UPPSALA
UNIVERSITET

Living in a Variable Environment

Reproductive Decisions in Wild Bird Populations

MÅRTEN B. HJERNQUIST

Dissertation presented at Uppsala University to be publicly examined in Zootissalen, EBC, Friday, January 9, 2009 at 10:00 for the degree of Doctor of Philosophy. The examination will be conducted in English.

Abstract

Hjernquist, M B. 2008. Living in a Variable Environment. Reproductive Decisions in Wild Bird Populations. Acta Universitatis Upsaliensis. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 584. 32 pp. Uppsala. ISBN 978-91-554-7369-3.

In nature, environments are often variable and heterogeneous influencing ecological and evolutionary processes. This thesis focus on how animals interact with their environment and how that affects the reproductive decisions they make. Using empirical data collected from wild collared flycatcher populations, experiments and molecular approaches I try to unveil some of these relationships and the evolutionary, ecological and conservation implications of these findings are discussed.

Firstly, collared flycatchers were shown to use breeding densities of their own and other species using similar resources when assessing costs and benefits associated to breeding in specific habitats. However, species will vary in how informative they are, and the worst competitor – with whom you overlap most in resources needs – also provides the best source of information. Collared flycatcher parents will also benefit differentially from investments in sons and daughters due to habitat characteristics and dispersal differences between the sexes. Here, I show that they will produce more of the sex that will give the highest expected fitness return given the environment they are in. These results also provide a reciprocal scenario to Clark's (1978) classical study of sex ratio adjustment in relation to local resource competition (LRC), as more of the natal philopatric sex is produced when LRC is low.

Secondly, the effect of elaborated ornaments on paternity in the socially monogamous collared flycatcher was shown to be of more importance in areas where the intensity of intra- and intersexual conflicts are expected to be elevated. Hence, ornamentation by environmental interactions determines paternity, illustrating that sexual selection through extra-pair paternity is context dependent.

Finally, even though the collared flycatcher populations that this thesis is based on have been studied on their breeding grounds for more then 25 years, we know little of where they are when they are not breeding. Here, stable isotope signatures in winter-grown feathers suggests that they may spend their winter with their breeding ground neighbours and do so repeatedly over years. Differences between breeding populations at this small scale should have many impactions for evolutionary and ecological processes as it will, for example, determine with whom individuals interact throughout their life.

Keywords: evolutionary ecology, competition, sex allocation, paternity, EPP, inadvertent social information, migration, breeding density, territory quality, territory availability, great tit, blue tit, Ficedula albicollis

Mårten B. Hjernquist, Department of Ecology and Evolution, Norbyv 18 D, Uppsala University, SE-75236 Uppsala, Sweden

List of Papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals:

I   Hjernquist, M.B., Thuman Hjernquist, K.A., Forsman, J.T., and Gustafsson, L. Sex allocation in response to local resource competition over breeding territories. *Behavioral Ecology* (In Press).

II   Forsman J.T., Hjernquist, M.B., Taipale, J., and Gustafsson, L. 2008. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. 2008. *Behavioral Ecology*, 19: 539-545.

III Forsman, J.T., Hjernquist, M.B., and Gustafsson, L. Experimental evidence for the use of density based interspecific social information in forest birds. *Ecography* (In Press).

IV   Hjernquist, M.B., Sheldon, B.C., and Gustafsson, L. Ornamentation and environment interact to determine paternity in a territorial bird. *Submitted manuscript*.

V   Hjernquist, M.B., Veen T., Font, L., and Klaassen M. High repeatability and population differentiation in stable isotope ratios in winter-grown collared flycatcher feathers. *Submitted manuscript*.

Contents

Abbreviations

EPC	Extra-pair copulation (see box 6)
EPP	Extra-pair paternity (see box 6)
EPY	Extra-pair young (see box 6)
ISI	Inadvertent social information (see box 4)
LMC	Local mate competition (see box 5)
LRC	Local resource competition (see box 5)
MC	Migratory connectivity (see box 7)
PI	Personal information (see box 4)
SI	Social information (see box 4)

Introduction

A central topic in evolutionary ecology is to understand how and why communities are shaped as they are, and what effect this has on community members. A good start is then to study the factors that influence the distribution of individuals and the resources upon which they rely. As resources often are limited and unevenly distributed in both time and space, and given that individuals of the same species and of species with similar needs co-occur at least during some part/parts of their life, the overall demand for resources often exceeds the amount available, resulting in competition between individuals. Environmental variation can influence the quality and quantity of resources, impacting how these resources vary over time and in space (e.g. Begon et al., 1996). The fitness of individuals depends on both the total amount of resources they can acquire in this competitive environment (e.g. Begon et al., 1996), and how they allocate these limited resources. Such decisions of resource allocation between traits important to fitness are referred to as life-history trade-offs, and the optimal strategies of allocation depend on the state of the individual and the environment (e.g. Frank, 1990; Roff, 2002). For example, collared flycatchers invest differently into current or future reproduction depending on their age and condition (e.g. Gustafsson and Sutherland, 1988). Furthermore, environmental conditions will directly or indirectly affect the cost and benefit returns at a given place and time and thus influence the fitness return of each investment unit.

It is also important to recognize that organisms acquire resources in different ways depending on the type of resource and how resources are distributed. For example, resources such as food may be successfully acquired through finding and processing the food at a faster, more efficient rate than competitors (scramble competition), or alternatively by aggressively excluding competitors from territories in which the food is located (interference competition). Not only do individuals vary in their success at acquiring such territories, the territories themselves may vary in quality (the amount of resources contained within). However, competitive ability is not the only factor determining which individuals occupy available territories. Resources may be more or less important to different individuals within the same population. These differences are often particularly striking for males and females (e.g. Frank, 1990), and sex-specific utilisation of resources leads to differences in how parents should optimally allocate resources to sons and daughters (sex allocation) in various environments. (Box 5). One way to allocate resources differentially to sons and daughters is to adjust offspring sex

ratio. For example, when competition over local resources is intense, the greater galago (*Galagos crassicaudatus*), a primate species, produces more offspring of the sex that will disperse to reduce local resource competition (LRC) (Clark, 1978). Primary sex ratios among offspring birds also show widespread variation in nature, although there has been considerable debate over whether this variation reflects adaptive sex allocation. A recent meta-analyses on sex allocation in birds, or more specifically on primary sex ratio adjustment, came to the conclusion that there were strong support for adaptive sex allocation (West and Sheldon, 2002). Ewen et al. (2004) later criticised those conclusions showing only weak support for facultative sex ratio adjustment in their meta-analysis, and only for the few studies concerning breeding territory quality (see Cassey et al. (2006) for corrections). It is therefore important that we study sex allocation across environments to improve our understanding of how environmental variation affects differential resource allocation decisions to offspring of different sex (I, II).

Not only do interactions between individuals within a community affect how resources should be allocated, but it will also affect various other ecological and evolutionary processes. While high breeding densities increase overall levels of competition, it also creates more opportunities for males and females to seek extra-pair copulations. Thus, the level of intra- and intersexual conflicts are expected to be influenced by changes in breeding densities. Increased conflict between and within the sexes will affect evolutionary processes potentially accelerating adaptive or maladaptive evolution (Andersson, 1994) and possibly also speciation (Arnqvist and Rowe, 2005). Similarly, variation in other resources and the environment is expected to affect sexual selection. Incorporating environmental variables and their interactions in studies of sexual selection will therefore present a more accurate and complex picture of the evolutionary dynamics in nature (IV). Until now I have focused attention on the dynamics of intraspecific competition. However, resource availability is influenced by the densities of any other species with overlapping resource usage (e.g. Gustafsson, 1987). Such negative effects of competition has lead to the principle of competitive exclusion, which states that two competing species coexist in a stable environment only if they have differentiated their realized niches (Gause, 1934). However, recent studies suggest that competitative exclusion may take considerable time (Hubbell, 2001) and there might also be benefits associated with breeding in areas with heterospecific competitors under specific circumstances (e.g. Forsman et al., 2002, Monkkonen et al., 1997). For example, other species may indirectly signal the presence or abundance of predators through their breeding density and may also provide defence against predators. Similarly, the occurrence of close heterospecific competitors will be linked to the abundance of mutual resources in that habitat, hence, associated to habitat quality. Such effects are generally not considered in traditional models of habitat selection, metapopulation dynamics and species coexistence, and understanding more about these dynamics is crucial for our understanding of evolutionary and ecological processes within communities (II, III).

Thesis aims

The community structure, the environment and the interactions between them are key factors for many ecological and evolutionary questions. In the following chapters of this thesis I will discuss how variation in the environment influences reproductive events. Focus will be on reproductive decisions and their outcome in a variable environment, ranging from reproductive settlement, investment and allocation decisions to mating behaviours and ornamentation. The emphasis of the first part (I-III) is on how interactions between individuals, of both the same (conspecifics) and of different species (heterospecifics), and their environment affect reproductive settlement and investment decisions as well as resource allocation. In the first paper, I test how patterns of sex allocation change between areas with different levels of intraspecific competition over local resources. The second paper continues to investigate how patterns of sex allocation are related to environmental variables, this time focusing on interspecific competition. Further, competition between animals is traditionally thought of as something negative for one of the parties involved, but in paper II and III focus will be made on both the benefits and costs of living with con- and heterospecific competitors. Both papers test if information regarding resources within in a specific area is obtained from other individuals, and whether this influences reproductive decisions. As stated above, sexual selection is expected to be affected by environmental variation and paper IV examines how female mating behaviour varies across environments. These questions will be addressed using emperical data both from nature as well as from experiments. Focus is on the collared flycatcher (*Ficedula albicollis*) as a model migratory species, in addition to interspecific interactions involving two species of resident titmice (*Parus* spp.). These species and the study sites will be presented in more details in the following chapter. Finally, despite extensive knowledge of their breeding ecology, we lack information on the ecology of collared flycatchers in their African wintering grounds. The environmental variation and community structure an individual encounters each winter could affect subsequent breeding events and thus, to fully understand the reproductive decisions of migratory organisms we need detailed information of their entire life cycle. The structure of wintering communities of collared flycatchers was inferred using stable isotopes, in order to test the strength of winter site philopatry and how migrants from different breeding populations are distributed on their wintering grounds (V). To conclude this thesis, major findings will be summarized, future directions outlined and limitations of the studies of which this thesis is based on will be discussed. A short summary is also presented in Swedish. For more details on methodology not presented here see the paper/s to which the chapter/s refer.

The study site and species

The island of Gotland

The island of Gotland (57°30'N, 18°30'E) is 3,140 km^2, and is situated in the Baltic Sea (Fig. 1). It is made up of limestone from the Silurian period and the common soils are either sand based or consists of different moraines (Geological Survey of Sweden, http://www.sgu.se). About half of the island's surface is covered with forests, 90% of which is coniferous (76 % Scots pine (*Pinus sylvestris*), and 13 % Norway spruce (*Picea abies*)) (Hjernquist et al., 2008). The remaining tenth of the forests consists of deciduous trees (Hjernquist et al., 2008). The majority of the study sites are situated in these deciduous woodlots, where English oak (*Quercus robur*), common ash (*Fraxinus excelsior*), common hazel (*Corylus avellana*) and silver birch (*Betula pendula*) dominates (pers. obs.). However, some study sites are situated in mixed coniferous-deciduous forests, and one is a pure coniferous forest. Installed in all study sites are nest-boxes favoured by collared flycatchers (*Ficedula albicollis*, the study species), pied flycatchers (*F. hyperleuca*), and great (*Parus major*) and blue tits (*Cyanistes caeruleus*). Other animals utilizing the nest-boxes in small numbers (<1% of boxes), are other passerine birds such as coal tits (*Periparus ater*), Eurasian wrynecks (*Jynx torquilla*) and Eurasian nuthatches (*Sitta europaea*), and mammals such as brown long-eared bats (*Plecotus auritus*), northern bats (*Eptesicus nilssonii*) and yellow-necked mice (*Apodemus flavicollis*) (pers. obs.). The Uppsala University nest-box project's core areas on southern Gotland have been annually monitored since 1980 and two main expansions have followed in 1990 and 2003 (Fig. 1). After 2003, additional areas have also been included (Fig. 1). Today, more then 2000 nest-boxes are installed over the island. Some additional data also comes from another long-term nest-box project on Gotland, started in 1976 by Johan Träff (Fig. 1).
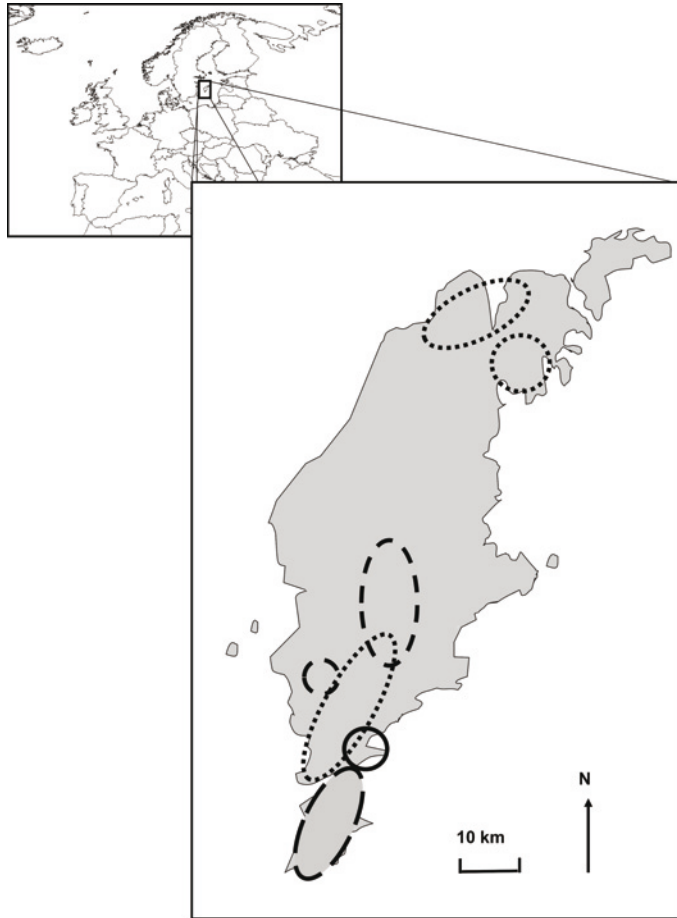
Figure 1 *Maps of Europe and Gotland, the island where all study sites are situated. The area within the long-dashed line represents the southern core area where study sites have been annually monitored since 1980 (annual population size of almost 400 collared flycatcher pairs, used in article I, IV to V). The solid line circles the area where study sites belonging to the long-term project administrated by Johan Träff, which have been annually monitored since 1976 (annual population size of about 200 collared flycatcher pairs, used in article V). Areas within dashed lines represent forests where nestboxes were installed in study sites in 1990 (annual population size of about 120 collared flycatcher pairs, used in article I, IV and V) while dotted lines circles the area where nest-boxes were installed in study sites in 2003 or later (annual population size of about 200 collared flycatcher pairs, used in article I - III and V).*

11

Collared flycatchers

The main focus of the work in this thesis is on a wild population of collared flycatchers. The collared flycatcher is a small (~13g), long-distance migratory passerine bird within the family of Old World flycatchers (*Muscicapidae*). They arrive at the breeding areas situated on the island of Gotland in the beginning of May from their wintering grounds in sub-Sahara Africa (box 1). Males then compete over and establish breeding territories surrounding a natural cavity in a tree or a nest-box, preferably in deciduous forest. Males that obtain a breeding territory then attempt to attract females using vocal, morphological and behavioural signals. The best studied of these is perhaps the white forehead patch (e.g. Qvarnström et al. 2000). Females use not only these secondary sexual signals when choosing mates, but also favour males with high quality breeding territories (e.g. Alatalo et al., 1985). Once paired, the female starts to build a cup-shaped nest using dried up grass, bark and leaves. The females lay one egg per day, and single clutches contain four to seven eggs (mean = 6.1 (± 0.8SD) (Svedin et al., 2008). These are incubated by the female for two weeks, and chicks are provisioned by both parents for an additional two weeks before they fledge (Pärt and Gustafsson, 1989). On average, each collared flycatcher brood produces 3.8 (± 2.5SD) fledglings (unpublished data). After juveniles have fledged, little is known of how the parents and offspring interact but it is commonly thought that parents continue to feed the offspring for about two additional weeks, as indicated by feeding rate estimates determined in nature (FREDIN) (pers. com. S. Hasp). Collared flycatchers can live up to nine years in nature (pers. obs.), but of those that survive the first year, the average lifespan is roughly two years (Svedin et al., 2008). The majority of collard flycatchers are socially and genetically monogamous with seasonal pair bonds (Gustafsson and Qvarnström, 2006). About 25-35% of all nests contain offspring not fathered by the social father (Sheldon and Ellegren, 1999, IV) and about 9 % of all males attract a second female to an additional breeding territory (Gustafsson and Qvarnström, 2006). Just prior to migration to their African winter grounds (box 1), birds born that year have a partial moult, and adults have a complete moult into their autumn plumage (Svensson, 1992). At the wintering grounds both first year and older birds go through a partial moult into their breeding plumage (Svensson, 1992). The partial moult includes all feathers except the primaries and their coverts and about half to three quarters of their outermost secondaries and their coverts (Svensson, 1992). For distribution maps and pictures see box 1.

The collared flycatcher also rarely hybridizes with closely related species, of which the pied flycatcher is the only one breeding in the study area (Veen et al., 2001). On Gotland, mixed pairs of flycatchers make up about 5% of the breeding flycatcher population whereas pure pied flycatcher pairs approximately make up an additional 5 % (Veen et al., 2001).
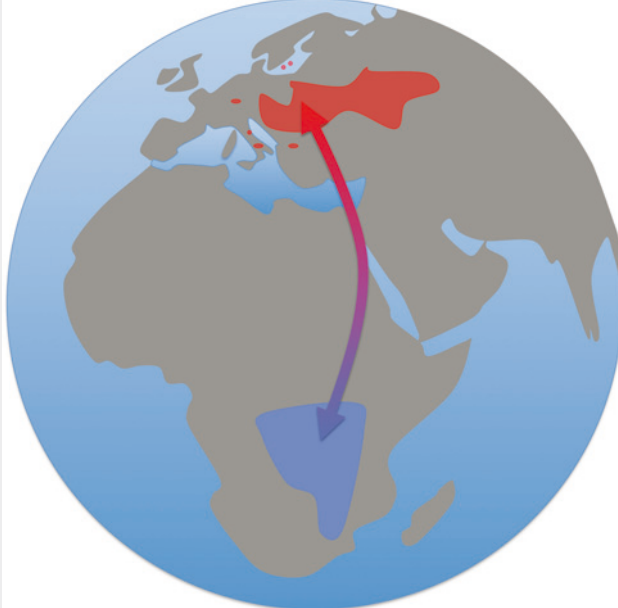
Box 1 Collared flycatcher A singing one year old male collared flycatcher in the spring trying to establish a territory and attract females (top left and bottom right picture) like the female on the botton left picture. When paired up the female starts nest building (top right picture – female with nest material). On young males it is easy to see what feathers that has been moulted in Africa (black) during the partial moult, and which has been moulted last summer (brown) during the complete moult. The map illustrates the breeding distribution (red areas) and the African winter grounds for collared flycatchers (blue area) as well as the approximate migration route (arrow) (details from Cramp and Perrins 1993).

Great and blue tits

The great (box 2) and blue tit (box 3) are partially residential birds in Sweden, meaning that a part of the Swedish population migrates a short distance southwards to overwinter, while the others are resident. Most breeding on Gotland are year-round residents. The great tit is found in both deciduous and pine forests whereas the blue tit prefers deciduous forests. Both nest in tree cavities and nest-boxes similar to collared flycatchers, and adult titmice also eat and feed their

Box 2 Great tit

Both great (picture to the left) and blue tits (box 3) nests in open areas, meadows, gadens and in forests. A meadow with many bushes (e.g. hazel and hawthorn) and trees (e.g. oak and ash) as seen picture to the right shows a typical habitat for both great and blue tits as well as collared and pied flycatchers. Such areas are also rich on caterpillars and other food resources important to juveniles of all the above species.

Great tits on Gotland:

Clutch size	9 eggs on average
Number of clutches per breeding season	1 (less then 5% have a second clutch)
Incubation time	approximately two weeks

For more details see e.g. Gustafsson (1987, 1988) and referrences therein.

offspring similar food to collard flycatchers, resulting in interspecific competition (Gustafsson, 1988, Gustafsson, 1987).

Both species start nest building and egg laying earlier than the collared flycatcher, often by more then two weeks (Gustafsson, 1988). Titmice densities in areas without nest-boxes often do not exceed two pairs per hectare (Gustafsson, 1987) whereas in areas with nest-boxes densities may be as high as four pairs per hectare (II, III) or higher. Titmice densities consist of about two thirds great tit and one-third blue tit pairs (pers. obs.).

Box 3 Blue tit

Both blue (picture to the left) and great tits (box 2) builds a cupformed nest using moss, wool, feathers and grass. Before incubation starts the eggs are covered with nest material. Both blue and great tits nest in the same nest-boxes as collared and pied flycatchers do. On the picture to the right morphological measures and blood samples are collected from an adult bird in a typical decidious habitat where both titmice and flycatchers nest.

Blue tits on Gotland:

Clutch size	11 eggs on average
Number of clutches per breeding season	1 (a few second clutches)
Incubation time	approximately two weeks

For more details see e.g. Gustafsson (1987, 1988) and referrences therein.

Living together in a variable environment

By definition, co-existing with competitors, regardless if they are conspecifics or heterospecifics, is associated with costs (Begon et al., 1996). As argued above, these cost will depend on the distribution, quantity and quality of the resource, how many individuals that are utilising the resource, as well as the overlap in resource niche between individuals (Begon et al., 1996). Further, the availability of alternative resources and variation in competitive abilities between individuals will also influence the intensity of competition. (Begon et al., 1996). Despite the costs of breeding in areas with heterospecific competitors, recent studies have suggested that there are also benefits. This is mainly due to the fact that the densities of heterospecific competitors are positively correlated with the abundance of resources and/or negatively associated with the abundance of predators (e.g. Forsman et al., 2002). When the reproductive season is short and individuals are time-limited, as is the case for most migratory birds, breeding in areas with some competitors may be an adaptive strategy for locating resource-rich territories or areas with low predation levels. Copying the habitat choice of others with similar resource needs reduces costs associated with gathering personal information (PI) (e.g. Monkkonen et al., 1997, Monkkonen et al., 1990, Forsman et al., 2002). Paradoxically, species that are the strongest competitors should provide the most reliable information on habitat quality. Because of the cost of intense competition when densities of heterospecific competitors are elevated, the highest fitness returns are expected in intermediate breeding densities (Forsman et al., 2002, Forsman et al., 2008).

Box 4. Personal and social information
First, a broad and short definition of what information is – information is anything that reduces uncertainty. Most organisms are using some sort of information e.g. when making reproductive decisions (I, II, III). Information can either be acquired by individuals interacting with their physical environment learning through trail and error, i.e. personal information, or be vicariously acquired through observing cues and signals produced by others, i.e. social information. Personal information (PI) is usually divided into private (which is inaccessible to others) and public (which produces social information). Social information can in turn be intentionally communicated as signals (communication) or inadvertently advertised as cues (inadvertent social information (ISI)). For review see e.g. Danchin et al. (2004).

Organisms can benefit from acquiring and using information provided by con- and heterospecifics (box 4). This information can then be used when deciding where to settle, how much to invest into current reproduction, and how to allocate resources to maximize the fitness return. For example, if the fitness of sons and daughters is different in any given environment, theory predicts that parents will invest in, or even bias the offspring sex ratio towards the sex that will provide the highest fitness return (Box 5). Thus, according to sex allocation theory, parental investment should be biased towards offspring of the philopatric sex if the quality of the breeding territory or area is favourable, and towards the dispersing sex if local conditions are unfavourable (Box 5). As male collared flycatchers are philopatric to their natal area, in areas where vacant territories (an otherwise limiting resource) are widely available, pairs would benefit from producing more sons (Pärt, 1990).

Most sexually reproducing organisms still have to live, at least for a short time, with conspecifics to be able to reproduce. Competition over reproductive opportunities is generally stronger in males as the number of potential female partners limits their reproductive success (Andersson, 1994). Females on the other hand are expected to be choosy about with whom they should mate. Competition among males may be indirect (through being most attractive to females), or direct (through defending breeding territories against other males in order to be considered by females). In collared flycatchers, the outcome of male-male and female-male interactions can be predicted by the size of a white patch on the forehead of males (Qvarnström et al., 2000), a condition-dependent ornament (Gustafsson et al., 1995). Environmental factors may influence the degree of this competition in several ways. Low availability of breeding territories, or large variance in their quality increases reproductive variance, increasing sexual selection. The same is true for breeding densities, as the intensity of sexual selection among males and females is expected to increase with elevated breeding densities, hence, increased likelihood of encountering extra-pair partners. Although the majority of collared flycatchers are socially monogamous (Gustafsson and Qvarnström, 2006), extra-

Some examples of organisms that have been shown to use ISI:

Norwegian rats (*Rattus norvegicus*) smell the breath of other rats when faced with a novel food resource (Galef and White, 1997).

Collared flycatchers are using reproductive success of conspecifics as a cue for dispersal decisions (Doligez et al., 2002).

Migratory birds, such as collared flyctchers (e.g. II) and teals (*Anas crecca*) (Elmberg et al. 1997) are attracted to resident birds with similar resource needs.

pair paternity (EPP, Box 6) is common (Sheldon and Ellegren, 1999, IV), and polygamy occurs at low frequency. Because more ornamented males sire more of their own offspring, sexual selection acting through EPP is expected to be density-dependent (Sheldon and Ellegren, 1999, IV). Thus, interactions between conspecifics and heterospecifics over any resources will influence evolutionary processes through both sexual and natural selection.

In articles I, II and III, experimental manipulations of the level of competition between both con- (I) and heterospecifics (II and III) were conducted to test the effect on reproductive decisions, such as where to settle, how much to invest into reproduction and how to allocate these resources to sons and daughters in the collared flycatchers specifically (I and II), and for migrating passerines in general (I, II, III). We can thus examine the role of environmental variation in reproductive decisions and thereby improve our understanding of how the direction and strength of evolutionary processes may vary with current conditions. We also tested whether or not collared flycatchers (II) and other migrating birds (III) acquire and use social information (SI, Box 4) when making these reproductive decisions. In article IV the effect of male ornamentation on the level of extra-pair paternity (EPP) is extended incorporating environmental variation (breeding densities and the quality of breeding territories) and interacting effects (ornament by environment effects) and will therefore tell us if processes of sexual selection are context dependent.

Finally, many birds, including collared flycatchers, breeding in the northern hemisphere are migrants, causing individuals to experience different environments throughout their life cycle, and for many organisms these environmental shifts reoccur every year (Alerstam, 1982). Different phases in a migrant's annual cycle are not independent, and factors affecting an individual in one phase can have consequences for that individual in subsequent phases (Fretwell, 1972). It is generally assumed that such carry-over effects between phases or seasons are widespread, having important consequences for the ecology, evolution and conservation of migratory organisms (Gill et al., 2001, Webster et al., 2002; Norris, 2005). Despite the equal importance of performance in all phases for an individual's fitness, most migratory species are studied extensively only during the breeding season. We often lack detailed knowledge on where they spend the winter and how they are distributed on the wintering grounds. For example, the ecology, current evolutionary processes and their evolutionary past (and much more) of the collared flycatchers breeding on Gotland have been studied for more then 25 years resulting in numerous doctoral theses, peer-reviewed publications, books and book chapters, but still we cannot be more precise about where they spend their winter or how they get there, than that they fly down eastern Europe and overwinter in sub-Sahara Africa (Veen et al., 2007 and references therein). Further, although carry-over effects are assumed to be common (Webster et al., 2002) we do not know how they affect individuals, their reproductive decisions

and the ecological and evolutionary processes that they experience. In article V, one step towards increasing our knowledge of the winter quarters of collared flycatchers is made using the stable isotope approach.

Nest site selection and Reproductive investment decisions

Migration is a behavioural adaptation associated with seasonally oscillating environmental conditions, like food abundance and reproductive opportunities (e.g. Lundberg, 1988). For example, birds will move to areas with great abundance of resources, like the northern hemisphere during the spring and summer, and away from areas with little resources, like the northern hemisphere during autumn and winter (Alerstam, 1982). These shifts in resources are also often linked to reproductive opportunities. Because these abundant resources are limited to short time-spans, migratory birds, such as collared flycatchers, benefit from breeding soon after arrival (Sheldon et al., 2003). Time wasted on surveying vacant habitats for territories of the highest quality (obtaining personal information – PI) thus has important ramifications for fitness. Copying the choice of others with similar resource needs is one strategy to decrease costs associated to obtaining PI. Collared flycatchers were observed to rely on titmice breeding densities as a cue of the expected overall fitness returns of breeding in a given area (II). Forests where they were expected to gain the highest fitness return, i.e. with intermediate titmice densities, were selected first (II). However, given that titmice densities were experimentally manipulated, uncoupling titmice densities from habitat quality, collared flycatchers did not make reproductive decisions matching their fitness outcome (II) (Fig. 3). Hence, experimentally illustrating that animals' can acquire and use SI, when making reproductive settlement decisions.

Interspecific interactions also affected collared flycatchers' reproductive decisions of how much to invest in reproduction and of how to allocate resources into sons and daughters (II) (Fig. 3). Again, due to manipulation of titmice densities, collared flycatchers made a mismatch in their reproductive investment decision, producing larger clutch sizes and more of the philopatric sex in intermediate titmice densities. This demonstrated that they relied on titmice densities as a cue for habitat quality and intensity of competition. Interspecific information use has many ecological and evolutionary implications not considered in models of e.g. habitat selection, population dynamics, metapopulation dynamics and species coexistence (II).

Even though many migrating birds seem to use resident competitors as a cue for habitat quality and for the level of competition within a specific site, the association between resident and migrant breeding densities may not always be unimodal (III). The unimodal relationship is expected for species that most overlap in resource needs, i.e. when the costs exceed the benefits in high densities

Box 5. Sex allocation

Frequency dependent selection should lead to an equal parental investment in sons and daughters (Fisher, 1930, Frank, 1990). Assuming equal costs of producing sons and daughters, when a population is skewed towards one sex, the benefits of investing in the other sex increases (Fisher, 1930, Frank, 1990). However, if the fitness of sons and daughters is affected differently by e.g. environmental factors, theory predicts that parents should invest more, or if possible, only producing offspring of the sex with the highest fitness return for each investment unit (e.g. Trivers and Willard, 1973, Charnov, 1982, Hamilton, 1967, Clark, 1978, Frank, 1990).

In 1967 Hamilton showed that parental fitness would increase if more resources were allocated to daughters when competition between brothers were high, and vice versa. This theory of sex allocation, the Local Mate Competition theory (LMC), took the first modern day steps improving our knowledge of sex allocation since Darwin (1859, 1871). Local Resource Competition (LRC) has great similarity to the theory of LMC and was suggested to explain biased sex allocation in primates (Clark, 1978). Clark (1978) suggested that parents limit competition among philopatric daughters by producing sons who will disperse. Further, according to sex allocation theory, parental investment to sons and daughters and/or sex ratios should also be biased towards the philopatric sex if the quality of the breeding territory or habitat is favourable and towards the dispersing sex if local conditions are unfavourable (e.g. Julliard, 2000). Thus, the basic idea of any sex allocation theory is that if a population deviates from equal allocation to sons and daughters, this must be explained either in terms of selection or evolutionary constraint.

Differential sex allocation has been observed in several taxa (Clark, 1978, Hamilton, 1967) and avian sex ratio adjustment has been reported to correlate with many life-history traits (e.g. Sheldon et al., 1999, Heg et al., 2000, Thuman et al., 2003) and some environmental variables (e.g. I, II). However, today we lack knowledge of the underlying mechanism/s for sex ratio adjustment in birds and mammals, a crucial part that is needed to fully understand how animals can adjust their sex ratio. Nevertheless, recent meta-analyses on avian sex ratio adjustment conclude that there is an adaptive sex ratio variation in wild bird populations (strong support according to West and Sheldon (2002), whereas Ewen *et al*. (2004) only found a weaker support and only for studies concerning breeding territory quality – see Cassey *et al.* (2006) for corrections).

Above picture shows five male and two female four days old collared flycatchers.

Box 6. Extra-Pair Paternity (EPP)

Mating systems for sexually reproducing species can be divided into two main groups, monogamy (were one individual reproduce by mating with only one other individual) and polygamy (were one individual reproduce by mating with several other individuals). These two main groups can of course again be separated based on numerous variables and characteristics of e.g. if one or both sexes engage in multiple matings. Monogamy is a relatively common mating system in nature, at least in vertebrates, where a male and a female form a social pair. However, only a few species are truly monogamous. For example, in birds less the 25% of the socially monogamous species are genetically monogamous (Griffith et al., 2002).

Engaging in copulations outside the social pair, i.e. extra-pair copulations (EPC), is expected to be costly (Griffith et al., 2002, Arnqvist and Kirkpatrick, 2005 and references therein) and why and how EPP has evolved and is maintained in socially monogamous species is a question that have received much attention during the last decades. Given these expected costs, the main hypotheses for the function and maintenance of females to mate outside the social pair have focused on the benefits for females to engage in EPCs and EPP is thus driven by females seeking copulations that will maximize their fitness outcome (review by Griffith et al., 2002). These costs and benefits are listed below (e.g. Griffith et al., 2002, IV and references therein).

Costs
Reduced parental care
Increased risk of sexually transmitted deceases

Benefits
Direct benefits (non-genetic benefits e.g. obtaining food).
Indirect benefits (genetic benefits such as avoiding infertile or less fertile males, genetically diversification of offspring or enhancing genetic compatibilies, or obtaining good genes e.g. genes for sexy sons).

In contrast to the above theory of the function of EPP a recent comparative study by Arnqvist and Kirkpatrick (2005) instead concluded EPP to be male driven. They argue that existing empirical evidence shows that indirect selection for females to engage in EPCs are weak at best and that selection against EPP is thought to be strong. Thus, Arnqvist and Kirkpatrick invoke the traditional view that males seeking mating opportunities outside their social pair can explain the occurrence of EPCs. Males should then defend his social partner from encountering other males to maximize his fitness and females should resist costly (listed above) extra-pair encounters. Variation in the dynamics of these sexual conflicts or differences in the cost-benefit balance can explain variation in the level of EPP between populations and species. Although such variation in EPP is also attributed to environmental variation (Rubenstein, 2007, IV).

(Forsman et al., 2002). As seen in article III, the relationship between resident titmice density and the densities of migrating species besides collared flycatchers is instead positively linear. Again, titmice densities were experimentally manipulated, resulting in a response in migrating birds to actual titmice densities. These results illustrate how the relationships between species using and providing density-based SI seem to vary depending on the overlap in mutual resource needs, the intensity of competition, and the costs and benefits associated to within and between species interactions. Variation between species in their ecology and evolutionary past as well as the environmental variation they experience influences the cues an individual uses when making its reproductive decisions. Hence, the information content of any cue varies widely according to receiver, and the same cue may signal different information to different species and populations and in different contexts.

Thus, the community's composition may play an important role in many evolutionary processes and may also prove to be important in practical conservation biology. For example, conspecific attraction has been used as a tool for attracting endangered species into safer nesting habitats and the same idea can be extrapolated to heterospecific cues as well (II).

Intraspecific interactions will also affect reproductive decisions. The observed bias in primary sex ratio toward more sons in areas with many available breed-
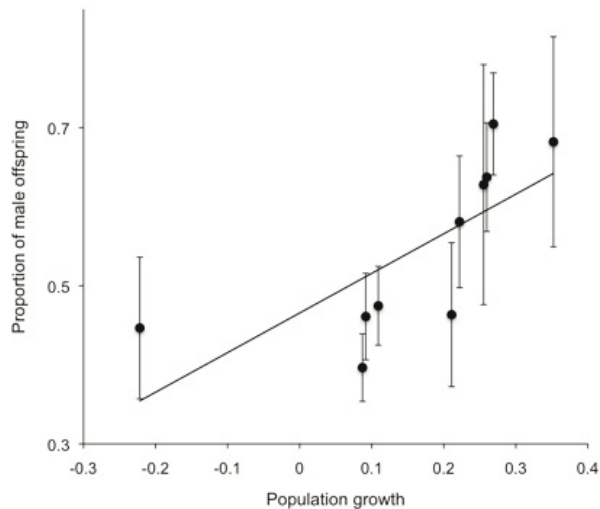

Figure 2 *Primary sex ratios in collared flycatcher broods in ten forests were significantly associated to the number of available breeding territories in that year Circles show population mean and bars indicate s.e. Population growth rate lower or higher than zero indicates a decrease or an increase in population size to the next year, respectively, which was used as an estimate of number of available breeding territories in the first year.*

22

ing territories (Fig. 2) is in agreement with the theory of sex ratio adjustment in response to LRC (Clark, 1978) (Box 5). However, it constitutes a reciprocal scenario to that described by Clark (1978), as more of the philopatric sex is produced due to low levels of competition over local resources (I). A meta-analysis by Ewen et al. (2004) supported the occurrence of facultative sex ratio adjustment within birds in response to changing territory quality (Cassey et al., 2006). To my knowledge, no study has previously shown such an effect of territory availability on sex allocation and sex ratio bias in avian species. Given that the potential for manipulating sex ratios exists in birds, breeding territory characteristics may be a general and important factor affecting sex allocation in birds. However, as that the underlying mechanism for sex ratio adjustment in birds is unknown (Pike and Petrie, 2003), the extent to which this is possible is unclear.
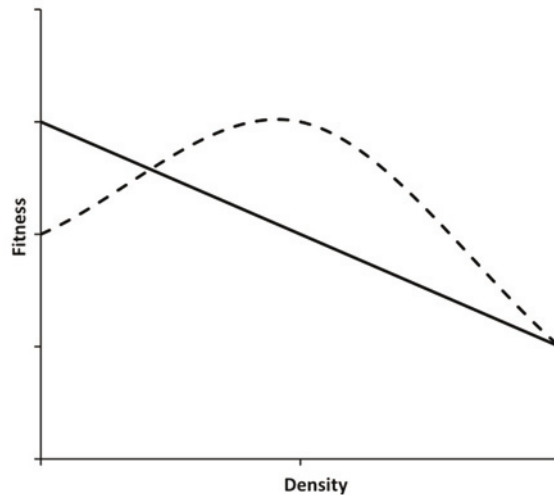
Figure 3 *Illustration of the theoretical predictions for the experimental manipulation in article II and III. If migrating birds, such as collard flycatchers, use resident titmice densities as an indicator of habitat quality and intensity of interspecific competition their investment into reproduction should follow a unimodal fitness curve (dashed line). However, this relationship is strongest for species that have the highest overlap in niche utilization and reource needs. Given that titmice densities were experimentally manipulated, in article II and III, the costs of nesting in low titmice density areas and benfits of breeding in intermediate titmice density areas are removed and the reproductive success is thus expected to be negativly linear associated to titmice densities (solid line). Hence, there will still be costs associated with breeding with competitiors but no benefits. Collared flycatchers preferred breeding at and invested most in intermediate titmice density areas (laid more eggs, biased their sex ratio accordingly), while their reproductive outcome was negatively linear related to titmice densities, which is in agreement with our theoretical predictions (II). Thus, they made a missmatch in their investment decisions illustrating that they did rely on titmice densities as a cue for habitat characteristics and costs of competition. For migrating birds that did not overlap to the same extent in resource need, this relationship was not evident (III).*

Paternity and environmental interactions

More then 75 % of socially monogamous passerines engage in copulations out-side of their social pair, i.e. extra-pair copulations (EPC) (Box 6). This seemingly common behaviour is thought to be costly for females seeking EPCs, as it can lead to reduced paternal care and increased risk of sexually transmitted diseases (Box 6). Females may also directly (non-genetically) or indirectly (genetically) benefit from these extra-pair encounters, although, the costs have been argued to outweigh the benefits in most avian species (Box 6). Thus, an alternative expla-nation for the occurrence of EPC is that EPCs are driven by males gaining more benefits (through greater paternity) than costs. This creates a sexual conflict over EPCs, with males seeking them and females resisting such costly endeavours. At
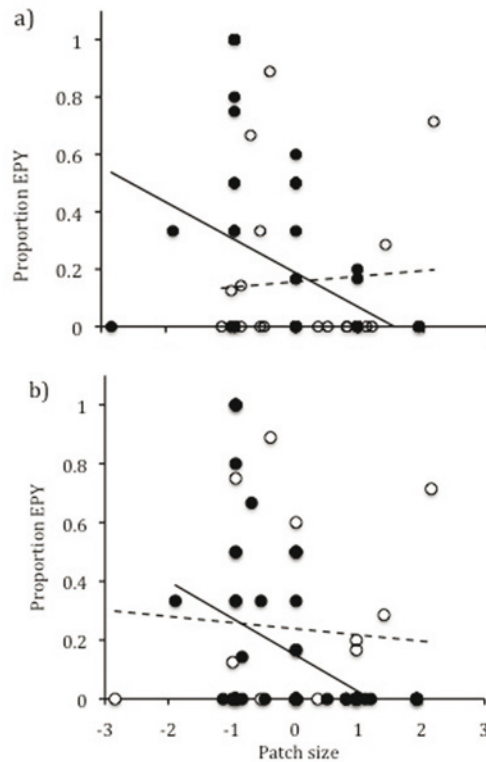
Figure 4 *The efect of male ornamentation, i.e. the width of the white forehead patch, on EPP is environmental dependent varying with both a) breding density and b) breed-ing territory quality. The effect of ornamentation was highest for males in a) high breed-ing densities (filled circles and solid line) and with b) high quality breeding territories (filled circles and soild line). For males in a) low breeding territories (open circles and dashed line) and with b) low quality breeding territories (open circles and dashed line) the association between ornamentation and the proportion of EPY was less pronounced.*

the same time, males must defend their social partner from intruding extra-pair males (Box 6).

The finding that more ornamented males tend to be more successful at gaining EPCs and siring more of the offspring in their own nests (Sheldon and Ellegren, 1999, IV) is consistent with both hypotheses. Females may choose to be more faithful to their social partner if he is more attractive or carries good genes (indirect benefits through good genes (sexy son) hypothesis). Alternatively, male ornamentation may be linked to his ability to defend his social partner against other males as it has previously been associated to males abilities to compete with other males (Pärt and Qvarnström, 1997). In article IV, the importance of ornamentation in male collared flycatchers on the levels of EPP was elevated in high breeding densities (Fig. 4), suggesting that the intensity of sexual selection increases with increasing breeding densities. Further, males with high quality breeding territories always sired more of their own offspring (Fig. 4). There was also a tendency for ornamentation to be of less importance for males with low quality territories as they always sired less of their own offspring (fig. 4). These results are predicted whether EPCs are driven by female choice or male coercion, and further illustrate how the interactions between and within the sexes can be influenced by environmental variation. EPCs are generally studied without respect to the environmental factors that may influence their adaptiveness. Improved insight into the variables influencing the dynamics of mating behaviours and secondary sexual characters may help us to better understand the evolutionary processes explaining EPCs (Eliassen and Kokko, 2008), and mating systems in general.

Studying the whole life cycle of migrating organisms

Collared flycatchers breeding in different woodlots on the island of Gotland differed in isotope ratios in their winter-grown feathers and did so over consecutive years (V). These isotope signatures are often used as a sort of geographic coordinate, as isotopic variation can be attributed to variation linked to the environment. In terrestrial habitats, variation in isotope signatures in Carbon ($\delta^{13}C$) is mainly attributed to the ratio of primary producers using either C3 or C4 photosynthetic pathways although variation within primary producers may vary (reviewed by Kelly, 2000). Further, terrestrial plants may vary widely in their nitrogen isotope signatures ($\delta^{15}N$) (e.g. Shearer et al., 1983) mainly due to soil differences (e.g. Shearer and Kohl, 1989). There is also a tendency for $\delta^{15}N$ in plants to be higher in arid regions (e.g. Shearer et al., 1983), which has consequences for $\delta^{15}N$ at higher trophic levels. In addition, as shown in mammals, higher $\delta^{15}N$ can result from water stress (Cormie and Schwarcz, 1996), potentially increasing the association between $\delta^{15}N$ and habitat aridity (Kelly, 2000, but see Kempster et al., 2007). The differences between populations observed in article V (Fig. 5) are

based on differences in $\delta^{15}N$ and thus, differences in wintering habitat for the populations are most likely attributed to differences in soil and aridity between their wintering areas. The repeatability of all isotope signatures was high suggesting that individuals experience similar winter habitat characteristics every year (Fig. 6).

Collared flycatchers have previously been shown to exhibit strong natal (Pärt, 1990) and breeding-site philopatry (Pärt and Gustafsson, 1989). A likely explanation for the observed repeatability between years in isotopic signatures (V) (Fig. 6) is that individuals are also philopatric to their winter grounds. An alternative hypothesis is that individuals from the same breeding population are utilizing similar winter habitats/food resources every year, but not necessarily at the same location. Natal and breeding site philopatry in collared flycatchers are considered behavioural adaptations minimizing costs of habitat selection (e.g. Pärt, 1991, Pärt, 1994), maximizing reproductive success (e.g. Doligez et al., 2002), and improving competitive abilities (e.g. Pärt, 1994). Winter site philopatry could be beneficial for similar reasons.

The observation that individuals within breeding populations share a more similar isotope signature than those from other breeding populations (V, Fig. 5) has two potential explanations. First, members of a breeding population might have
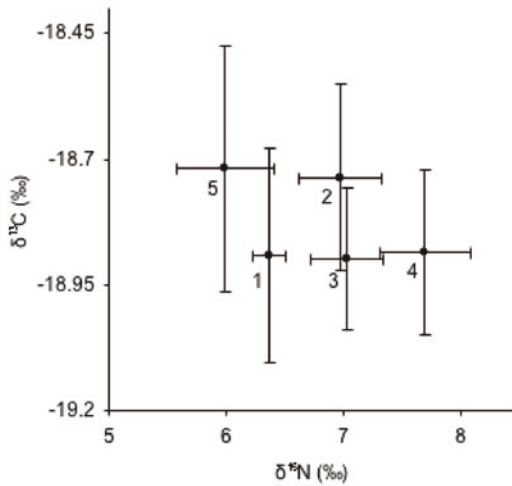
Figure 5 *Carbon (‰$\delta^{13}C$, y-axis) and nitrogen (‰$\delta^{15}N$, x-axis) stable isotope ratios as measured in winter-grown median tertial feathers of individual collared flycatchers from five breeding populations (circles are population mean isotopic signature ± SE) on Gotland (numbers refer to breeding populations, see Fig. 1 in V). Individuals from the same breeding population had more similar "winter"-isotope ratios compared to birds from other populations and the observed difference between populations was explained by differences in $\delta^{15}N$.*

similar habitat/food utilization in the wintering grounds. Secondly, there may be strong migratory connectivity (MC, box 7) on a small spatial scale. The latter posits that whoever breeds together, winters together. For the first explanation to hold, one needs to understand why differences in winter habitat utilisation between breeding populations could arise when all such populations are situated in very similar/identical breeding habitats. As seen in article V, there was no difference in quality of population members nor any difference in time at arrival at breeding grounds, which could have provided further explanations for why populations differed in isotope ratios. However, if birds inherit their winter habitat preference either genetically or socially, and populations have diverged, such differences in winter habitat preferences are expected. Either way, both explanations will have many important implications for a range of fields within ecology, conservation and evolutionary biolog and the awareness of migratory connectivity and its implication on the annual life cycle of migratory organisms is increasing (e.g. Rubenstein et al., 2002, Webster et al., 2002). It is very likely that such links between winter and breeding populations can be present on a much finer scale than previously considered, as paper V suggests. However, to fully understand variation in migratory behaviours, one needs information on the underlying processes determining why, where, when and how animals migrate. Experimental studies have revealed some information on the quantitative genetics of migratory behaviours in the past (Bearhop et al., 2005 and references therein). Using long-term data sets coupled with pedigree information and quantitative-genetic statistics (such as the Animal Breeding Model, reviewed in Kruuk, 2004) may prove to be a powerful approach in the future.
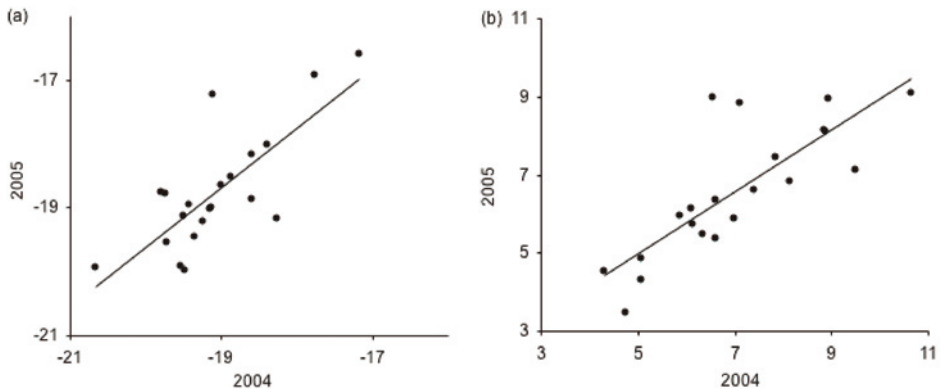

Figure 6 *Scatter plots of (a) carbon (‰ $\delta^{13}C$), (b) nitrogen (‰ $\delta^{15}N$) stable isotope ratios in a median tertial feather of individuals sampled in 2005 versus measurements on median tertials from the same individuals sampled in 2004. All isotope ratios ($\delta^{13}C$: r = 0.76, $\delta^{15}N$: r = 0.80) showed high repeatability between years, suggesting that isotope pattern in Fig. 5 is consistent between years and that collared flycatchers are wintering at the same sites/habitats over consecutive years. A significant year effect was found for $\delta^{13}C$ and a near significant tendency for $\delta^{15}N$, implying that habitat characteristics at the wintering sites changed between years.*

Box 7 Migratory connectivity

Knowledge of the degree of isolation between populations is fundamental to many fields within biology such as evolutionary and conservation biology and ecology. For migrating animals, the degree of isolation will not only depend on the level of migration between populations at the breeding ground, but also at their winter site. The degree of isolation between populations in migratory species is defined as migratory connectivity (MC). Total mixing of breeding populations at the wintering site, as found in the North American black-throated blue warblers (*Dendroica caerulescens*), at least with respect to breeding longitude (Rubenstein, et al. 2002), and completely separated wintering sites as shown in the aquatic warbler (*Acrocephalus paludicola*) breeding in Europe (Pain, et al. 2004) represent the extremes of a weak and strong MC, respectively. Of course, a reciprocal scenario to that of the American black-throated blue warbler, where animals from the same breeding population winter at different sites, also represents weak MC.
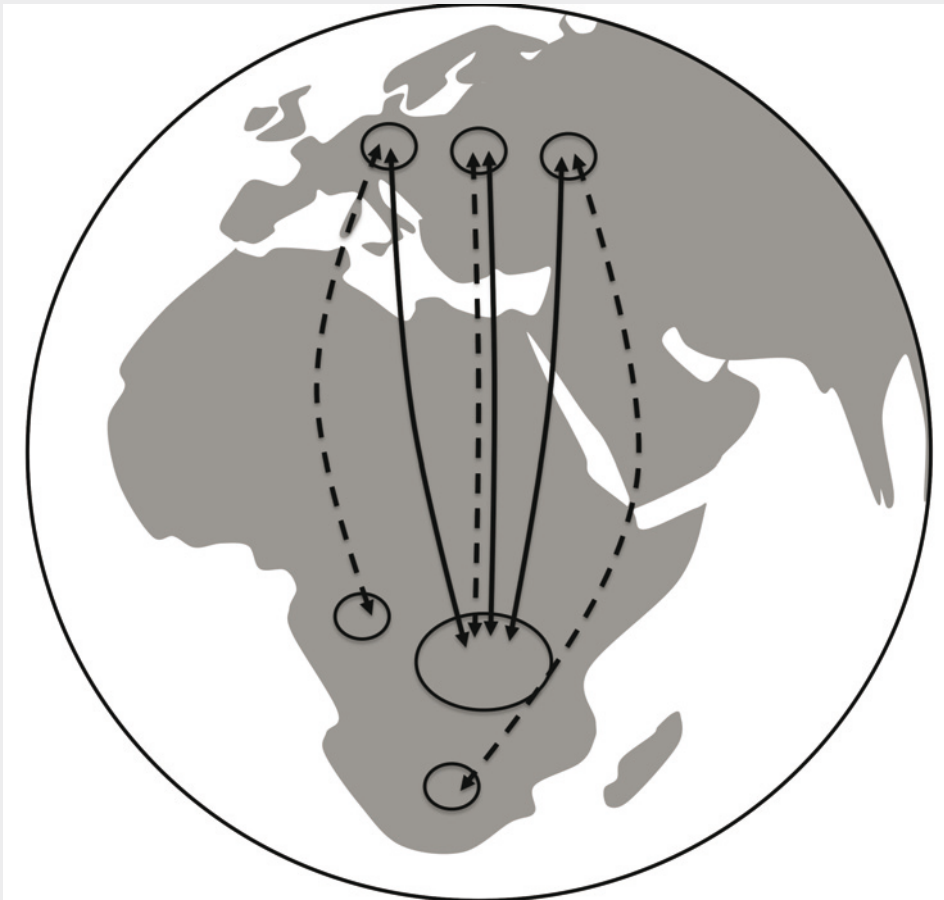
The above figure illustrates examples of strong and weak MC. Individuals from the three breeding areas in Europe and western Asia either share (migrating according to the solid arrows) their winter location in Africa with each other, i.e. weak MC, or have seperated (migrating according to the dashed arrows) winter quarters, i.e strong MC.

Concluding remarks

Most evolutionary and ecological process in nature, including many highlighted in this thesis, are affected by environmental factors, and information concerning these interrelated processes is crucial to fully understanding evolutionary and ecological dynamics in nature. The main focus of this thesis has been on how the quality of the environment affects animals' reproductive decisions, as well as the outcome of such decisions. The first three articles focus on how animals adjust their reproductive decisions based on costs and benefits associated with breeding densities of con- and heterospecific using SI provided by competitors. How they acquire this information is currently not known, although vocal signals (as well as visual) are a likely candidate (unpublished experimental data, M.B. Hjernquist) for avian species. One such reproductive decision was for parents to differentially allocate resources to sons and daughters depending on differential costs and benefits to each sex associated with intra- and interspecific breeding densities and habitat quality (I, II). Flycatchers invested more into or produced more sons when the fitness return of sons is expected to be greater than that of daughters. Future testing of the actual fitness of sons and daughters in such situations will help clarify the gains achieved by such a strategy. The generality of sex allocation in avian species is currently debated, and this thesis suggests that characteristics of breeding territories may affect facultative sex ratio adjustment in many bird species (I).

That interspecific competitors, especially those that overlap most strongly in niche, can have benefits (II, III) is not generally considered in current models of habitat selection, population dynamics, metapopulation dynamics and species coexistence (II). However, the finding that migratory birds can use cues from the distribution of competitors to discern habitat quality, without the costs of habitat assessment highlights one way in which limited numbers of competitors may provide benefits. Conservation management of endangered species should acknowledge that the removal of species that are ecological competitors may have some negative impacts on the focal species. Furthermore, this attraction to their own or other species can also be utilised in management programs designed to attract endangered species to 'safe' areas.

As in articles I-III, article IV also focuses on how reproductive decisions change along environmental gradients. The strength of sexual selection in males that is driven by extra-pair copulations is context dependent, varying with breeding den-

sities and breeding territory quality (IV). To fully understand the evolution and maintenance of EPCs in socially monogamous organisms, one needs to quantify the costs and benefits for males and females. Previous fitness estimates of EPP in collared flycatchers suggest that female benefits from EPC (Sheldon et al., 1997), although, variation in EPP is assumed to reflect variation in EPC, which might not be the case. Because of logistic difficulties, assessing costs and benefits associated to females engaging in EPC is something that has not yet been done. Further, focusing on how individuals are influenced by environmental factors (as in Rubenstein, 2007 and IV) will provide us with more insights into female mating behaviours in general. Such information will aid our efforts in better understanding the evolutionary processes leading to EPP, and its maintenance in socially monogamous species.

To fully understand the ecology of and evolutionary processes affecting organisms, especially in nature, we need detailed knowledge concerning their entire life cycle. This thesis, and the work on which it is based, uses a wild migratory bird, the collared flycatcher, as the model species. The species has been studied extensively for more then 25 years, yet we know very little about their ecology and distribution when not breeding. The same is true for most migrating species. Stable isotopes from feathers produced while wintering in Africa (V) suggest that collared flycatchers may spend their winter alongside their breeding neighbours, and that they are faithful to their winter grounds. These results suggest that MC may occur on much smaller spatial scales than previously considered (V), and raises the possibility that breeding neighbours may have substantial previous experience with one another prior to their arrival to the breeding grounds. Future studies should examine factors determining migratory behaviours (e.g. inheritance), as well as the ecological and evolutionary implications of this year round connectivity of populations.

Summary in Swedish (sammanfattning)

De flesta evolutionära och ekologiska processer i naturen påverkas av och växelverkar med miljöfaktorer. En viktig uppgift inom ekologiska och evolutionsbiologiska studier är att försöka förstå denna växelverkan bättre. Jag försöker i denna avhandling att beskriva hur miljöns påverkan på reproduktionen. Den första delen tar upp frågor rörande hur reproduktionen påverkas av nackdelar och fördelar relaterade till konkurrens inom och mellan arter. En annan aspekt som diskuteras är hur individer kan utnyttja andra individer, oavsett arttillhörighet, som en informationskälla för att uppskatta dessa kostnader och fördelar. Fördelarna och nackdelarna vägs emot varandra innan de fattar reproduktiva beslut om var de ska häcka, hur mycket de ska investera i reproduktion och hur de ska fördela resurserna mellan söner och döttrar (I, II, III). Halsbandsflugsnappare, en liten tätting som fått fungera som modellorganism i denna avhandling, föredrar att häcka i områden där fördelarna överstiger nackdelarna – vilket visade sig bero på intensiteten av konkurrens inom och mellan arter, samt vilken kvalité området är av t.ex. i förhållande till födotillgång och predationsnivåer.

Halsbandsflugsnappare dras till optimala häckningsområden där nackdelarna kopplade till konkurrens mellan arter övervägs av fördelarna av områdets kvalité. Väl där investerar de mer i reproduktionen och producerar även fler av det könet som ger föräldrarna den högsta reproduktiva vinsten. I dessa områden där den relativa fortplantningsframgången är högre produceras därför fler söner eftersom hanar kommer att komma tillbaka till födelseplatsen för att häcka och därigenom själva kunna utnyttja fördelarna av området de föddes i till skillnad från honorna som sprider sig till andra områden (II). Skeva könskvoter observeras också i förhållande till intensiteten av konkurrens över borevir inom arten – halsbandsflugsnappare producerade fler söner i områden med mindre inomartskonkurrens, återigen för att maximera den reproduktiva vinsten för varje investeringsenhet (I). Hur informativ en art är för en annan beror på hur mycket överlapp de har i resursutnyttjande. Den värsta konkurrenten är samtidigt den som bäst signalerar de faktiska förhållandena (II, III). Att arter kan använda sig av information från andra arter och att det finns fördelar med att leva med konkurrenter är faktorer som tidigare inte vägts in i evolutionära och ekologiska modeller. Dessutom kan man använda sig av arters "attraktion" till sin egen och andra arter inom tillämpad bevarandebiologi genom att attrahera hotade arter till skyddade områden.

Det finns två huvudtyper av parningssystem där individer antigen bildar ett troget

par, s.k. monogami, eller reproducerar sig med fler än en partner, s.k. polygami. Monogami förekommer i många taxa men brukas ofta beskrivas med exempel från fåglar. Genetiska studier har dock avslöjat att arter som vi tidigare ansett vara monogama ofta istället är mer eller mindre polygama, samtidigt som de lever i parförhållanden. Mer än 75 % av de arter som är socialt monogama är inte genetiskt monogama eftersom de söker parningstillfällen utanför sitt parförhållande. Att förstå varför otrohet är så pass vanligt har varit fokus för många studier. Hos halsbandsflugsnapparen påverkar storleken på hanliga ornament sannolikheten för otrohet. Otrohet begränsas dock av både tätheten av häckande halsbandsflugsnappare och kvalitén på hanens revir (IV). Alltså, vikten av att ha ett stort ornament är beroende på den miljö hanen är i. Det visar på att processer av sexuell selektion är beroende och påverkas av miljön. Att förstå hur miljön och evolutionära processer växelverkar är en förutsättning för att vi ska förstå varför otrohet förekommer inom socialt monogama arter och de underliggande evolutionära processerna som kan förklara arters olika parningssystem.

När det gäller flertalet flyttfåglar, inklusive halsbandsflugsnapparen, vet vi ytterst lite om var de befinner sig och vilka faktorer som påverkar dem när dem inte är på sina häckningsplatser. Man vet dock att flyttfåglar påverkas av den miljö de upplever på övervintrings- och rastplatser vilket indirekt påverkar deras beslut och resultatet av dessa beslut på häckningsplatsen. I artikel V tas ett viktigt steg att införskaffa mer kunskap om var halsbandsflugsnapparna befinner sig på vintern. Genom att studera skillnader och likheter mellan individer i isotopsignaturer av grundämnen som finns i fjädrar som vuxit ut på övervintringsplatsen kan man fastställa om de övervintrat på samma/liknande platser eller inte. Detta p.g.a. att isotopsignaturer speglar miljöförhållanden som fågeln upplevt när fjädern vuxit ut. De populationer som häckar på olika ställen på Gotland skiljde sig från varandra vilket tyder på att individer från samma häckningsområde också troligen övervintrar tillsammans. Vi vet sedan tidigare att halsbandsflugsnappare är ortstrogna både till sin födelse- och häckningsplats, och vi kan nu konstatera att de troligen är lika ortstrogna när det gäller övervintringsplatsen. Artikel V representerar ett nödvändigt steg som visar att framtida evolutionärbiologiska och ekologiska studier måste förbättras så att effekterna av miljöfaktorer och händelser i alla livsmiljöer som en individ utnyttjar under sitt liv beaktas.

Acknowledgements

A very wealthy and successful man once said, "*show me someone without an ego, and I'll show you a loser*". Although being egocentric is a wonderful character for any man or woman, at times, being humble is too. So, let the thank you begin.

First off all, this thesis wouldn't have been possible without The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning who funded my research and my position at Uppsala University with a grant to my supervisor Lars Gustafsson. Also, for finacial support, thanks to Zoologiska stiftelsen, Liljewalchs foundation, The Royal Swedish Academy of Science, Knut and Alice Wallenberg foundation.

Secondly, I would like to thank all the people that have been directly involved in the work leading up to this thesis. First of all to my supervisor Lars Gustafsson – thanks for giving me the opportunity and for being a good friend. Jukka Forsman have contributed to many parts of this thesis – thanks for that, and for all the other non-scientific contributions as well. Anna Qvarnström, my second supervisor – I appreciate your help and our collaborations over the years and hope that they will continue in the years to come. Thor Veen, you are a good birder and you like GT's and are therefore one of my best mates, it's as simple as that. Johan Träff – you've help me since the first day I started to work with the flycatchers on Gotland sharing some of your great knowledge of the *Ficedula* flycatchers, providing comments and data for which I owe you more then just a thank you. Ben Sheldon – you contributed both as a co-author and by providing excellent comments to other manuscripts and for that I'm very grateful. Jennie Taipale was en hard working master student of mine and Jukka and I will never forget your ability to get lost, anywhere (☺). You did a great job! Marcel Klaassen and Laura Font – for among other things, your isotopic wisdom. To Katherine Thuman Hjernquist – you have been an important part of all work leading up to this thesis. For that, and for the support over the years I'm grateful. Many thanks to Niclas Kolm – you helped me to focus on the right things in the critical last months before handing in my thesis. And maybe even more importantly, for all the great chats about everything from science to genetically modified Olympians. Anna Qvarnström, Chris Wiley, and the pre-defense committee; Andreas Rudh, Björn Rogell, Niclas Kolm, Alejandro Gonzalez Voyer and Pim Edelaar, all provided helpful comments on earlier versions of parts of, or the entire thesis, for which I'm very grateful. I would also like to thank everybody that has been involved in

Cited literature

Alatalo, R. V., Lundberg, A. & Ulfstand, S. 1985. *Ficedula hypoleuca*. In *Habitat Selection in Birds.* (ed. M. L. Cody), pp. 59-83. San Diego, CA: Academic Press.

Alerstam, T. 1982. The course and timing of bird migration. In *Animal migration.* pp. 9-54. Cambridge: Cambridge University Press.

Andersson, M. (1994) *Sexual Selection,* Chichester: Princeton University Press.

Arnqvist, G. & Kirkpatrick, M. 2005. The evolution of infidelity in socially monogamous passerines: The strength of direct and indirect selection on extrapair copulation behavior in females. *American Naturalist,* **165:** S26-S37.

Arnqvist, G. & Rowe, L. (2005) *Sexual Conflict,* Oxfordshire: Princeton University Press.

Bearhop, S., Fiedler, W., Furness, R. W., Votier, S. C., Waldron, S., Newton, J., Bowen, G. J., Berthold, P. & Farnsworth, K. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science,* **310:** 502-504.

Begon, M., Harper, J. L. & Townsend, C. R. (1996) *Ecology - Individuals, Population and Communities,* Oxford: Blackwell Science Ltd.

Cassey, P., Ewen, J. G. & Moller, A. P. 2006. Facultative primary sex ratio variation: a lack of evidence in birds (vol 271, pg 1277, 2004). *Proceedings of the Royal Society B-Biological Sciences,* **273:** 3129-3130.

Charnov, E. L. (1982) *The Theory of Sex Allocation,* Princeton: Princeton University Press.

Clark, A. B. 1978. Sex ratio and local resource competition in a prosiminian primate. *Science,* **201:** 163-165.

Cormie, A. P. & Schwarcz, H. P. 1996. Effects of climate on deer bone delta 15N and delta 13C: Lack of precipitation effects on delta 15N for animals consuming low amounts of C4 plants. *Geochimica et Cosmochimica Acta,* **60:** 4161-4166.

Danchin, E., Giraldeau, L.-A., Valone, T. J. & Wagner, R. H. 2004. Public Information: From Nosy Neighbors to Cultural Evolution. Science, 305: 487-491.

Darwin, C. (1859) *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life,* London: John Murray.

Darwin, C. (1871) *The descent of man and selection in relation to sex.,* London: John Murray.

Doligez, B., Danchin, E. & Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. *Science,* **297:** 1168-1170.

Eliassen, S. & Kokko, H. 2008. Current analyses do not resolve whether extra-pair paternity is male or female driven. *Behavioral Ecology and Sociobiology,* **62:** 1795-1804.

Ewen, J. G., Cassey, P. & Moller, A. P. 2004. Facultative primary sex ratio variation: a lack of evidence in birds? *Proceedings of the Royal Society of London Series B-Biological Sciences,* **271:** 1277-1282.

Fisher, R. A. (1930) *Genetical Theory of Sex Allocation,* London: Clarendon Press.

Forsman, J. T., Hjernquist, M. B., Taipale, J. & Gustafsson, L. 2008. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. *Behavioral Ecology,* **19:** 539-545.

Forsman, J. T., Seppänen, J.-T. & Mönkkönen, M. 2002. Positive fitness consequences of interspecific interaction with a potential competitor. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **269:** 1619-1623.

Frank, S. A. 1990. Sex Allocation Theory for Birds and Mammals. *Annual Review of Ecology and Systematics,* **21:** 13-55.

Fretwell, S. D. (1972) *Populations in a seasonal environment,* Princeton: Princeton University Press.

Gause, G. F. (1934) *The struggle for existence* Baltimore, MD: Wil-liams & Wilkins.

Gill, J. A., Norris, K., Potts, P. M., Gunnarsson, T. G., Atkinson, P. W. & Sutherland, W. J. 2001. The buffer effect and large-scale population regulation in migratory birds. *Nature,* **412:** 436-438.

Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology,* **11:** 2195-2212.

Gustafsson, L. 1987. Interspecific competition lowers fitness in collared flycatchers Ficedula albicollis an experimental demonstration. *Ecology,* **68:** 291-296.

Gustafsson, L. 1988. Interspecific and Intraspecific Competition for Nest Holes in a Population of the Collared Flycatcher Ficedula-Albicollis. *Ibis,* **130:** 11-16.

Gustafsson, L. & Qvarnström, A. 2006. A Test of the "Sexy Son" Hypothesis: Sons of Polygynous Collared Flycatchers Do Not Inherit Their Fathers' Mating Status. *American Naturalist,* **167:** 297-302.

Gustafsson, L., Qvarnström, A. & Sheldon, B. C. 1995. Trade-Offs between Life-History Traits and a Secondary Sexual Character in Male Collared Flycatchers. *Nature,* **375:** 311-313.

Gustafsson, L. & Sutherland, W. J. 1988. The cost of reproduction in the collared flycatcher Ficedula albicollis. *Nature,* **335:** 813-817.

Hamilton, W. D. 1967. Extraordinary sex ratios. *Science,* **156:** 477-488.

Heg, D., Dingemanse, N. J., Lessells, C. M. & Mateman, A. C. 2000. Parental correlates of offspring sex ratio in Eurasian Oystercatchers. *Auk,* **117:** 980-986.

Hjernquist, M. B., Hjernquist, M., Hägerroth, J.-E., Johansson, T. & Martinsson, M. (2008) *Kungsörnsymposium 2007,* Visby: Gotlands Ornitologiska Förening & Länsstyrelsen i Gotlands Län.

Hubbell, S. P. (2001) The Unified Neutral Theory of Biodiversity and Biogeography, Princeton, NJ: Princeton University Press.

Julliard, R. 2000. Sex-specific dispersal in spatially varying environments leads to habitat-dependent evolutionarily stable offspring sex ratios. *Behavioral Ecology,* **11:** 421-428.

Kelly, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* **78:** 1-27.

Kempster, B., Zanette, L., Longstaffe, F. J., MacDougall-Shackleton, S. A., Wingfield, J. C. & Clinchy, M. 2007. Do stable isotopes reflect nutritional stress? Results from a laboratory experiment on song sparrows. *Oecologia,* **151:** 365-371.

Kruuk, L. E. B. 2004. Estimating genetic parameters in natural populations using the 'animal model'. *Proceedings of the Royal Society of London Series B-Biological Sciences*: 873-890.

Le Boeuf, B. J. & Laws, R. M. (eds.) 1994. *Elephant seals : population ecology, behavior, and physiology,* Berkeley: University of California Press, cop.

Lundberg, P. 1988. The evolution of partial migration in Birds. *Trends in Ecology & Evolution, 3:* 172-175.

Monkkonen, M., Helle, P., Niemi, G. J. & Montgomery, K. 1997. Heterospecific attraction affects community structure and migrant abundances in northern breeding bird communities. *Canadian Journal of Zoology-Revue Canadienne De Zoologie, 75:* 2077-2083.

Monkkonen, M., Helle, P. & Soppela, K. 1990. Numerical and Behavioral-Responses of Migrant Passerines to Experimental Manipulation of Resident Tits (Parus Spp) - Heterospecific Attraction in Northern Breeding Bird Communities. *Oecologia, 85:* 218-225.

Norris, D. R. 2005. Carry-over effects and habitat quality in migratory populations. *Oikos, 109:* 178-186.

Pain, D. J., Green, R. E., Giessing, B., Kozulin, A., Poluda, A., Ottosson, U., Flade, M. & Hilton, G. M. 2004. Using stable isotopes to investigate migratory connectivity of the globally threatened aquatic warbler Acrocephalus paludicola. *Oecologia, 138:* 168-174.

Pärt, T. 1990. Natal Dispersal in the Collared Flycatcher - Possible Causes and Reproductive Consequences. *Ornis Scandinavica, 21:* 83-88.

Pärt, T. 1991. Philopatry Pays - a Comparison between Collared Flycatcher Sisters. *American Naturalist, 138:* 790-796.

Pärt, T. 1994. Male Philopatry Confers a Mating Advantage in the Migratory Collared Flycatcher, Ficedula-Albicollis. *Animal Behaviour, 48:* 401-409.

Pärt, T. & Gustafsson, L. 1989. Breeding Dispersal in the Collared Flycatcher (Ficedula-Albicollis) - Possible Causes and Reproductive Consequences. *Journal of Animal Ecology, 58:* 305-320.

Pärt, T. & Qvarnström, A. 1997. Badge size in collared flycatchers predicts outcome of male competition over territories. Animal Behaviour, 54: 893-899.

Pike, T. W. & Petrie, M. 2003. Potential mechanisms of avian sex manipulation. *Biological Reviews, 78:* 553-574.

Qvarnström, A., Pärt, T. & Sheldon, B. C. 2000. Adaptive plasticity in mate preference linked to differences in reproductive effort. *Nature, 405:* 344-347.

Roff, D. A. (2002) *Life History Evolution,* Sunderland, MA: Sinauer Associates.

Rubenstein, D. 2007. Territory quality drives intraspecific patterns of extrapair paternity. *Behavioral Ecology, 18:* 1058-1064.

Rubenstein, D. R., Chamberlain, C. P., Holmes, R. T., Ayres, M. P., Waldbauer, J. R., Graves, G. R. & Tuross, N. C. 2002. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. *Science, 295:* 1062-1065.

Shearer, G. & Kohl, D. H. 1989. Estimates of N_2 fixation in eco-systems: the need for and basis of the ^{15}N natural abundance method. In *Stable isotopes in ecological research.* eds. P. W. Rundel, J. R. Ehleringer & K. A. Nagy), pp. 342-374. New York: Springer-Verlag.

Shearer, G., Kohl, D. H. & Virginia, R. A. 1983. Estimates of N_2-fixation from variation in the natural abundance of ^{15}N in Sonoran Desert plants. *Oecologia,* **56:** 365-373.

Sheldon, B. C., Andersson, S., Griffith, S. C., Ornborg, J. & Sendecka, J. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature,* **402:** 874-877.

Sheldon, B. C. & Ellegren, H. 1999. Sexual selection resulting from extrapair paternity in collared flycatchers. *Animal Behaviour,* **57:** 285-298.

Sheldon, B. C., Kruuk, L. E. B. & Merila, J. 2003. Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. Evolution, 57: 406-420.

Sheldon, B. C., Merila, J., Qvarnstrom, A., Gustafsson, L. & Ellegren, H. 1997. Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. Proceedings of the Royal Society of London Series B-Biological Sciences, 264: 297-302.

Svedin, N., Wiley, C., Veen, T., Gustafsson, L. & Qvarnstrom, A. 2008. Natural and sexual selection against hybrid flycatchers. Proceedings of the Royal Society B-Biological Sciences, 275: 735-744.

Svensson, L. (1992) *Identification guide to European passerines,* Stockholm: L. Svensson.

Thuman, K. A., Widemo, F. & Griffith, S. C. 2003. Condition-dependent sex allocation in a lek-breeding wader, the ruff (Philomachus pugnax). *Molecular Ecology,* **12:** 213-218.

Trivers, R. L. & Willard, D. E. 1973. Natural selection of parental ability to vary sex ratio of offspring. *Science,* **179:** 90-92.

Veen, T., Borge, T., Griffith, S. C., Saetre, G. P., Bures, S., Gustafsson, L. & Sheldon, B. C. 2001. Hybridization and adaptive mate choice in flycatchers. Nature, 411: 45-50.

Veen, T., Svedin, N., Forsman, J. T., Hjernquist, M. B., Qvarnström, A., Thuman Hjernquist, K. A., Träff, J. & Klaassen, M. 2007. Does migration of hybrids contribute to post-zygotic isolation in flycatchers? Proceedings of the Royal Society of London Series B-Biological Sciences, 274: 707 - 712.

Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S. & Holmes, R. T. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution,* **17:** 76-83.

West, S. A. & Sheldon, B. C. 2002. Constraints in the evolution of sex ratio adjustment. *Science,* **295:** 1685-1688.

Acta Universitatis Upsaliensis

*Digital Comprehensive Summaries of Uppsala Dissertations
from the Faculty of Science and Technology* 584

Editor: The Dean of the Faculty of Science and Technology

ACTA
UNIVERSITATIS
UPSALIENSIS
UPPSALA
2008