that received an insect-rich diet exhibited a slower cooling rate, which was probably a reflection of their better insulation and higher body mass. It seems reasonable to assume that the insufficient amount of animal protein in the low-insect diet, and an improper quality of the fish proteins, was reflected in the less-developed temperature regulation in chicks fed these diets. Food-restricted Japanese quail chicks may regulate their metabolic rate at a lower level. Their ability to increase heat production is maintained by shivering, which is used to compensate the decrease in diet-induced/growth related thermogenesis (Marjoniemi 2000).

Shivering and fluffed plumages were obvious in the seven-day-old chicks. According to Marjoniemi *et al.* (1999) shivering was detected in one-day-old domestic fowls, and two-day-old grey partridges and Japanese quails. Shivering was also obvious in the willow grouse (Aulie 1976, Aulie & Moen 1975) at the age of 2–3 days, or even earlier (Myhre *et al.* 1975). It was also assumed, that the thermogenic processes in muscles were fully developed at the age of five days, since the maximal thermogenesis did not increase after that time (Marjoniemi *et al.* 1995). Improved cold resistance later on would then result from increased body mass and improvement of the insulation (Jurkschat *et al.* 1989, Marjoniemi *et al.* 1995, Hohtola & Visser 1998). The development of insulation may be considered stepwise, an obvious shift from the age of 11 to the age of 15 days could be seen, (II, Marjoniemi *et al.* 1995). It must be kept in mind, that at this age chicks are still dependent on parental warming, at least at nighttime. In Finland, most of the grey partridge chicks hatch in the beginning of July (Moilanen 1981, Putaala & Hissa 1998), when ambient temperatures may occasionally drop below 0 °C.

5.8 The main detoxication route in galliforms may not be the liver

According to McArthur *et al.* (1991) there are at least six physiological mechanisms, which may be used for diminishing the effects of plant secondary compounds. Of these, formation of less reactive complexes, modification of the environment to inhibit reactions (for instance pH), and degradation, are taking place in the gut. Inactivated or degraded compounds may not have any harmful effects after absorption. If these defences fail, and absorption of these compounds occur, liver is the main site for addition of functional groups, and conjugation reactions (to change solubility). Kidneys, lungs, brain and intestinal mucosa contribute these processes.

Plant secondary compounds entail an effective detoxication mechanism or adaptation to certain levels of chemicals in herbivores. The biotransformation system – including both cytochrome P450 (CYP) enzymes and conjugation reactions, is considered to be the most important process against toxication in herbivores (Gonzales & Nebert 1990). The CYP enzyme system is closely related to feeding habits with specialised requirements for enzymatic detoxication of xenobiotics in the food (Walker *et al.* 1987, Walker & Ronis 1989, Fossi *et al.* 1995, Walker 1998, Dearing *et al.* 2000).

Intraspecific differences, that is, differences between wild and hand-reared birds of each species were found (IV). Wild capercaillies had significantly lower EROD and PROD activities than hand-reared birds, which may have reflected the decreasing effect of some phenolic compounds on the enzyme, at least EROD activity (Baer-Dubowska *et al.* 1998, Mimica-Dukic *et al.* 1999, Stupan *et al.* 2000). According to Lindén (1984b), Sjöberg and Lindén (1991), and Spidsø and Korsmo (1994) the pine needle diet of the capercaillie is rich in phenolic compounds (resins). Also in the grey partridge PROD activity was lower in wild birds in comparison to hand-reared birds. Naturally, delayed sampling could cause low enzyme activity values, but in this case it could not explain the whole decrease in the enzyme activity (IV). Wild and hand-reared birds of either of the species had similar COH activity. It is possible that secondary compounds present in the birds' diets did not induce the activity of these certain CYP enzymes. However, bird species feeding on totally deviant diets may share similar hepatic biotransformation activities (Rivière *et al.* 1985).

EROD and PROD activities were similar in both species, and the only interspecific difference was found in COH (IV). The exact connection between the CYP enzymes used and secondary compounds in the diet of these birds still remains unknown, since studied CYP enzymes represented only a minor part of the large CYP enzyme family and did not completely reflect the detoxication capacity. Sampling may have affected the results, because it is shown that different parts of the liver show various enzyme activities (Gillette *et al.* 1972). The small number of birds used in this study may have had its impact on the results.

In the feeding trial with birds fed control, tannin and natural diets (V), the hepatic enzyme activity did not show any differences between diet groups with any of the substrates used. EROD activity seemed to be lower in the tannin group birds, but the difference was not significant. Enzymes used in this study are easily induced by several environmental toxins (e.g. Mattson *et al.* 1998), but natural substrates, like plant secondary compounds, may not induce these enzymes (H. Raunio, pers. comm.).

Induction of EROD and PROD in polychlorobiphenyl-fed captive grey partridge males is reported (Abiola *et al.* 1989). According to Pelkonen *et al.* (2000) COH activity may be connected to coumarin-type alkaloids rather than tannins.

In addition to the hepatic detoxication enzymes, herbivores also have symbiotic micro-organisms in their caeca which may have an important role in the catabolism of secondary compounds (Hanssen 1979b, Hewitt *et al.* 1997). High CYP values are known from the *duodenum* of the grey partridge (Rivière 1980). This may reveal the main route for detoxication in birds to be the intestinal metabolism, and that the tannins are not absorbed from the intestine to blood circulation, thus not entering the liver for detoxication. Tetraonids probably detoxify resins in their caeca, where they are concentrated and excreted as energy-rich caecal droppings (Moss 1973, Pendergast & Boag 1971b). The increased length of the small intestine in tannin fed birds (V) may indicate an increased gastrointestinal detoxication activity.

Salivary tannin-binding proteins are found in mule deer *Odocoileus hemionus*, American black bears *Ursus americanus* (Robbins *et al.* 1991), root vole *Microtus oeconomus* (Juntheikki *et al.* 1996), and moose *Alces alces* (Juntheikki 1996), which may reduce fecal nitrogen losses (per unit of ingested tannin). However, such salivary proteins have not been found in birds. In animals which do not produce tannin-binding proteins, at least part of the condensed tannin are absorbed (McArthur *et al.* 1991). Galliform birds may also have a high resistance to secondary compounds, as suggested for the greater snow goose *Anser caerulescens atlantica* (Gauthier & Bédard 1990).

5.9 A deep divergence between the two lineages of the grey partridge

DNA technology provides with suitable markers to study the genetic structure of populations, species, and communities (Hewitt 2000). MtDNA was chosen because of several reasons: it is considered to be a marker that is evolving fast (Brown *et al.* 1979), and not recombining (Hayashi *et al.* 1985). It is also considered a neutral marker, which means that environmental factors do not affect it (Brown *et al.* 1979, but see Ballard & Kreitman 1995, Fry 1999). Further, it is only matrilineally inherited (Wilson *et al.* 1985). These properties make mtDNA widely used in genetic studies on populations and subspecies (Shields & Wilson 1987b, Avise & Nelson 1989, Lucchini & Randi 1988, Tarr & Fleischer 1993, Kvist *et al.* 1998, 1999a,b, Uimaniemi *et al.* 2000), and also on phylogenetic relationships between species (Edwards & Wilson 1990, Crowe *et al.* 1992, Kvist *et al.* 1996, Randi 1996, Marshall & Baker 1997, Kimball *et al.* 1999, Gutiérrez *et al.* 2000, Randi *et al.* 1998, 2000, Ruokonen *et al.* 2000, Young *et al.* 2000). The control region, which is the most variable region of the avian mtDNA, is divided into three domains (Baker & Marshall 1997). Intraspecific variation in birds is commonly found in the domains I and III, the central domain (II) being most conserved (e.g. Wenink *et al.* 1993, 1994, Marshall & Baker 1997, Lucchini & Randi 1998, Uimaniemi *et al.* 2000, Young *et al.* 2000).

The mean nucleotide composition in the CR1 of the grey partridge was similar to several other bird species (Lucchini & Randi 1998, Holder *et al.* 2000, Uimaniemi *et al.* 2000). The amount of divergence (3.6 %) found in the CR1 between the basic eastern and

western mtDNA lineages was of the same magnitude as the divergence between Sicilian and Alpine haplotypes of the rock partridge (Lucchini & Randi 1998). The Palaearctic lesser white-fronted goose also exhibited two main lineages, eastern and western, with a mean divergence of 2.0 % (Ruokonen *et al.*, manuscript).

In this study substantial variation was found in the nucleotide diversity between populations. Low diversity areas have suffered large-scale environmental changes, and have been under severe hunting pressure. Of these, the Greek population has been bottlenecked during the last century (B. Alexiou, pers. comm.). The NW German population did not contain any variation at all in the CR1, which may result from a local population crash following the hard winters of 1978/79 and 1979/80, and from the continuous decrease in population size since 1991 (E. Strauss, pers. comm.). Close inbreeding may be expressed in the loss of genetic variation (O'Brien 1994b). In grey partridge, however, close inbreeding does not occur, because of differential dispersal of sexes, and the female mate choice from other than her own winter covey (Potts 1986). Extremely high nucleotide diversities together with high haplotype diversities, found in the Oulu region, Ireland and Bulgaria, can be explained by the finding of both mtDNA lineages in these populations.

5.10 Past and present populations

According to Hewitt (1999) "population structure is the distribution of genotypes in space and time, and is the result of both present processes and past history". Conspecific populations may be structured at a variety of evolutionary depths: slight molecular separations may reflect more recent population subdivisions, whereas deep subdivisions may evidence a major source of intraspecific evolutionary gene pool diversity (Avice 1992). The population structuring of the grey partridge was relatively strong when compared with the blue tit *Parus caeruleus* (Kvist *et al.* 1999b), or the greenfinch *Carduelis chloris* (Merilä *et al.* 1997), but of the same magnitude as the rock partridge (Lucchini & Randi 1998), and the dunlin *Calidris alpina* (Wenink *et al.* 1996). This may reflect allopatric divergence of refugial populations, and subsequent low maternal gene flow between the populations. The grey partridge is considered a relatively sedentary bird, with a short natal dispersal and high site-fidelity of adults. The mean dispersal distance of released grey partridges is 5.96 km \pm 1800 m (SE) (Finnish Game and Fisheries Research Institute; Ringing Centre, Finnish Museum of Natural History). On the average the breeding dispersal distance of radio-tagged wild hens is 3.1 km \pm 525 m, and that of released hens 2.32 km \pm 764 m (Putala & Hissa 1998). The negative correlation between the geographical distance and genetic variation in the populations can be explained by the genetic similarity among distant populations of Bulgarian, Greek, Finnish and Irish birds.

A star-like minimum-spanning network structure has been found among several bird species using either the mtDNA RFLP (Ball *et al.* 1988, Ellsworth *et al.* 1994, Seutin *et al.* 1995) or mtDNA control region (Merilä *et al.* 1997, Kvist *et al.* 1999a). This type of network may be an expression of rapid population expansion. The ancient history of the grey partridge was reflected in the minimum-spanning network. There were at least two

separate refuges where ancestral *Perdix perdix* bottlenecked but survived the glaciations. A marked increase in the population size followed the retreat of the continental ice. Both lineages exhibited a star-like haplotype network, which referred to expanding populations.

In the eastern lineage, the expansion of the population was supported by the observed distribution of pairwise genetic distances, and the significantly negative Tajima's *D*. Deviations from the neutral patterns of nucleotide variation expected at equilibrium may result from past changes in population size (Aris-Brosou & Excoffier 1996, Fry & Zink 1998). In the western lineage the observed distribution of pairwise genetic distances did not follow the expected distribution of either the expansion or the equilibrium model. A very recent population crash, maybe back in the 1950s, was reflected in τ , which was 0 (Rogers & Harpending 1992). This would explain the close kinship of a large part of the birds. The significantly negative Tajima's *D* and the shape of the minimum-spanning network reflected a population under expansion.

5.11 The impact of ice ages can be seen in present day grey partridge populations

When examining the geological time chart, the most interesting period concerning the grey partridge is the Quaternary period, which is divided into two epochs, namely the Pleistocene (1.7–0.01 Myr BP) and the Holocene (0.01 Myr BP – present). The northern hemisphere ice sheets have varied in size for at least the last 2.5 Myr. About 100 000 year cycles of glacial-interglacial periods have forced species to evolve as a response to changes in climate and biosphere (Webb & Bartlein 1992, Hewitt 1999), with series of bottlenecks and expansions in population size and range (Hewitt 1996, 1999, 2000). The last European, so-called Weichselian, glaciation started ca. 120 000 years ago. It lasted about 100 000 years, having its coldest period ca. 18 000–20 000 years ago. At that time ice covered the entire northern Europe southwards to the Pyrenees, the Alps, and the Balkans (Webb & Bartlein 1992). Glaciations caused a series of bottlenecks that species had to survive (Hewitt 1996, 1999, 2000), but even during the coldest periods, some southern parts of Europe and the easternmost parts of the continent provided several plant and animal species with suitable habitats to survive (Taberlet *et al.* 1998, Hewitt 2000). According to Mourer-Chauviré (1993) a primitive form of the grey partridge, *Perdix palaeoperdix*, was a characteristic species from the Lower to Middle Pleistocene in western Europe. *Perdix perdix* has inhabited Europe from the Late Pleistocene on (Tyrberg 1998).

After the last glaciation the northern regions of Europe were recolonised from the Iberic and the Balkanic refuges, but the Alpine barrier isolated the Italian lineages (Taberlet *et al.* 1998, Hewitt 1999, 2000, see also Bilton *et al.* 1998). In the grey partridge the western mtDNA lineage was found primarily in England, France, Germany, Austria, and Poland. The possible refuge areas for this lineage were considered to be the Iberic and the Italic refuges. The two Italian haplotypes found in the wild birds may be remains of this Italic refuge. In contrast to this, at least the great bustard *Otis tarda* populations

were reported to follow the biogeographic model of Bilton *et al.* (1998), with the Mediterranean Peninsula as a geographical isolate, and a non-Iberian source of European mainland populations (Pitra *et al.* 2000).

In the western populations the nucleotide diversity values showed a south-north oriented cline from the Pyrenees to Poland. This may follow the grey partridge postglacial recolonisation route from the Iberian refuge to Central Europe (Hewitt 1996, 2000, Merilä *et al.* 1996, 1997). Non-continental populations (England and Ireland) deviated from this cline. These populations included some unique haplotypes, which may be remainders of historical introductions on the Isles (Westerskov 1958). Among the eastern populations no clinal variation was detected. The Balkanic and the easternmost (Caucasian) refuges (Taberlet *et al.* 1998, Hewitt 2000) may be considered as the two potential refuge areas for the eastern lineage. This is supported by the finding of the eastern lineage mtDNA from Kazakhstan and Russia in addition to Bulgarian, Finnish and Greek samples. However, more Russian samples would be needed to draw final conclusions about this recolonisation route.

The 2 %/Myr mutation rate gave a divergence time of 1.1 Myr (i.e. in early Pleistocene) for the two lineages. This is, in general, earlier than the average phylogenetic subdivision time for several avian species (Shields & Wilson 1987a, Wenink *et al.* 1993, Lucchini & Randi 1998, Kvist *et al.* 1999b, Uimaniemi *et al.* 2000). The 20.8 %/Myr mutation rate gave a divergence time of 173 000 years (i.e. in late Pleistocene), which in turn refers to a clearly later subdivision (VI). Because of this ambiguity the use of divergence time estimates is questionable, and may require a calibration of the molecular clock for each genus separately (Ruokonen & Kvist 2001, manuscript).

5.12 Morphology and genetic variation may go hand in hand

Many species are divided into subspecies based on a limited number of morphological characteristics. According to Van Wagner and Baker (1990), Merilä *et al.* (1997), Mundy *et al.* (1997), Lucchini and Randi (1998), Barrowclough *et al.* (1999), and Holder *et al.* (2000) subspecies may also be distinguished by genetic variation, but the morphological classification and genetic differentiation may not be strictly comparable (Avise *et al.* 1992, Ball & Avise 1992, Seutin *et al.* 1995, Fry & Zink 1998, Questiau *et al.* 1998, Bensch *et al.* 1999).

The grey partridge subspecies may be determined on the basis of the plumage colour, even though it may, in some cases, depend on factors like soil consistency (Potts 1986). The grey partridge subspecies can be divided into two classes based on plumage colour. More dark/rufous-brown subspecies (*P. p. hispaniensis*, *italica*, *armoricana*, *sphagnetorum*) originate from the west, and paler/greyer subspecies (*P. p. lucida*, *canescens*, *robusta*) from the east. The nominate *P. p. perdix* may be considered an intermediate form. Relatively high amount of genetic variation (80.74 %) was associated with the plumage colour variation. Morphological patterns (plumage types among subspecies) also reflected in the neighbour-joining tree and genetic divergence in the rock ptarmigan (Holder *et al.* 2000). The NW German samples were from the assumed distribution area of *P. p. sphagnetorum* and the eastern Polish from the area of *P. p. lucida*

(Potts 1986), but the mtDNA sequences were mainly identical with the basic western haplotype (VI). Two different haplotypes with a systematic difference of one/two nucleotides from the main western type were found in the wild population in Italy, and one different haplotype with one systematic deviant nucleotide came from the Pyrenees. In the distribution areas of the French subspecies, *P. p. armoricana* (FR1, FR2), the basic western haplotype together with four other closely related haplotypes were found. Pairwise comparisons revealed a significant difference between all other expected subspecies except between *P. p. perdix* and *P. p. sphagnetorum*. Genetic markers other than the control region, such as nuclear microsatellites, may be needed to examine the divergence at the level of morphological subspecies.

In addition to plumage colour disparities, grey partridge subspecies may have ecological, physiological and behavioural differences as well. Some of these can be considered as adaptations to the climatic conditions of their distribution area. In Finland, grey partridges have an extremely high clutch size with up to 24 eggs (Putala & Hissa 1998). They are also known to form large winter flocks, where covey mixing is possible (Pulliainen 1965). The ambient temperature may be well below $-30\text{ }^{\circ}\text{C}$, strengthened by an icy wind in the open fields. To avoid the freezing effects of frost and cutting wind, birds reduce heat loss by spending nights huddled together (Pulliainen 1965, Putala *et al.* 1995). Finnish grey partridges are able to maintain their body temperature in ambient temperature as low as $-52\text{ }^{\circ}\text{C}$ (Hohtola *et al.* 1991). Additionally, they are able to dig through the snow cover for food. An ice layer on the snow, or snow cover $> 50\text{ cm}$ may impede feeding (Siivonen 1957, Sulkava 1964). The easternmost populations of *P. p. lucida* may have hard weather movements, and even migration, and the long-winged easternmost subspecies *P. p. robusta* is known to migrate south in autumn (Potts 1986). Grey partridges from eastern Bulgaria, Finland, and Greece represented the eastern mtDNA type, which also seems to be adapted to geographically more extreme areas. The liver samples were from a study population in Greece, which inhabits a mountainous area about 1 km asl (B. Alexiou, pers. comm.).

5.13 Introductions – work for hunting or conservation?

Hand-rearing and releasing can be used for conservation of endangered species or biodiversity (Kleiman *et al.* 1994, Cade & Temple 1995). On the other hand, conservation efforts may fail because maladaptive traits are introduced into populations when hand-reared individuals are released into the wild. Despite the previous releasing actions of grey partridges (Putala & Hissa 1998), only five grey partridges of the western lineage were found in the wild population in Finland, which, in general, represented the eastern mtDNA lineage. On the other hand, the farm stocks represented the western lineage as well. The Irish and Swedish populations consisted of both mtDNA lineages, which was probably an evidence of historical releases of imported birds (Westerskov 1958).

The wild population in Italy consisted of two different haplotypes, while the Italian farm stock consisted mainly of the basic western haplotype. According to Lovari (1975) the native Italian *P. p. italica* still existed back in 1975 in the district of Tuscany, the same area from where the samples of this study were collected in 1998. *P. p. italica* as its purest

form is presumed extinct (Matteucci 1988), because of the intensive releasing of farm birds in Italy (Matteucci 1988, Montagna *et al.* 1990). Both *P. p. italica* and *P. p. hispaniensis* are listed as endangered subspecies of the grey partridge in the Annex I (http://europa.eu.int/comm/environment/nature/directive/perdix_perdix_hispaniensis_en.htm, and http://europa.eu.int/comm/environment/nature/directive/perdix_perdix_italica_en.htm, 10.5.2001) of the European Union (EU).

Despite the numerous releases of grey partridges, amazingly few marks of these could be seen in continental Europe. One possible explanation, in addition to natural selection (Darwin 1859), may be found in the Haldane's rule (Haldane 1922), which states: "when in the F₁ offspring of two different animal races one sex is absent, rare or sterile, that sex is the heterozygous [heterogametic] sex". Haldane based his rule on a study of 45 Lepidopteran, 10 bird and six mammalian crosses. In birds, female is the heterogametic sex (ZW) and will show sterility in interspecific matings, even though males were still fertile. In twenty-one avian species hybrid female offspring is known to be partially or completely inviable, and in thirty species hybrid female offspring is sterile (for review, see Laurie 1997). Because mtDNA is maternally inherited, the possible reduced viability or even sterility of the hybrid female offspring of two different subspecies may explain the slight expression of the massive releasing activity in mtDNA in the present populations. However, this aspect remains to be studied.

Unsuccessful introductions may result from the maladaptation of birds to climatic or environmental conditions of the introduction areas. In hand-rearing for conservation purposes, the genetic origin of the animals should be compatible with the wild ones of the releasing site (Rave *et al.* 1994, Glenn *et al.* 1999). The genetic similarity of wild and hand-reared birds should preserve local adaptation and avoid harmful effects of outbreeding (Templeton 1986). Even though animals are released only for hunting purposes, without any target for increasing the population size, this does not totally remove the risk for outbreeding depression. Some of the released individuals may survive in the wild and breed later. The hybridisation between the released alien and local subspecies may reduce fitness and adaptation to local conditions by a disruption of adaptive gene complexes (Templeton 1986).

5.14 Practical gamebird management in light of this study

Wild and hand-reared capercaillies differed from each other in many morphological and physiological features (I). Similar results were obtained on grey partridges (Putala & Hissa 1995). Thus, the difference between wild and traditionally hand-reared gamebirds may be considered as well documented. Hand-rearing affects GI tract as well as the flight muscles in both of these species.

Grey partridge chicks fed a diet rich in invertebrates were heavier than chicks fed a low-insect diet or a fish diet. They also had better developed wing primaries, and a superior temperature regulation ability (II). This result highlights the importance of natural food for the growing chicks. Grey partridge chicks should be provided with invertebrates at least during the first weeks of their life.

The abrupt change in diet from pelleted commercial poultry food to natural food (III, V) caused a mass loss in grey partridges, and the body mass stayed at a lower level during the feeding trial than in control birds. They also had to increase their food intake to compensate the high fibre and low energy content of the natural food compared with the commercial food. However, feeding on natural foods only improved the gizzard mass in grey partridges. Plasma analyses did not reveal any dramatic disparities between traditionally or naturally fed grey partridges (III, V). As a consequence of these feeding trials we may summarise, that preconditioning of birds to natural food is beneficial, but a six-week period may not be long enough for acclimation of the birds.

The parameters used for studying power production showed a clear difference between wild and hand-reared capercaillies. The cytochrome-c oxidase activity, glycogen content of the muscles and the size of the heart may reflect differences in take-off and flying abilities. High plasma thyroxine concentration can indicate low metabolic level, which may affect the power production and flying ability. These results support the earlier suggestions about the benefits of large rearing aviaries, where birds can exercise their muscles and heart. It would probably be worth trying to teach hand-reared birds to recognize predators, as a valuable adjunct to predator-naïve birds after release (Dowell 1989, McLean *et al.* 1995, Griffin *et al.* 2000).

An interesting finding in this study was the slight impact of introductions that could be seen despite the centuries long introduction actions in Europe. The genetic disparity between wild and hand-reared Finnish grey partridges in the mtDNA was considerable deep. The control region 1 differed by 13 substitutions and 1 deletion/insertion between wild main eastern and hand-reared main western birds (VI). The history of hand-rearing and releasing of grey partridges is long; birds have been moved from one place to another, and it was of great interest to find some of the Irish grey partridges to be identical to those from Finland, Bulgaria, Russia or Greece. The crash of the grey partridge population in Finland may be a consequence – at least partly – of the use of more southern subspecies for introductions. The Finnish natural population represents, without any doubts, a more eastern mtDNA lineage. Genetic compatibility of released birds to the native population of the releasing site should be ensured before any releasing actions are put into practice.

Some of the game management economics are addressed to hand-rearing and releasing gamebirds. However, the survival of hand-reared birds after the release is poor. Hand-reared birds differ from their wild conspecifics in many morphological, physiological and behavioural ways, which may explain their high mortality. Before any releasing activities are started, it is more important to take care of the habitat. There is no use in trying to reintroduce galliform birds to areas where the habitat has become unsuitable or even hostile because of human activity, farming or forestry practices. It may be a strong statement to advocate predator-control (Maa- ja metsätalousministeriö 1999). It is preferable to determine how habitat changes have negatively affected gamebirds, and then direct management to reverse these negative changes.

If hand-rearing and releasing are carried out for hunting purposes only, the quality of birds is not of great importance. However, if the aim is to increase the population size, or even to reintroduce a species, the quality of the birds is vitally important. According to this study, more natural rearing methods are preferable. Hand-reared birds should be fed natural food, and should be able to exercise their flying muscles and heart, for which an adequate area for flying is required. However, the most important thing is to ensure that

the birds represent proper subspecies. Further, grey partridges should be managed population-by-population. Releasing birds without any genetic adaptation to the environmental conditions, into which they are released, is a waste of time and money.

6 Conclusions and further study visions

This work consists of six studies investigating the background of the poor survival of hand-reared galliform birds released into the wild. The aim of these works was to clarify those morphological, physiological, and genetic differences between wild and hand-reared birds, which may explain the high mortality of released birds. Hand-rearing and releasing gamebirds may not only be game management, but also species or biodiversity conservation activities. Accordingly, the subspecies of the birds raised for releasing purposes must be of the same genetic stock as the birds from the releasing site. The rearing methods should be conducted in a way that enables the birds' morphology and physiology to develop in natural ways. This includes feeding practices as well as rearing aviaries, which should, at least to some extent, mimic life in the wild.

Further studies can be easily designed based on the results of the present studies. It would be of interest to study more closely the detoxication mechanisms of galliform birds. What happens in the caeca and small intestine and what kinds of microbes take part in the detoxication activities? Is the hepatic detoxication enzyme activity inducible with other plant secondary compounds, like terpenoids or alkaloids? Do birds produce proline-containing proteins in their saliva as protection against plant secondary compounds?

In the field of molecular marker analyses, and their applications, several fascinating visions can be seen. The easternmost parts of the European continent and the whole Asian distribution area of the grey partridge are still open questions regarding the genetic structure of the populations. By sequencing grey partridges from these areas we could get more detailed information about the post-glacial colonisation routes of the European grey partridges. Other molecular markers, such as microsatellites, could be used to validate or deepen this approach. The viability and fertility of the hybrid offspring of grey partridges representing eastern and western mtDNA lineages should be verified.

Both the grey partridge and the capercaillie have suffered from human impact on their natural environments. Thus, both species may be considered as bioindicators, when environmental questions are studied both in agriculture and forestry contexts. As I think that the grey partridge is the most beautiful bird in the world – and the capercaillie probably the second most beautiful – I may conclude that the beauty of these birds is worth saving as a value itself.

7 References

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