Individual reproductive strategies in the dusky warbler (*Phylloscopus fuscatus*): female and male perspectives

Dissertation zur Erlangung des
naturwissenschaftlichen Doktorgrades
der Bayerischen Julius-Maximilians-Universität Würzburg

vorgelegt von

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München

Würzburg 2001

Eingereicht am: ....

Mitglieder der Promotionskommission:

Vorsitzender: ....

Gutachter : ....

Gutachter: ....

Tag des Promotionskolloquiums: ....

Doktorurkunde ausgehändigt am: ....

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1. Introduction

Darwin’s theory of evolution (Darwin 1859) may represent one of the greatest if not *the* greatest advancement ever made in biological sciences. He argued that a population evolves according to the relative success of individual members of this population in the ‘struggle of life’. The fact that natural selection discriminates against badly performing individuals is often encapsulated in the expression ‘survival of the fittest’. However, Darwin also recognised that some evolved traits, such as the tail of a peacock, do not appear to improve an individual's prospects of survival. Darwin proposed that these traits had evolved as a consequence not of natural selection, but rather of sexual selection. An elaborate tail confers a mating advantage on a male peacock, such that the male will reproduce more successfully than males with less elaborate tails. Generally speaking, sexual selection is acting if one individual produces more progeny than another, as a result of differences in mating success. Modern life-history theory (Stearns 1995) states that reproduction and not survival is the ultimate goal of existence. The concept of ‘survival of the fittest’ is therefore perhaps of less relevance to the processes of evolutionary selection than ‘reproduction of the fittest’, as this encompasses both natural and sexual selection.

Possibly due to the development of molecular methods that allow the identification of an individual's genetic parents, sexual selection has recently become the dominating topic in the field of behavioural ecology. Sexual selection can be split up into two components: (1) intra-sexual selection, or male-male competition, in which males typically compete with each other for access to females and (2) inter-sexual selection, or female choice, in which females, typically the choosy sex, may prefer one male over the other as a mate (Andersson 1994). I say ‘typically’, because cases of sex-role reversal do occur, although this is of limited relevance to the following introduction. Generally, males compete to fertilise females, and females try to select their optimal partner. The way in which this is achieved, however, can be quite sophisticated. On the one hand, males may differ individually in their strategies how to gain access to females (Gross 1996). On the other hand, mate preferences may vary between different females of the same species, and even within the same female, according to her changes in her situation and needs (Gowaty 1996).

In most bird species, where males defend territories and help females with raising the young, females want more than just the sperm of the most attractive male (i.e. ‘good genes’[1]). Direct benefits that can be obtained from choosing the right partner may be more important than such indirect genetic benefits (see Andersson 1994). They might include breeding on a high-quality territory (providing abundant resources), or having a social partner who is ready to participate substantially in brood care (a ‘good parent’). However, most females are unlikely to find a partner who will maximise all of these potential benefits (e.g. resources, good parenting and good genes). Possible trade-offs will necessitate a compromise solution. The most dominant male may own the best territory, but he may invest relatively little in parental care (Ketterson & Nolan 1999). A good parent, on the other hand, may be of low genetic quality (see Griffith et al. 1999, Sanz 2001). In principle, the latter problem could be overcome by having extra-pair copulations with males of higher genetic quality (a very widespread phenomenon in birds; e.g. Petrie & Kempenaers 1998), but if female unfaithfulness induces the social partner to reduce his parental efforts (Dixon et al. 1994; Møller & Cuervo 2000, Møller & Tegelström 1997, Westneat & Sargent 1996), females may still face a trade-off between direct and indirect benefits.

These trade-offs may result in alternative female mating strategies. Some females (e.g. inexperienced individuals or individuals in poor condition) may strongly depend on male assistance in brood care. Thus they may search for a ‘good parent’ and accept lower-quality territories and genetic partners. Other females, that are more capable of raising their young without male assistance, may adopt a more ‘emancipated’ strategy. If they are prepared to forgo male help, they may be free to settle in the best territory they can find, and to have their offspring sired by the most attractive male in the area.

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[1] Note that there are several other indirect benefits besides ‘good genes’ that females may gain from choosing particular copulation partners (see Jennions & Petrie 2000). I here emphasise ‘good genes’ because while there is some evidence for the importance of ‘good genes’ in the dusky warbler (Chapter 10), there is no support for alternative hypotheses.

If female mating strategies are aimed at different kinds of benefits, this may promote variation in male strategies. Individuals varying in their competitive abilities, parenting abilities and sexual attractiveness may invest differentially in competition, brood care and sexual display to maximise their overall mating success.

Up to here I have used the term ‘strategy’ in a rather broad sense. Although such loose treatment is widespread in the biological literature (e.g. Krebs & Davies 1993), I will now introduce a terminology and some background information on alternative mating behaviours, which should help to avoid ambiguity (Box on page 3). This terminology is largely adopted from Dominey (1984), but is also meant to summarise a common sense in the literature on this field. These definitions are a necessary background for the Discussion Chapter (11).

The aim of this thesis is to investigate individual variation in reproductive behaviours, from both the female and the male perspectives. For two reasons special attention is given to female mating behaviour. Firstly, individual variation in female behaviour has so far received only very limited attention (see e.g. Gross 1996 and Introductions to Chapters 4, 5 and 6). Secondly, as female mate choice may have major effects on reproductive tactics applied by males (Alonzo & Warner 2000), understanding the first is a prerequisite for the study of the latter.

Phylloscopus warblers in general provide very interesting study systems. They typically show a variable mating system at both the social and the genetic level. In all of the three well studied European species, the willow warbler, *P. trochilus*, the chiffchaff, *P. collybita* and the wood warbler, *P. sibilatrix*, social polygyny occurs regularly (e.g. Neergaard & Arvidson 1995, Rodrigues 1996a, Temrin & Jakobsson 1988) and extra-pair paternity does often occur at a very high rate (Bjørnstad & Lifjeld 1997, Fridolfsson et al. 1997, Wilson 2000). Such variable mating systems offer the opportunity to look for individual variation in mating behaviours.

The study of another *Phylloscopus* species, that was almost completely unknown when this study was initiated, appeared very promising, as new systems often allow new insights. The population of dusky warblers, *Phylloscopus fuscatus* Blyth, that I studied near Magadan in the Russian Far East between 1997 and 1999, inhabits a coastal tundra ecosystem that is free of anthropogenic change to the habitat. In contrast to the circumstances normally found in Central Europe, this allows to study a mating system under natural conditions. Thus a main aim of the present thesis was to embed this study into a broad ecological framework, describing the likely key-factors for habitat quality, namely variation in food availability and predation pressure (see Forstmeier 1998). A diploma thesis conducted by Ingo Weiß (2000) helped greatly to understand the influence of ecological factors on this mating system.

Hans-Heiner Bergmann, who began to study the dusky warbler in 1995 in another area near Magadan (Bergmann 1996), suggested me to continue this work. Preliminary results indicated that the behaviour of the dusky warbler differed from that of most other passerine species in some very remarkable ways. In the vast majority of passerine species, males closely follow their female partners during the period when they are fertile to prevent them from having extra-pair copulations (‘mate guarding’; Birkhead & Møller 1992). Instead of guarding their mates, male dusky warblers spend most of the daytime singing when females are fertile. This suggests that song is of outstanding importance for the mating system of this species. Besides that, dusky warblers are unusual with regard to the fact that they show territoriality throughout the summer, even during the period of post-nuptial moult when virtually all bird species abandon territorial behaviour (Schüz 1942, Haukioja 1971, Hegner & Wingfield 1986, Logan & Carlin 1991, Logan & Hyatt 1991, Yamagishi 1991, Lawn 1994, Weggler 2000). This indicates that male-male competition over the possession of territories may be an important aspect of sexual selection in this warbler.
My studies subsequently showed that polygyny and extra-pair paternity occurred at a high rate, which is not very surprising for a *Phylloscopus* warbler, although the observed rate of extra-pair paternity was actually one of the highest found among birds (see Petrie & Kempenaers 1998).

The following thesis starts with a short introduction to the study area (Chapter 2) and to the natural history of the study species (Chapter 3). Subsequently, there follows an analysis of female mating strategies (Chapters 4 to 6), which sets the frame for the subsequent treatment of variation in male mating behaviours (Chapters 7 to 10).

Box: Behavioural strategies: definitions and background

A strategy is a genetically fixed decision rule. It describes the range of phenotypic plasticity of the behaviour of one individual. Typically it tells an individual at which point it should switch between two tactics when circumstances are changing. A tactic is a phenotypic behaviour. Tactics should be defined discontinuously, otherwise two tactics cannot readily be distinguished. They should also be mutually exclusive, but serve the same function. Normally, a strategy gives instructions like ‘apply tactic 1 (i.e. behaviour 1), if such and such circumstances (e.g. weather, population density etc.) are given, and tactic 2, if such and such circumstances are given’. However, in extreme cases there can also be a strategy saying ‘apply this tactic under any given circumstances’.

Very often, circumstances are defined by an individual’s status. If the status is influenced by factors like age or non-heritable components of condition or body size, then the term ‘conditional strategy’ is used (Gross 1996). For instance, ‘fight if you are old and sneak if you are young’ is a conditional strategy and such types of strategies appear to be the most widespread among all kinds of animals.

If we observe discrete alternative reproductive behaviours, then there are two questions that need to be answered. (1) What is the origin of the different behaviours? Is the origin genetic or environmental? (2) What are the payoffs? Are they equal, or is one ‘making the best of a bad job’ (Dawkins 1980)? Obviously, two behavioural tactics need not have equal payoffs. A young sneaking male may be making the best of a bad job, but he may be able to apply the more successful fighting tactic when it is older. However, if there are two or more different strategies (meaning different genotypes carried by different individuals), then payoffs have to be equal to maintain these strategies. Changing environmental conditions may allow exceptions to this rule (Austad 1984, Sinervo et al. 2000), but this means only that *at the long run* payoffs have to be equal.

In the literature there are rather few (but famous) examples for the existence of discrete alternative strategies, where heritable rather than conditional factors decide about which tactic will be applied (e.g. Shuster & Wade 1991, Ryan et al. 1992, Lank et al. 1995). In these cases the switchpoints between alternative tactics that are defined by the strategies lie at extremes. This means that one genotype will under nearly all circumstances apply one tactic, while the other genotype applies the other. Such extreme behavioural dimorphisms are typically maintained by negative frequency-dependent selection (classical ESS models, Maynard Smith 1982).

However, what if strategies (not tactics!) are not discrete? What if there is continuous genetic variation for switchpoints, leading to an infinite number of gradually varying strategies? Classical ESS models are inadequate for describing such situations. The difficulty of theoretical treatment may partly be responsible for the fact that such cases are typically ignored (e.g. by Gross 1996), although they may even represent the most common situation (Dominey 1984).

Most recently, a model by Alonzo & Warner (2000) has introduced another mechanism by which alternative mating strategies may be maintained in a population. While models so far have focussed on interactions within one sex, it is now argued that interactions between the sexes will influence the evolution of alternative reproductive behaviours. For example, variation in female choice caused by female condition-dependence may allow the maintenance of alternative male strategies, even if there is no frequency-dependence in male reproductive success.

Exactly this situation may be given when female birds face trade-offs between different kinds of benefits. As outlined above, variation in female emancipation caused by differences in the ability to raise the brood unassisted, may facilitate the coexistence of two male tactics. Attractive males may concentrate on sexual display, while others may compensate for their lower attractiveness by showing a greater readiness to participate in brood care.

In Chapter 4 I explain the origin of polygyny and how this relates to female mate choice. I then analyse individual female characteristics that covary with their mating behaviour, firstly at the social (Chapters 4 and 5) and secondly at the genetic level (Chapter 6). The following Chapters 7 and 8, deal with male-male competition for access to females. I analyse how males invest in competition over territories in accordance with their individual characteristics. These chapters focus on the social mating system, while the final two chapters (9 and 10) deal with the genetic mating system. I show how males try to ensure paternity in their own nests, while they also try to gain extra-pair copulations with neighbouring females. I attempt to find out why there is no mate guarding but such extensive singing in this species (Chapter 9). Finally I look at what traits make males attractive as copulation partners and what females gain from engaging in extra-pair copulations. In this context, the relationship between the attractiveness of individual males and how much these invest in competition for territories is of special interest (Chapter 10).

The Discussion (Chapter 11) summarises the major findings of the seven previous chapters, and is aimed to conclude on the following questions: What are the origins of alternative behaviours, how are they determined and what are their payoffs? Which of them represent ‘making the best of a bad job’ and which are real alternatives conferring equal fitness gains? Finally, I state the ways in which this study advances parts of the general theory on mating systems, namely the ‘polygyny-threshold model’ (Verner 1964, Orians 1969), the ‘constrained-female hypothesis’ (Gowaty 1996) and the ‘fertility-announcement hypothesis’ (Møller 1991), and how it contributes to the fields of ‘resource competition’, ‘honest signalling’ and sexual selection in general.

Publication of the results

The main chapters of this thesis have been submitted for publication to scientific journals with the following authorships and titles:

Chapter 4: Forstmeier, W., Kuijper, D. & Leisler, B. Polygyny in the dusky warbler (*Phylloscopus fuscatus*): the importance of female qualities. Accepted for publication in *Animal Behaviour*.

Chapter 5: Forstmeier, W., Leisler, B. & Kempenaers, B. (in press) Bill morphology reflects female independence from male parental help. *Proceedings of the Royal Society of London, Series B*.

Chapter 6: Forstmeier, W. Extra-pair paternity in the dusky warbler (*Phylloscopus fuscatus*): a test of the “Constrained-Female Hypothesis”. (submitted to *Behavioral Ecology*).

Chapter 7: Forstmeier, W. Factors contributing to male mating success in the polygynous dusky warbler (*Phylloscopus fuscatus*). (submitted to *The Auk*).

Chapter 8: Forstmeier, W. Differences in the motivation of males to arrive early at breeding grounds. (submitted to *Journal of Animal Ecology*).

Chapter 9: Forstmeier, W. & Balsby, T. J. S. Why mated dusky warblers sing so much: territory guarding and male quality announcement. (submitted to *Animal Behaviour*).

Chapter 10: Forstmeier, W., Kempenaers, B., Meyer, A. & Leisler, B. A novel song parameter correlates with extra-pair paternity and reflects male longevity. (submitted to *Nature*).

2. The study area

In the following, the study area, its habitats and climate is described briefly, focussing on those aspects that might be important for the breeding biology of the dusky warbler. A more detailed geo-botanical, geological and meteorological description is provided by Haese (1999). Details on habitats, food availability and predators can be found in Weiß (2000).

Location and surroundings

The study area is situated at the mouth of the river Malkachan, 190 km east of Magadan (ca. 40,000 inhabitants) in the Russian Far East (154° 14’ E; 59° 51’ N; Figure 2.1). The area is located on the west coast of the Shelikhov Gulf, part of the Sea of Okhotsk, opposite the Kamchatka peninsular. Yamsk (33 km to the south of Malkachan) and Tachtoyamsk (47 km to the north) with approximately 150 and 600 mostly native inhabitants are the closest-by permanent villages. Caused by the cooling influence of the Okhotsk Sea the area is situated at the transition between the northern boreal and the hemi-arctic zone (Tuhkanen 1984). Altogether the region belongs to the forest tundra ecotone (Walter & Breckle 1986), where isolated trees, tundra and forest vegetation alternate mosaically. Hence there is tundra-like vegetation near the coast and taiga forest stands are found further inland.

The Malkachan river is approximately 100 km long and 50-100 m wide, and forms an extensive delta together with the somewhat smaller river Habata which flows into the Okhotsk Sea directly north of the Malkachan mouth. The surrounding area is characterised by a great diversity of habitats. Directly to the north there are mountains of up to 895 m height (m. Iretskaya). To the south, between Malkachan and Yamsk, there stretches an extensive sea terrace with open tundra holding a large number of small, shallow lakes. Further inland, to the west, there are *Larix*-dominated taiga forests. The delta of the Malkachan and Habata rivers are in a shallow bay with large tidal mudflats, which are partly separated from the open sea by a 6 km long island. Approximately 90 km to the south-east there are the Yamsk Islands, which probably hold one of the largest seabird colonies of the world.

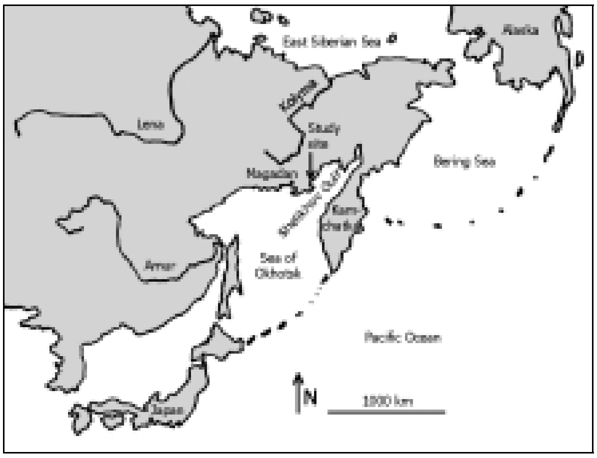


Figure 2.1. Location of the study area

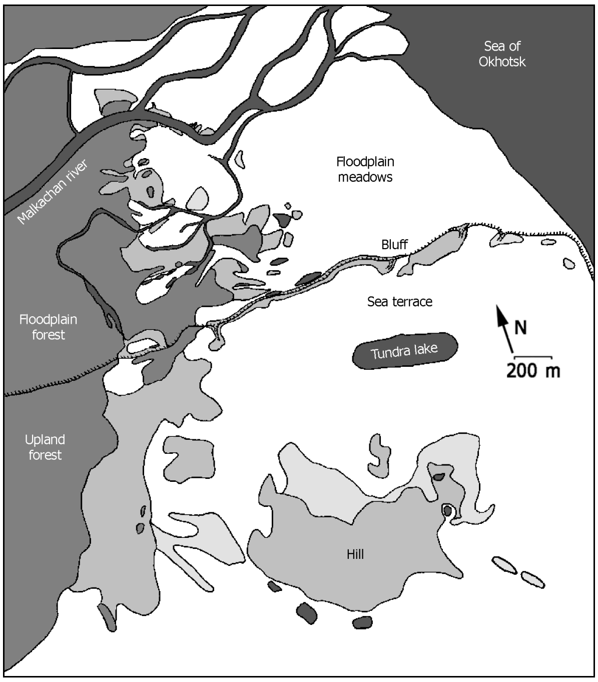


Figure 2.2. Schematic map of the study area showing the Malkachan river and the Okhotsk Sea, the inland forest and the bluff in east-western direction, separating the floodplain (top half) from the sea terrace (bottom half). Bushlands are found along the forest edge, along the bluff and on the hill which is south of the tundra lake. The two grey tones indicate areas of bush cover of above 20% (darker grey) and below 20% (lighter grey), respectively. See Figure 8.1 for the distribution of dusky warbler territories.

The habitats

A schematic map (Figure 2.2) gives an overview of the study area. Most of the area is covered by tundra vegetation or meadows, bordered by the seacoast in the east and taiga forest in the west. At the transition between taiga and tundra, there are extensive bushlands (the only habitat occupied by the dusky warbler). An approximately 10 m high bluff running from the west to the east separates the floodplain of the Malkachan river in the north (just above sea-level) from the upland sea terrace in the south (10-28 m above sea-level). South of a small lake there is a maximally 28 m high hill standing out from the otherwise flat tundra area.

Figure 2.3. Pine bushes near the forest edge seen from the helicopter. Note that large parts of the floodplain are still covered with snow (May 22nd 1999; Photograph: Schmidt-Eisenlohr).

Figure 2.4. Dusky warbler habitat at the edge of the floodplain forest. On the right hand side is the bluff which separates the floodplain from the sea terrace (Photograph: Schmidt-Eisenlohr).

Figure 2.5. Willow bushes along the Malkachan river: the most preferred habitat where up to five females were nesting within a single male territory.

Figure 2.6. The camp site at the forest edge.

As the study area is characterised by discontinuous permafrost soils, well drained areas (the hill and the bluff) and forest edges allow the growth of bushes. These bushlands are dominated by *Pinus pumila* (brush pine; 61%) and *Betula middendorffii* (22%) with some admixture of *Alnaster fruticosus* (5%), *Alnus hirsuta* (5%), *Larix cajanderi* trees (5%) and *Salix* sp. bushes and trees (2%). The given values are averages from vegetation measurements collected for 54 dusky warbler territories. On average, two thirds of all the territorial areas are covered with bushes or trees, the remainder being tundra or meadow.

From the point of view of the dusky warbler, these bushlands vary with respect to food availability (arthropods) and predator or brood parasite densities (most noticeably the Siberian chipmunk, *Tamias sibiricus*, and the Horsfield’s cuckoo, *Cuculus saturatus horsfieldi*; see Weiß 2000). By far the highest food densities are found in *Alnus hirsuta* and *Salix* vegetation growing along the sides of the Malkachan river and along a small stream crossing the floodplain area (for methods of arthropod sampling see Chapter 5). The poorest habitats are on the upland, namely the northern side of the hill and most of the area along the forest edge (south of the bluff). Chipmunks are completely absent only from the island in the delta of the Malkachan river. In the northern parts of the floodplain and on the hill they are found in rather low densities, while highest abundances are reached along the bluff and in the southern parts of the floodplain. Note that chipmunk numbers can show tremendous between-year fluctuations. Cuckoos are numerous in the floodplain, less common along the bluff, but virtually absent on the hill. For more details see Weiß (2000).

Climate and weather

The climate in the study area is characterised by very low temperatures and outstandingly strong storms during the wintertime, and moderately warm and rather dry weather in summer (see Table 2.1 for climate data from Yamsk). When the first dusky warblers arrive in the area (end of May), parts of the habitat still may be completely snow covered (on average there is a closed snow cover from November 2nd to May 17th; data from Yamsk). In years with delayed snow melting this may have strong impact on the patterns of territory establishment, as wind-exposed areas have no snow, whereas there may be snow drifts, several meters deep, at forest edges. During this study, however, most of the territories were essentially free of snow at the time when the great bulk of male dusky warblers arrived. Mid to end of May the ice of the Malkachan river breaks, which typically sets the lower parts of the floodplain under (shallow) water. This may also happen (about once per five years) during unusually high spring tides of the Okhotsk Sea (8 m tidal amplitude). Typical temperatures at the end of May, when male dusky warblers arrive, are –3°C during the night and +5°C during the day. Warbler mortality caused by unusually cold weather was never observed. In summer, during the nesting period, the most extreme temperatures ranged from 0°C to +29°C, but typically were around +5°C at night and +20°C during the day. The lowest temperature recorded during autumn migration was –4°C.

Generally, there was very little precipitation. Due to monsoonal influences rain was more frequent in late as compared to early summer, but hardly ever lasted for more than one day. Misty weather occurred regularly in late May and early June (especially during night), the time when the ice on the sea breaks. During daytime, winds are typically from the east, bringing rather cool air from the sea, while there is normally no wind from evening to late morning. This is due to the sun heating up the inland air much faster than the air above the sea. When there are winds from the west (a couple of days every summer), temperatures typically raise to about 27°C. Because of high latitude, it does not get completely dark during the nights in late June, and the activity of dusky warblers may last from about 04:00h to 22:00h.

Table 2.1. Climate data from Yamsk (means and extreme values from a 30-year period).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	total
Temp. mean (°C)	-20.5	-21.0	-17.2	-9.1	-0.6	5.8	12.0	12.1	7.7	-1.5	-10.5	-16.5	-4.9
Temp. min (°C)	-44	-51	-44	-41	-22	-4	1	1	-8	-25	-31	-38	-51
Temp. max (°C)	0	0	2	6	17	29	28	27	21	12	6	4	29
Precipitation (mm)	42	44	27	23	16	25	36	59	56	102	54	35	519
Wind mean (m/s)	5.8	5.6	4.3	4.9	3.9	4.4	5.1	5.3	6.1	6.0	7.5	8.0	5.6
Wind max (m/s)	52	40	40	40	34	24	24	40	40	40	40	34	52

3. Natural history of the dusky warbler

The literature contains only limited information on the breeding biology of the dusky warbler (see Glutz von Blotzheim & Bauer 1991). I therefore briefly describe some aspects of its natural history that might be relevant for the following chapters. Note that part of the information given here is rather anecdotal, based on incidental observations and small sample sizes. As the following chapters do not normally include this kind of information, it is presented here in some greater detail.

Distribution

The dusky warbler breeds throughout southern Siberia from the Ob river in the west to the Pacific coast in the east. In the Yenisei river valley it reaches at least as far north as 62° (Bourski & Forstmeier 2000), and at the Pacific coast the breeding range extends to about 64° of northern latitude. The species winters in south-eastern Asia, mostly in Thailand, Burma, Laos, Cambodia and Vietnam (Dementiev & Gladkov 1968), which is about 6,000 km to the south west of the study area.

Plumage and morphology in relation to age and sex

The dusky warbler has a sexually monomorphic, dull brownish plumage (Figure 3.1). Juvenile birds that have not yet moulted their body feathers (moult was found to start as early as eight days after fledging) can be distinguished from adults by a more greyish coloration (Figure 3.2).

Figure 3.1. Colour-ringed three-year-old male dusky warbler sitting on a brush pine (Photograph: Schmidt-Eisenlohr).

Figure 3.2. An 11-days-old nestling which is almost ready to fledge (Photograph: Schmidt-Eisenlohr).

Morphological measurements can be used to unequivocally sex full grown birds (for sexual dimorphisms see Figure 7.4). This is more difficult when wings and tail are not full grown. A discriminant analysis based on tarsus length and body mass of 11 days old nestlings was able to correctly classify 99% of 76 molecularly sexed female nestlings and 89% of 82 molecularly sexed male nestlings (molecular sexing following Griffith et al. 1998). Measurements from wings and tails can also be used to distinguish individuals in their first year (still wearing juvenile wing and tail feathers) from older individuals with some confidence (94% of females and 91% of males of known age were correctly classified; see Figures 4.3 and 7.1).

Songs and calls

The song of the dusky warbler consists of discrete strophes of 1-2 seconds duration that are separated by pauses of typically 3-5 seconds. There are two very distinct song types. First, a stereotypic, individually specific song type which allows individual recognition (called S-song), and second, a variable song type which comprises large individual syllable repertoires (called V-song). For details and spectrograms see Chapter 9. The alarm call of the dusky warbler is a very characteristic, short, harsh ‘tack’ (Spectrogram depicted in Cramp 1992). However, unlike stated in Cramp (1992), it is used only very rarely in combination with song (as shown in Schubert 1982). In addition, there is a much softer call which is described as ‘drrr’ or ‘drp’, which is typically heard between strophes of V-song (as shown in Glutz von

Blotzheim & Bauer 1991), but is also frequently used in communication between sexes.

Nestlings start producing begging calls at an age of about four days. These can be heard only from a short distance, but the amplitude increases with age and appears to significantly increase the risk of nest predation by carnivores during the late nestling stage (Weiß 2000). As soon as the young fledge they start producing the above ‘tack’-call to maintain contact with their parents. This juvenile call is noticeably softer than the adult alarm call, but this difference disappears gradually as juveniles grow older. Juvenile males start producing a form of sub-song in late August, but this is not comparable to full adult song, and I never observed it provoking any aggressive response by territorial adult males.

Phenology

The first males typically arrive at the study area in the last days of May. In 1997, most of the males had already arrived when the study began (June 8th). In 1998 the first male was seen on May 26th and in 1999 on May 29th. About 10 days later, the great majority of males arrive (see Chapter 8) together with the first females. Female arrival is more concentrated, thus the difference between the arrival dates of the average male and the average female is only six days. The latest females arrive about four weeks after the earliest male.

In 1997 the first egg of the season was laid on June 11th, in 1998 on June 15th and in 1999 on June 19th, interestingly, always by the same individual female. The fact that males defend their territories until they depart to their winter quarters (see below and Chapter 8) allows us to observe the timing of their departure. The first males left the study area on August 21st, the great bulk departed around August 27th, and on August 30th only three males out of 21 were still defending territories (observations from 1997). In 1998, the last male was observed singing on September 4th. Females appear to leave the study area earlier than males, as revealed by mist-netting during August. Between August 1st and August 23rd, 28 juvenile males and 20 juvenile females were trapped, whereas from August 24th to August 31st, 21 juvenile males but only three juvenile females were captured ($\mathrm{Chi}^2 = 6.3$, $p = 0.016$). A similar pattern appears to apply to adult birds, although the sample sizes are more limited there.

Habitat choice, foraging behaviour and food

The dusky warbler is one of the *Phylloscopus* warblers that is specialised on habitats with dense bush vegetation (Gaston 1974, Forstmeier et al. 2001). No other *Phylloscopus* species that occurs in the surroundings of the study area, nests in the same habitat (i.e. *P. borealis*, *P. plumbeitarsus*, *P. inornatus*, *P. proregulus* and *P. collybita*). The dusky warbler is the dominant passerine species breeding in the bushlands of the study area. The most common other species, in decreasing numbers, are yellow-breasted bunting (*Emberiza aureola*), yellow wagtail (*Motacilla flava*, nesting in tundra), Siberian rubythroat (*Luscinia calliope*), pine grosbeak (*Pinicola enucleator*), redpoll (*Carduelis flammea*), stonechat (*Saxicola torquata*, nesting in tundra) and lanceolated warbler (*Locustella lanceolata*).

Foraging in dense bush vegetation means that locomotion is predominantly on foot with little use of the wings, and prey is typically captured by gleaning techniques (Forstmeier & Keßler 2001). Females that search for prey under time constraint, e.g. during pauses from incubation, appear to use sallying techniques more frequently (own observations; see also Nyström 1990). Early in the season (i.e. the earliest arriving males) are sometimes seen to forage directly on the ground, where they apparently hunt for spiders. Later in the year, birds were only very rarely observed on the ground. Parents that were provisioning their young were most often seen to collect caterpillars, but they also regularly fed spiders and flies to the nestlings. Locally, in territories with *Alnus hirsuta* bushes, small cicada are the predominant food item. Large prey items are also used, e.g. a dragonfly of the genus *Coenagrion* was seen to be fed to an 11-days-old nestlings.

Territoriality

Males defend an exclusive area as a breeding territory, where they tolerate no other adult male. The territory area is marked by the individually specific S-song of a male (see Chapter 9). Territory size ranged from 0.5 to 6 ha (mean 2.1 ha; n = 52 territories from 1998). Early in spring, males typically defend larger areas that shrink in size as new males arrive and settle. During the period of post-nuptial moult (i.e. late July to late August) territories may be further reduced in size when some of the males move to high-quality habitat to establish a new territory. Dusky warblers are unusual with respect to being territorial even during the moulting period. This late territoriality appears to function as a preoccupation of territories with respect to the following year. However, not all males engage in such late territoriality (see Chapter 8). In 1999, when there was a strongly reduced population density (see below and Chapters 4 and 8), the size of territories tended to be somewhat larger than in the previous year. This effect was small because high-quality habitat (see Chapter 4) was occupied almost as densely as in the previous year, while low-quality habitat remained unoccupied.

Territory boundaries hardly ever changed during the breeding season (i.e. during the time when there are no new males arriving to an area, which is normally from mid June to the end of July). Real fights over the possession of a territory occurred only very rarely, and this happened only when a female had just settled on that territory. Such fights may last for long periods (up to two days) and are very energy consuming as they involve mutual chasing and singing to each other (see Chapters 7, 8 and 10). Physical contacts were never observed. Non-territorial floaters appear to occur only exceptionally (see Chapter 4).

Social system

Females that nested within a male’s territorial area were always also socially paired to that male, as judging from overt courtship display and male presence at the nest. The number of different females that nested on a territory (‘harem size’) varied from zero to five, thus the social mating system is facultatively polygynous. Sometimes females nested in an area where no male had ever been observed singing, as males usually avoid singing near the nest (see Chapter 9). However, there was never any doubt about who was the social partner of such a female.

Very rarely, i.e. on three occasions, I observed a neighbouring male that once fed at a nest in another male’s territory. In two cases the territory owner was absent at that moment, while in the third case the ‘helper’ was vigorously chased away by the female’s social partner. Intriguingly, in none of these cases had the neighbouring male sired any of the young in that nest. Two of these males simultaneously had nestlings on their own territory which they were feeding as well. One other case, however, was difficult to classify. A female was paired monogamously with a male and had just finished building a nest on the territory of that male, when a new male settled in an adjacent territory. On that day, the female was seen staying in close proximity to the newly arrived male for several hours, as is typical for social pairing. The first male was not seen to attack the new neighbour but entered the territory of that new male to copulate with the female. The female finally bred in the nest that she had already built and both males were seen to regularly provision the nestlings without being aggressive to each other. The males still maintained exclusive singing territories, but the first male tolerated the second male, which typically collected food in his own territory and then had to fly across all of the other male’s territory to reach the nest. The male that had settled later provisioned the young more frequently than the first male, and paternity analysis showed that he also had sired all the offspring.

To classify this case in a way that is consistent with the other classifications I use, I consider the first male to be mated monogamously (as the female nested on his territory), while the second male is regarded to be unmated (as he did not attract a female to breed on his territory). This classification is used in chapters that deal with the social mating system (Chapters 4, 5, 7 and 8). For analysis of extra-pair paternity (Chapters 6 and 10), I refer to this as a case of social polyandry, and treat it separately from normal cases of extra-pair paternity, as there were also direct benefits (parental care) involved.

Pairing and copulation

Females pair with a male soon after their arrival, although some females were seen to visit several territories before they settled (see Chapter 4). Males spend much time close to the female on the day of pairing and they sing less than normal on that day, but later males do not guard their females (see Chapter 9). Within-pair copulations are performed visibly e.g. on top of a bush, but they appear to be infrequent, as I observed only a few of them (less than ten). Copulations were seen a few days before and during the period of egg-laying. Copulation-solicitation display by females was additionally seen twice around the time of hatching (July 13th and 25th), apparently to stimulate the social partner to participate in brood care. In both cases, secondary females that had made replacement clutches, displayed towards their polygynous male partners. Extra-pair copulations appear to take place secretively at special places that provide visual cover, thus they were never seen directly (see Chapter 9). Courtship feeding was never observed.

Nests and eggs

Only the female builds the nest. The main construction of the closed nest with a side entrance (Figure 3.3) is completed within three days of nest building. Such a nest consists of about 500 blades of grass and some other materials, and has a dry weight of 20 ± 6 SD g (see Schubert 1998). The inner parts are lined with feathers (171 ± 83 SD; n = 18 nests), most commonly with white body feathers of the willow grouse (*Lagopus lagopus*). Nests are placed in low bushes, rarely directly on the ground, mostly 10 to 30 cm above the ground (maximally 70 cm; see Weiß 2000). Four out of 101 nests were not situated in bushes, but in high grass.

Females started laying eggs almost invariably eight days after arrival at breeding grounds (see Chapter 4). Normally one egg per day was deposited early in the morning, but occasional irregularities were observed. Clutch size varied from three to seven (mean = 5.16, n = 84) and strongly declined over the season (see Chapter 4). Eggs are whitish (Figure 3.4) and measure on average 16.37 ± 0.70 SD mm x 12.65 ± 0.35 SD mm (n = 221; excluding one aberrant egg of 14.7 mm x 10.8 mm that did not hatch). Average egg size of a clutch was significantly repeatable between clutches laid by the same female, but did neither correlate with any female trait nor with female status, nor did egg size significantly vary between years or between different territories (data not shown).

Figure 3.3. Nest with the side entrance facing to the camera (Photograph: Bergmann).

Figure 3.4. Nest with three dusky warbler eggs and one egg of the Horsfield's cuckoo (Photograph: Schmidt-Eisenlohr).

Eight out of 40 nests (20%) that were found before the deposition of eggs, were parasitised by the Horsfield's cuckoo (*Cuculus saturatus horsfieldi*; see Chapter 9). Cuckoo eggs were whitish with red-brown spotting (Figure 3.4) and measured 19.54 ± 0.80 SD mm x 14.20 ± 0.65 SD mm (n = 11 eggs from eight nests; one nest contained three cuckoo eggs). When laying their eggs, cuckoos always removed one host egg.

Brood care

Incubation normally started on the day when the last egg was laid, and lasted on average 13.2 days (range 12-15; n = 23 nests that were checked frequently enough). When females made replacement clutches late in the season, they typically initiated incubation before the last egg was laid. Consequently, the first nestlings hatched 12.3 days after the last egg was laid (range 12-13; n = 3), and thus one or two days before the last egg hatched. Altogether, 16 of 356 eggs (4.5%) from 70 nests did not hatch.

Both sexes participate in feeding nestlings, but polygynous males normally restrict their efforts to the nest of their primary female (see Figures 4.1. and 6.2.). Only the female appears to brood the young and typically spends the night inside the nest until the young are about eight to ten days old. The nestling period lasted on average 13.5 days (range 12-15; n = 35). Altogether, 224 of 340 nestlings (66%) from 70 nests fledged. Twenty-three nests suffered complete predation and four nest were partially depredated. No single nestling died from starvation. For more details on nest predation see Weiß (2000) and for details on female and male reproductive success see Chapters 4 and 7.

Nestlings were ringed and measured when they were 11 days old. Seventy-six molecularly sexed female nestlings had tarsi of 23.16 ± 0.53 SD mm (range 21.7 to 24.1 mm), while those of 82 male nestlings measured 24.84 ± 0.64 SD mm (range 23.2 to 26.1 mm; measured as illustrated in Schmid and Spitznagel 1985). Female nestlings weighed 9.88 ± 0.51 SD g (range 8.0 to 11.0 g), which is 4.7% above the adult female weight ($p < 0.0001$), and male nestlings weighed 11.08 ± 0.67 SD g (range 9.1 to 12.8 g), which is 10.9% above the adult male weight ($p < 0.0001$). Note that in European *Phylloscopus* species, nestling weight does not exceed that of adults (Tiainen 1978).

Both parents may care for fledglings, but most of the work is done by the female. As long as the female together with the young stayed on the territory, 23% of the feeds were done by the male (mean for 33 broods). In a very few cases broods were split up and males cared for two or three young until they reached independence. Most frequently, however, females left the territory together with the brood. This may happen already two or three days after fledging, but most often after about one week. About two weeks after fledging juveniles begin to reach independence and start to disperse. If nests are lost early in the season (before July 13th), females may initiate a replacement clutch (69% of 31 clutches were replaced; see Chapter 4), for which they always build a new nest. The latest replacement clutch was initiated on July 17th (see also Figure 9.4).

Moult

Adult birds have a complete postnuptial moult before their departure to winter quarters. The earliest moulting male was trapped on July 20th, and all males trapped between July 26th and September 1st were moulting (n = 22). Moulting females were trapped from July 23rd onwards, but captured individuals that still had to feed their young (n = 5), had either even not yet started their moult (August 7th and 12th), or had just begun to moult slowly (August 4th, 7th and 24th; see also Chapter 4). During moult, birds stay very hidden in bushes and are difficult to observe and catch, despite the fact that many of the males vigorously defend their territories (also against playback-simulated intrusions). As already mentioned above, juvenile birds have a partial moult after fledging, when they change their body feathers. During mid or late winter dusky warblers have a partial moult when they change body feathers, a variable amount of tail feathers and normally all three tertials. Moulted tail feathers can be easily distinguished from old unmoulted feathers and can be used as a key to distinguish first-year females from older females (see Chapters 4 and 7).

Population size and site tenacity

During the first season, studies were restricted to the central part of the study area, but were later extended to the north and south. Breeding populations in 1997 and 1998 were similar in size (17 vs. 16 territorial males in the central part of the study area), while there was a tremendous decline between 1998 and 1999 (28 vs. 58 territorial males in the overall area). This decline was caused by an unusually high winter mortality.

Return rates, based on colour-ringed males that held a territory in the study area for at least one month, were 43% between 1997 and 1998 (six of 14), but only 25% between 1998 and 1999 (12 of 48). Theses values are similar to the return rates observed in females (53% in 1998 vs. 14% in 1999; see Chapter 4). Two of 33 male fledglings (6%) and three of 26 female fledglings (12%) from 1997 returned to the study area in 1998. In the following year, two of 64 male fledglings (3%) and none of 65 female fledglings (0%) returned. These figures indicate that most juveniles disperse from their natal area, while almost all adults that survive the winter appear to return to the area where they bred the previous year.

Between-year movements of returning males (n = 19) were 240 m, on average (maximum 1.5 km), and returning females (n = 15) moved 530m, on average (maximum 2.3 km). Outside the study area, there is more habitat that is suitable for dusky warblers north of the Malkachan river (between Malkachan and Habata and also north of Habata). In 1998 and 1999 we searched for colour-ringed individuals in this population and also ringed 13 individuals (seven males, one female, five male juveniles) at this place in 1998. However, no exchange of individuals between the study area and this area was observed.

4. Polygyny from the female perspective

The polygyny-threshold model states that secondary females gain benefits from high territory quality that outweigh the costs of sharing a male. I aimed to test this prediction using the dusky warbler as a model species. I first show that neither the shifted sex-ratio hypothesis nor the no-cost models are likely to apply to the studied population. Secondary females settled in territories of higher quality (high food abundance, low predator density) and tended to have higher reproductive success than simultaneously settling monogamous females. However, there were strong indications that these two groups of females differed intrinsically. Secondary females were older than late monogamous females, and while they replaced lost clutches more often, they also tended to suffer from higher winter mortality. Consequently, it was impossible to tell whether differences in reproductive success were caused by differences in territory quality or in female qualities. The present study suggests that female choice may also depend on characteristics that are specific to the individual, and may therefore be more sophisticated than allowed for in traditional polygyny models. In other words, the polygyny threshold may be not the same for all individuals. A comparative analysis of studies on other polygynous bird species confirms the finding that late arriving females are more prone to mate as secondary females if they are old than if they are first-time breeders. I suggest that prior breeding experience may help older females to profit more from the benefits and to suffer less from the costs of polygyny than young females.

INTRODUCTION

Social monogamy is the prevalent mating system for the vast majority of bird species, and it is usually combined with bi-parental care of the offspring (Lack 1968, Ligon 1999). The most common deviation from monogamy is polygyny, which has been recorded in 39% of well-studied European passerine species (Møller 1986). More than 30 years ago, the polygyny-threshold model (PTM) was developed (Verner 1964, Verner & Willson 1966, Orians 1969), which explained territorial polygyny as an adaptive strategy originating from female choice. According to this model, a female can gain higher fitness by mating with an already paired male in a high quality territory in preference to joining an unpaired male in a poor territory. The cost of sharing the male's parental efforts with his primary female is offset by direct or indirect benefits from high breeding situation quality (BSQ), which may include territory quality, male parenting abilities and male genetic quality ("Sexy son hypothesis"; Weatherhead & Robertson 1979).

Since the proposition of the PTM, numerous field studies have been conducted to test the assumptions and predictions of this model empirically (reviewed in Davies 1989, Searcy & Yasukawa 1989, 1995, Slagsvold & Lifjeld 1994, Ligon 1999), and the interest in this topic is still active (Bensch 1996, Hansson et al. 2000). Generally it has been recognised that a single model is unable to explain all cases of territorial polygyny in birds (Searcy & Yasukawa 1989, 1995, Ligon 1999). According to Searcy & Yasukawa (1989), the most important alternatives that need to be considered are the skewed-sex-ratio model (Skutch 1935), the no-cost models (Lightbody & Weatherhead 1987) and the no-compensation models (Haartman 1969, Alatalo et al. 1981).

Rather few studies have supported the PTM (e.g. Pleszczynska 1978, Temrin & Jakobsson 1988, Petit 1991, Bensch 1996), while most studies have found that secondary females breed less successfully than simultaneously settling monogamous females (reviewed in Slagsvold & Lifjeld 1994, Johnson et al. 1994). The approach these studies have usually taken is to compare the reproductive success of secondary females with that of monogamous females settling simultaneously in the study area. This approach assumes that a key prediction of the PTM is that the breeding success of secondary females should at least equal that of simultaneous monogamous females. However, this is only the case if these two groups of females do not differ in their intrinsic qualities (Altmann et al. 1977, Davies 1989). If secondary females are of low quality, this might alternatively explain their low reproductive success as found in many studies (Slagsvold & Lifjeld 1994).

However, few studies have investigated the possibility that individual females may differ in their decision rules. Female choice may depend on qualities and characteristics that are specific to the individual, such as breeding experience or body condition (a conditional strategy; Caro & Bateson 1986). A similar idea was proposed by Gowaty (1996): according to the constrained-female hypothesis some females may depend more on the assistance of the male in raising offspring than others. This implies that the polygyny threshold might differ between individual females.

Here I report a case study of territorial polygyny in a migrant passerine, that illustrates the importance of individual variation among females. I firstly test whether the PTM can explain the occurrence of polygyny in the dusky warbler. I follow the instructions of Searcy & Yasukawa (1989) in testing between the possible alternative explanations. Assuming that polygyny in territorial birds is never based on male coercion (Searcy & Yasukawa 1989), the procedure consists of three steps. I have rearranged the order of these steps to make them easier to follow.

(1) I analyse whether secondary females were forced to pay the cost of polygyny because of the unavailability of unmated males (skewed-sex-ratio model) or whether there were unmated males present, that could provide secondary females with monogamous alternatives (balanced-sex-ratio models). (2) I investigate whether polygyny is costly to secondary females (cost models) or whether possible benefits from increased harem size do immediately outweigh these costs (no-cost models). (3) To distinguish between compensation (PTM) and no-compensation models is inherently difficult (Davies 1989, Searcy & Yasukawa 1989), but some predictions of the PTM can be tested: Firstly, do secondary females experience higher BSQ than simultaneously settling monogamous females? Secondly, is the occurrence of polygyny related to the magnitude of difference in BSQ between the best and worst territories?

Following the above outlined argument that intrinsic female qualities might influence female mating decisions (assuming that females do actively decide about their status) I test whether secondary females differ from simultaneously settling monogamous females in age or in other characteristics possibly related to their readiness to raise nestlings without male assistance.

MATERIAL AND METHODS

Study area

The study was conducted in pristine landscape at the mouth of the Malkachan river, 190 km east of Magadan, in the Russian Far East (154° 14’ E; 59° 51’ N). The area is characterised by the transition from inland taiga forests, that consist mainly of *Larix cajanderi* trees, to coastal tundra along the shoreline of the Okhotsk Sea. At this transition there are extensive bushlands of *Pinus pumila* with some admixture of *Betula middendorffii* and *Alnaster fruticosus*, typically 1-2m in height. On rich soils in close proximity of the Malkachan river, these bushes are replaced by faster growing *Salix sp.* and *Alnus hirsuta* bushes. The overall area measures 3 km x 3 km and contains approximately 1.5 km^2 of bushland, which is the habitat occupied by the dusky warbler.

I studied this dusky warbler population over three consecutive breeding seasons between 1997 and 1999. The dusky warbler is an insectivorous long-distance migrant passerine. It has a sexually monomorphic dull brown plumage and sexual dimorphism in body size is comparable to what is found in other congeneric species (males: mean ± SE = 10.0 ± 0.05 g, n = 128; females: mean ± SE = 9.4 ± 0.09 g, n = 78; for other species see e.g. Glutz von Blotzheim & Bauer 1991). Dusky warblers winter in south-east Asia (Glutz von Blotzheim & Bauer 1991) and are present in the study area from the latest days of May to the first days of September. I followed the birds for the duration of the breeding season, which comprises only a single brood (second attempts are only made when the first brood is lost early in the season) and an obligatory postnuptial, pre-migratory moult. In 1997 investigations were restricted to the central part of the study area described above (area A), and were extended during the two following years to the north (area B) and south (area C; see Figure 8.1). Comparisons over all three years of study are only possible for area A.

Breeding data

Male dusky warblers, which arrived on average six days in advance of the females, were captured using mist-nets as soon as possible after their arrival, and fitted with a unique combination of plastic colour rings. Male territories were usually visited every day or second day, and song posts were plotted on a detailed map drawn from a 1 : 5000 satellite photograph of the area.

Females were captured and ringed either at arrival, when they moved through the different territories, or (mostly) later at their nests, when incubating or feeding nestlings. Sixteen percent of the females could not be trapped at all, e.g. when they deserted their nests early in the season as a result of nest predation. In contrast, I managed to ring all the males that held territories in the area and also mist-netted a small number of additional males, that were thought to be non-territorial floaters.

Dusky warbler nests, that are built by the females in low bushes near to the ground, were mapped and were frequently checked to determine the date of deposition of the first egg. In all cases where I was able to determine the date of female arrival, the first egg was laid either 7 or 8 days after arrival (n = 1 and n = 5 respectively). As a result of brevity of the breeding season females are constrained to start the clutch as soon as possible, and I assume that an interval of 7 or 8 days is the minimal time span required for nest building and egg formation. As I found hardly any variation in the length of this period, I defined the date of female settlement as being 8 days before deposition of the first egg of the first clutch.

I determined female ranks in polygynous relations by the order of female settlement. All non-primary females are referred to as “secondary females”, including the third, fourth and fifth females. In contrast to other *Phylloscopus* species (Rodrigues 1998, Gil et al 1999), males do not guard their females during the fertile period (Chapter 9). Overt courtship display and copulation were observed only between social partners (the female and the owner of the territory where the nest is located). Contacts between females and other males were always secretive and extra-pair copulations were never witnessed, despite the fact that they must have been frequent (Chapter 6). The mating behaviour of the territory owner towards secondary females did not differ appreciably from that directed to primary females. I therefore apply the term “social mating” to all groups of females.

Each nest was inspected frequently, and I determined clutch size, hatching date, hatching success, fledging date, fledging success and incidence of nest predation. On the 12th day of the nestling period, shortly before fledging, all nestlings were measured and banded. I measured body mass, wing length, tail length and tarsus length (as shown in Schmid & Spitznagel 1985), and fitted nestlings with metal and colour rings.

To quantify the amount of paternal investment the feeding behaviour of parents at nests was recorded during the nestling period. For a total of 72 nests data on the number of feeding trips performed by males and females were collected. When young were 1-15 days old, I counted male and female feeding trips during short (5-60 min) observation periods. Some nests were observed more than once a day. For each day and each nest, I calculated the proportion of male feeds (on total number of feeds). These values were then averaged over the nestling period to obtain an estimate of male participation in brood care. I also noted time of day and age of nestlings to allow controlling for these factors.

This study includes a total of 97 breeding seasons of 84 individual females. Eleven females were included twice and one female three times. I used female breeding seasons as independent observations. I feel this is justified by the fact that there was no strong association between individual females and their status in different years. In 8 of 13 replications females did change their status between successive years. Retention of status between years was no more frequent than expected by chance (by chance probability of 5 or more cases of retention is p = 0.335). The same methodology was adopted by Bensch (1996), who also found no repeatability of status in a sample of 40 females breeding more than once.

Territory quality

To estimate the quality of territories I measured aspects of (1) food availability, (2) potential nest-predation pressure and (3) availability of potential nest sites.

(1) During the nestling period (late July) in 1998 and 1999 the arthropod fauna of bush vegetation was sampled by shaking the content of branches into an umbrella. Foraging activity of dusky warblers is almost exclusively restricted to this vegetation type, and as a typical gleaning species it mostly catches prey of low mobility (Forstmeier & Keßler 2001). Observations at the nest were made to ensure that the most abundant food items (prey species and prey size) that were sampled were also fed by dusky warblers to their nestlings (unpublished data). Within each of 45

territories at least 30 samples per year were collected; each sample being taken from an approximately constant volume of bush vegetation. Sampling locations were spread more or less equally over the entire territory area. I summed up the volumes of all arthropods in a sample (measuring length, breadth and height on millimetre-paper) and calculated mean arthropod volume per sample for each territory and year. The resulting values were log-transformed to approach a normal distribution (non-transformed values varied by 47 times between the richest and poorest territory).

(2) The most important predator of dusky warbler nests in the study area appears to be the Siberian chipmunk (*Tamias sibiricus*), occurring in densities of approximately 20 individuals per ha (Weiß 2000). Chipmunk densities were estimated by carrying out line-transect counts (Burnham et al. 1980) for each territory in 1998 and 1999 (Weiß 2000). I applied a square-root transformation of resulting values to fit the density estimates to a normal distribution.

(3) On the basis of experience gained from a total of 101 dusky warbler nests found in the study area I estimated the approximate number of potential nest sites (number of bushes capable of holding a well-concealed nest) for each territory. Estimated numbers, ranging from 5 to 250 per territory, were log-transformed.

Morphology

I measured the following morphological characters of females: wing length, tail length, tarsus length (as shown in Schmid & Spitznagel 1985), footspan with claws, bill depth, bill width and body mass. Using the tarsus, footspan and bill measurements I extracted one principal component ("PC body size") that reflects body size independently of body mass and feather measurements.

Body mass was strongly dependent on the stage in breeding cycle of individual females ($r^2 = 0.60$, $n = 89$ measurements). Body weight increased from day 8 to day 3 prior to the deposition of the first egg by mean ± SE = 0.18 ± 0.09 g per day ($r = 0.62$, $n = 8$, $p = 0.10$). During egg-laying, females were mean ± SE = 1.9 ± 0.19 g heavier than the average weight outside the egg-laying period ($n_1 = 6$, $n_2 = 83$; T-test, two-tailed: $T_{87} = 9.9$, $p < 0.001$). From the day of deposition of the last egg to the day of fledging of young, female body mass decreased by mean ± SE = 0.065 ± 0.006 g per day ($r = -0.76$, $n = 75$, $p < 0.001$). Female weight measurements were standardised using residuals from the above regressions, in order to eliminate the influence of stage of breeding cycle.

In addition, weights were corrected for differences attributable to visible fat-deposition, that varies markedly with time of day. Fat-deposition, estimated in 9 distinct classes (according to Kaiser 1993), accounted for 14% of the variation in weights that had been corrected for stage in breeding cycle as described above. Weights increased by 0.136 g per class of fat score ($r = 0.38$, $n = 89$, $p < 0.001$). The influence of fat score was eliminated by standardising weights with the residuals from this regression. If available, multiple values for the same female were averaged within seasons. Repeatability (calculated following Lessells & Boag 1987) of lean mass estimates for individual females was still low, but substantially higher than repeatability of untreated weight measurements (+0.23 vs. –0.36).

For each bird I recorded states of active moult and the extent of moult that had been performed in winter-quarters. Dusky warblers perform a complete postnuptial moult of body and flight feathers on the breeding grounds, which, in my study area, usually started around 25th of July. However, late breeding females, that were still feeding their offspring at this time, delayed the onset of moult until the independence of young, which was as late as the 20th of August. Inspection of museum skins revealed that dusky warblers can also moult some of their flight feathers (which, in migrant passerines, are subject to heavy wear and tear; Svensson 1992) in winter (see also Glutz von Blotzheim & Bauer 1991). A variable number of tail feathers (most commonly the central pair) and tertials (usually all of them) can be moulted in mid or late winter (unpublished data). These fresh feathers are easily distinguished from older feathers by very marked regular growing bars (these are always absent in feathers of postnuptial moult) and their better condition.

RESULTS

Skewed vs. balanced sex ratio

Table 4.1 lists numbers of territorial males and their mating status for various parts of the study area and for each year separately. The most striking observation is that the population size and especially the number of secondary females decreased dramatically from high levels in 1997 and 1998 to very low levels in 1999. This population decline was apparently caused by unusually high mortality outside the breeding season (Chapter 3). As a consequence, in 1999, only territories of high quality were occupied by males (shown below in detail). The consequences of this restriction to the optimal habitats provide circumstantial evidence for the origin of polygyny in the dusky warbler.

Table 4.1. Occurrence of polygyny in the study area from 1997 to 1999.

Area Year	A 1997	A 1998	A 1999	B & C 1998	B & C 1999
Number of territories	17	16	7	42	21
Unmated males	3	2	1	4	1
Monogamous males	9	12	5	23	19
Polygynous males (2 females)	4	1	1	4	1
Polygynous males (3 females)	1	1	0	2	0
Polygynous males (5 females)	0	0	0	1	0
Status unknown	0	0	0	8	0
Floating males *	+	+	-	+	-
Rate of polygyny	36 %	14 %	17 %	23 %	5 %
Breeding density (males/ha)	0.58	0.54	0.24	0.46	0.23
Secondary females	6	3	1	12	1

* Floating males were present in low numbers in 1997 and 1998, but were absent in 1999.

In 1997 and 1998 the number of secondary females exceeded that of unmated territorial males, suggesting a slightly unbalanced sex ratio (Table 4.1). However, in these years, I also observed a small number of unringed males in the study area that were thought to be floating males without territories. Assuming that unmated males were not successful in attracting females as a result of the low quality of the habitat that they were defending, these floaters may not have gained from establishing breeding territories in areas of even lower quality (see Searcy & Yasukawa 1989). In 1999, when the population size was much smaller, only the best habitats were occupied and not even a single unringed male was observed. In that year the number of secondary females equalled the number of unmated males (Table 4.1). Because in years of high population density, some males may not have defended territories (making them very difficult to detect), the sex ratio may have been balanced in all three study years.

As there is no indication of an unbalanced sex ratio, and as there were unmated males present in the study area, I conclude that the great majority of secondary females were not forced to mate polygynously through the lack of potential partners.

Cost vs. no cost of polygyny

In the dusky warbler, nest building and incubation is performed solely by females. Male parental effort is restricted to feeding of nestlings and, to a minor extent, fledglings. Nest defence by the male is restricted to warning of predators and was observed only at nests where the male was also feeding. Figure 4.1 shows how much males contribute to the feeding of nestlings. The data presented are raw means, not adjusted for differences in average nestling age and time of day at observation. Adjusting for these factors did not lead to any significant change of mean value. As male feeding activity declines markedly with the onset of postnuptial moult, first clutches and replacement clutches are depicted separately. Polygynous males concentrate their feeding effort almost exclusively on their primary female. Secondary females received no male help in most cases. Out of 16 secondary nests (11 secondary, 4 tertiary and 1 quarterny), where feeding data are available, only 4 nests (3 secondary and 1 tertiary) received a small amount of male help (on average 10% and maximally 18% of the feedings observed at the nest; Figure 6.2).

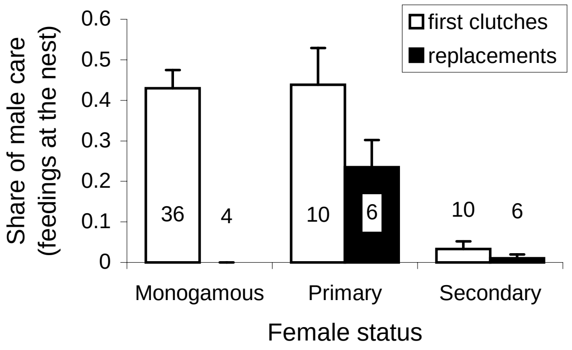


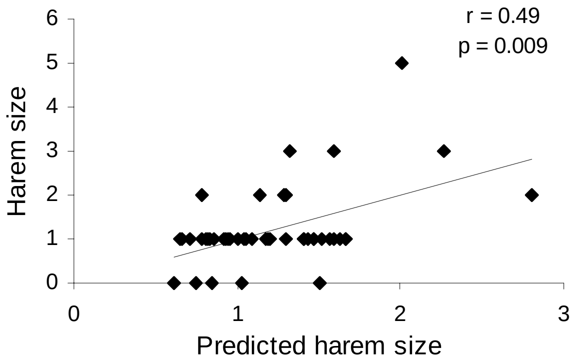
Figure 4.1. Proportion of male assistance at nests of monogamously mated females, of primary females of polygynous males and of all kind of secondary females (second to fourth) of polygynous males. Sample sizes (number of nests) and standard errors are given. Replacement clutches made after predation of the first clutch are depicted separately, as the intensity of male help significantly declined over the season.

The fact that secondary females encounter a clear cost of polygyny in terms of reduced male assistance is not a by-product of paternal care declining as the season progresses, but is clearly due to their social status (ANCOVA with date and status as main effects; date: $F_{69} = 17.7$, $p < 0.0001$; status: $F_{69} = 23.5$, $p < 0.0001$). In contrast, there appears to be little or no cost of polygyny to the primary females. Males always appeared to be reluctant to feed at a secondary nest, even when the nest of the primary female was depredated. Contrary to numerous studies on other polygynous bird species (reviewed in Slagsvold & Lifjeld 1994) I therefore do not find much potential for conflict between primary and secondary females. Aggressive encounters between females were never observed.

In order to reject the no-cost models of polygyny, we have to consider whether the cost of polygyny to secondary females could be immediately outweighed by direct benefits from increased harem size. Two possible direct benefits are mentioned in the literature (Searcy & Yasukawa 1989). (1) Large harems may reduce the risk of nest predation by communal nest defence or mutual warning from predators. This hypothesis cannot be tested directly by comparing rates of nest predation between monogamous and polygynous territories, as these territories differ in predator densities (see below). Nevertheless, if communal defence was an ultimate cause for polygyny, we would expect nests to be aggregated (Picman et al. 1988). To quantify nest dispersion I drew a circle around the nest of the primary female, large enough to cover exactly 50% of the territory area. From 18 nests of secondary females I found 9 situated within and 9 outside this circle, suggesting a random distribution with regard to between-nest distances. The average distance between primary and secondary nests was 72 metres (min. 15 m, max. 160 m). To human ears, alarm calls are perceptible only within 50-100 m distance. Two females simultaneously alarming against a predator or the observer were observed only in very few instances. These findings indicate that benefits from communal predator defence are marginal. (2) Social foraging may enhance foraging efficiency. As I have no indications of social foraging in the dusky warbler, this argument appears not applicable to the study species.

Do secondary females experience higher BSQ?

Because of small sample sizes in 1997 and low rates of polygyny in 1999 (Table 4.1), I concentrate on the data from 1998 to analyse how harem size depends on territory characteristics. A test for consistency in female choice (see below) indicates that the patterns were similar among years. As shown in Figure 4.2, harem size increased with arthropod and nest site densities, and decreased with predator densities (Siberian chipmunks). A multiple regression with these variables explains 24% of the variation in harem size and is significant at $p = 0.009$ ($n = 45$ territories). In a stepwise multiple regression, the first variable entering the model is predator density ($r = -0.33$, $p = 0.028$; $F_{43} = 5.17$). After accounting for variation in predator density, inclusion of arthropod density significantly improves the model ($r = 0.32$, $p = 0.025$; $F_{42} = 5.57$). Finally, availability of potential nest sites improves the model further, although not significantly ($r = 0.20$, $p = 0.178$; $F_{41} = 4.41$). The three factors used to explain variation in harem size are largely uncorrelated to each other. There is no correlation between food and predator densities ($r = 0.01$, $p = 0.962$), a weak correlation between predators and nest sites ($r = -0.23$, $p = 0.123$) and a weak trade-off between arthropods and nest sites ($r = -0.23$, $p = 0.131$).



(food r = 0.36 ; chipmunks r = - 0.28 ; nestplaces r = 0.20)

Figure 4.2. Multiple regression between harem size of 45 territories in 1998 and three measures of territory quality. Arthropod density (food) correlates positively, predator density (Siberian chipmunks) correlates negatively and abundance of possible nesting sites correlates positively with harem size.

One exceptional case of polygyny deserves special mention. A territory situated on a small island in the Malkachan river was the only place free of Siberian chipmunks. Four secondary females decided to settle there in 1998 and all of them raised a brood successfully, as did the primary female of the territory. Nests in the surrounding areas suffered from very high rates of nest predation (12 of 18 nests failed; Chi^2-exact test, two-tailed: $Chi^2 = 6.97$, $p = 0.014$). As food abundance was also quite high on this island I cannot conclusively decide which factor may have caused this unusual high concentration of secondary females.

Contrary to most studies on other species, polygynous territories tended to be smaller than monogamous ones (1.53 ha, n = 9 vs. 2.23 ha, n = 30; T-test, T = 1.38, p = 0.18). This is in accordance with the fact that high quality areas are populated more densely, and that females can nest close to each other without showing aggressive behaviour.

The PTM predicts that polygyny will occur only if the difference in BSQ between the best and the worst territories exceeds a certain threshold value. In 1999, when population density was much lower than the year before (Table 4.1), only the best territories were occupied by males. Territories occupied in 1999 had a mean predicted harem size (from the relationship between harem size and territory quality in 1998; see Figure 4.2) of 1.35, which differed significantly from those remaining unoccupied in 1999 (predicted harem of 0.97; T-test, two-tailed: $T_{32} = -2.38$, $p = 0.023$). The fact that the rate of polygyny was also decreased in 1999 (Table 4.1) is in accordance with the PTM.

The low rate of polygyny in 1999 and the small study area covered in 1997 render analysis of consistency of female choice by between-year comparison difficult. Moreover, patterns can be influenced by the same females returning to the same territory in consecutive years. Therefore, I look at those secondary females, that were new to the study area A in 1998 or to the overall area in 1999 (n = 4). All four of them settled on territories, that had been polygynous before in one of the previous years. The one-tailed by-chance probability of this is p = 0.04. In all these four cases the owners of polygynous territories were different from those that had occupied these territories in previous years.

Another prediction of the PTM is that polygynous territories are settled by primary females earlier than females settle on monogamous territories. Analysing the order of mating for 29 territorial males (5 polygynous and 24 monogamous males) in 1998, I find that polygynous males mated significantly earlier than monogamous males (T-test: $T_{28} = 3.78$, $p < 0.001$). Four days after the arrival of the first female all polygynous males were mated, while only 25 percent of the monogamous territories were settled by females. Besides territory quality, the BSQ may also depend on male quality. I have already shown that secondary females receive almost no direct benefits in the form of paternal care from their partners. However, females may also receive indirect benefits if offspring fitness is increased by heritable components of male fitness. Consequently, females may prefer territories of high quality not only because of direct benefits (more food, lower predation risk) but also because of the high genetic quality of polygynous males. If this is true, we would expect females to prefer polygynous males as genetic mates. In contrast, extra-pair paternity tended to be more frequent in nests of polygynous males as compared to monogamous males (Chapter 6), and polygynous males were not preferred as extra-pair fathers (Chapter 10).

In conclusion, BSQ for secondary females depends solely on territory quality, and secondary females experience higher territory quality than monogamous females.

Are secondary females different?

Before we look at whether increased BSQ sufficiently compensates secondary females for the costs of reduced male help, allowing them equal or higher reproductive success compared to simultaneously settling monogamous females, we have to check whether these groups of females differ intrinsically.

Table 4.2 shows a comparison of reproductive and morphological data between different groups of females. Note that morphological data reflect female traits, while reproductive data may depend on both, BSQ and intrinsic female qualities. As this comparison is aimed to make sure that female groups do not differ intrinsically, I highlight all differences with $p < 0.1$ and do not apply a Bonferroni correction (Rice 1989). Although this approach reduces the probability of statistical errors of type II, marginally significant results will require corroboration by other data sets.

Table 4.2. Reproductive and morphological data for four groups of females: primary (P1) and secondary (P2) females of polygynous males, as well as early and late breeding monogamous (M) females.

Female group	Date of first clutch	Clutch size	Clutch size corrected	Re-nesting frequ.	Age class	New tail feathers	Tail length (mm)	Wing length (mm)	PC body size	Mass residuals (g)
P1	18.6.	5.13	5.06	79 %	1.75	2.14	46.02	57.13	-0.50	0.015
	(15)	(15)	(15)	(7)	(8)	(7)	(15)	(15)	(14)	(14)
M early	18.6.	5.52	5.28	36 %	1.67	3.31	46.62	57.35	0.14	-0.012
	(20)	(20)	(20)	(11)	(12)	(16)	(20)	(20)	(18)	(18)
M late	22.6.	5.05	4.98	0 %	1.44	4.50	46.03	56.92	-0.01	-0.018
	(22)	(21)	(21)	(2)	(16)	(19)	(22)	(22)	(21)	(21)
P2	23.6.	4.97	5.26	100 %	1.79	2.19	46.52	57.27	0.09	0.043
	(22)	(17)	(17)	(10)	(14)	(16)	(22)	(22)	(20)	(20)
Test	T-test	T-test	T-test	Chi^2	Chi^2	Wilcox.	T-test	T-test	T-test	T-test
P2 vs. non-P2	**0.001**	0.209	0.482	**0.011**	0.352	0.104	0.534	0.691	0.518	0.507
P2 vs. M late	0.720	0.770	0.259	**0.015**	**0.072**	**0.036**	0.322	0.403	0.788	0.454

Sample sizes (in brackets) reflect numbers of females. Clutch size corrected reflects clutch size after removal of effects of laying date. Age class reflects mean age of females classified with significance by discriminant analysis as 1 (first-year) or 2 (older), including ringed birds of known age. New tail feathers are the number of tail feathers moulted in winter. Tail length is measured on old feathers, not moulted in winter. PC body size is a principal component on hind limb and bill measurements. Mass residuals are from a regression on PC body size.

Monogamous females were split into two groups, depending on settlement date. Within each year, I selected those monogamous females ("late monogamous") which best matched the secondary females of that year with regard to arrival date. There were no primary females arriving simultaneously with secondary females.

Variation in clutch size depended strongly on laying date and thereby also on the frequency of clutch replacement. After correcting for effects of laying date (clutch size declined by 0.0694 eggs per day; $r = -0.563$, $n = 82$, $p < 0.001$), secondary females did not lay fewer eggs than late monogamous females. More significantly, secondary females differed from monogamous females in their ability or readiness to replace lost clutches. Due to brevity of the breeding season, replacement clutches can be undertaken only when predation occurs rather early in the season. Nests lost after the 12th of July were never replaced and therefore excluded from the analysis. The data in Table 4.2 reflect how often clutches lost before the 13th of July actually were replaced. The validity of the finding that both secondary females and primary females replaced a much higher percentage of lost clutches than did monogamous females is not affected by differences in the mean date of nest predation. However, the relatively large clutches and the re-nesting ability of secondary females may be due either to differences in intrinsic female qualities, or to differences in environmental conditions, such as high food density in polygynous territories.

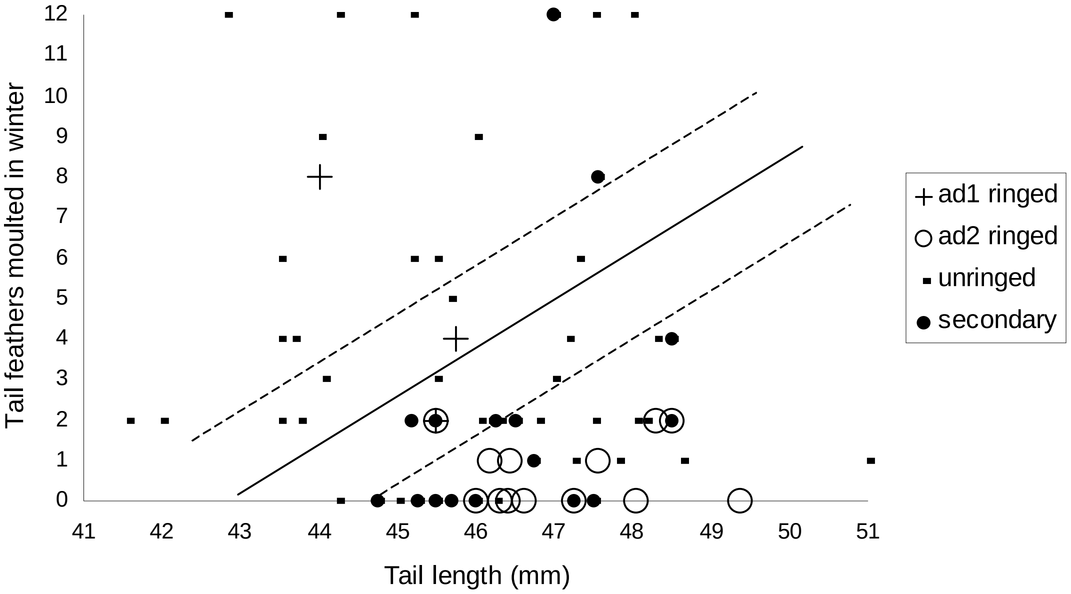


Figure 4.3. Scatter plot of tail length and winter moult for 68 individual females. Tail length is measured on unmoulted feathers with the exception of where all 12 feathers were moulted in winter. Three females were known to be first-year birds (ad1 ringed), 13 were known to be older than one year (ad2 ringed) and 52 were of unknown age (unringed). Tail characteristics of 16 secondary females (one ad1 ringed, two ad2 ringed, 13 unringed) are shown. A discriminant analysis is used to separate females into first-year and older (continuous line). Individuals beyond the broken lines were assigned with significance ($p < 0.05$).

There were also morphological differences between secondary and late monogamous females. Secondary females moulted significantly fewer tail feathers on their wintering grounds than late monogamous females did, and they tended to have slightly longer tails (measuring old, unmoulted tail feathers when available). There are strong indications that these two parameters are related to age, as shown in Figure 4.3. Thirteen out of 15 females that were captured in two consecutive years increased their tail length by more than 0.8mm (on average by 1.31 mm; paired T-test: $T_{14} = 5.6$, $p < 0.001$). Tail length therefore increases with age. Moreover, none of 13 females that were known (by ringing) to be older than one year had moulted more than two tail feathers in winter. In contrast, three first-year females (ringed as nestlings the year before), had moulted 2, 4 and 8 tail feathers. While only 54% of females had tails longer than 44.5 mm and no more than two winter-moulted tail feathers, this population included all 13 females known to be older than one year and 13 out of 16 secondary females (Figure 4.3).

I used tail length and winter moult in a discriminant analysis to assign females of unknown age to one of the two age groups (first-year vs. older; Figure 4.3). The discriminant function classified 15 out of 16 females of known age correctly and 51 females of unknown age were grouped into: 17 ‘confident’ first-years ($p < 0.05$), 5 ‘uncertain’ first-years ($p > 0.05$), 20 ‘confident’ older and 9 ‘uncertain’ older. Those which were determined with significance (later referred to as ‘confident’) plus those of known age class (referred to as ‘certain’) were included in the numbers given in Table 4.2, while those determined at $p > 0.05$ (referred to as ‘uncertain’) were excluded from the table. According to this, secondary females tended to be older than late monogamous females were (Chi^2-exact test, two-tailed: Chi^2 = 3.77, p = 0.072), suggesting that females with prior breeding experience more often decided to become secondary females than did inexperienced females.

As this finding is of great importance for the present study, I decided to implement a statistically more powerful analysis, to test whether the probability that a female will mate as a secondary female depended on her age, while controlling for the effect of arrival date. A logistic regression explaining female status (secondary vs. non-secondary) shows that the effect of age is significant (effect of arrival date: Beta = 5.8, p = 0.0004; effect of female age: Beta = 2.4, p = 0.0278; n = 50 females as in Table 2; entering year as a stratum variable; exact computation using LogXact 4.1 for Windows, Cytel Software Corporation). This result is robust to whether ‘uncertain-aged’ females are included or excluded (n = 67 vs. n = 50), and to whether ‘year’ is entered as a factor or as a stratum variable (p-values for the effect of age range from 0.0192 to 0.0278).

One additional finding supports the validity of the ageing technique presented here. Nine out of 15 females breeding in study area A in 1998 (see Table 4.1) were ringed there in the previous year, eight as adults and one as a nestling. Taking into account the very high site tenacity of adult female dusky warblers, the remaining six unringed females should be newly recruited first-year females. The discriminant analysis assigned five of them as confident first-year and one as uncertain older.

Measurements of wing length, body size and residual body mass (as a measure of body condition) revealed no significant differences between secondary and late monogamous females.

Compensation vs. no compensation

In the previous section I showed that secondary females differ from late breeding monogamous females in being older and in the higher frequency at which they replace lost clutches. Consequently, comparing the reproductive success of these two groups is not a legitimate test of the PTM, as effects of BSQ cannot be distinguished from effects of intrinsic female qualities. Nevertheless it is worthwhile examining the factors that contribute to differences in reproductive success.

Table 4.3. Parameters of breeding success for four groups of females: primary (P1) and secondary (P2) females of polygynous males, as well as early and late breeding monogamous (M) females.

Female group	Clutches per season (females)		Fledging success (nests)		Fledged young (females)		Fledging mass (nests)		Winter survival of females	
P1	1.44	(16)	0.52	(21)	3.31	(16)	10.33	(10)	46%	(13)
M early	1.17	(24)	0.44	(27)	2.17	(24)	10.26	(12)	42%	(15)
M late	1.03	(34)	0.40	(35)	1.91	(34)	10.61	(16)	32%	(13)
P2	1.52	(23)	0.47	(30)	2.83	(23)	10.57	(12)	17%	(20)
Test	Chi^2		Chi^2		U-test		T-test		Chi^2	
P2 vs. M late	< **0.001**		0.588		0.177		0.859		0.164	

Sample size of females or nests included in the analysis is given in brackets. The number of clutches includes first clutches and possible replacement clutches. Fledging success is the proportion of nests producing at least one fledgling. Fledging mass increased by 0.543 g per mm of tarsus length (r = 0.67, n = 235, p < 0.001) and was adjusted to fit the mean tarsus length of 24.0mm to eliminate effects of brood sex-ratio and heritable components of body size. Survival data are taken from Table 4.4 and the test between P2 and M late was calculated as in Table 4.4. The p-value is for a difference in the two years combined.

Parameters describing the reproductive success of the different groups of females are presented in Table 4.3. Secondary females tended (but non-significantly) to fledge more young per season than late breeding monogamous females. To a minor extent, this was caused by a higher fledging success of nest attempts as a result of slightly lower rates of nest predation. Nest predation was the most important factor determining fledging success, as there was no case of nestling starvation. The main factor leading to between-group differences in the number of fledged young was the number of clutches laid per season, i.e. the ability or readiness of females to replace lost clutches. Secondary females laid significantly more replacement clutches than late monogamous females (Chi^2-exact test, two-tailed: $Chi^2 = 18.9$, $p < 0.001$). The fact that primary females also tended to lay more replacement clutches than early monogamous females (Chi^2-exact test, two-tailed: $Chi^2 = 3.53$, $p = 0.08$), suggests that all females in polygynous territories may have been facilitated in the replacement of lost clutches by the same factor or combination of factors. Candidate factors, shared by primary and secondary females are: (1) age; both groups consisting mainly of females older than one year (Table 4.2) and (2) territory quality.

(1) Out of 31 females that lost their first clutch before 13th of July, 69% started a replacement clutch. There was no indication that the frequency of clutch replacement was lower in first-year females (6 of 8 replaced).

(2) There are indications that the territory per se influenced whether or not females replaced their lost clutches. Two out of 14 monogamous females that lost clutches before 12th of July in 1998 and 1999 bred in territories that had been polygynous in one of the previous years. Both of these replaced their clutches, compared to only 3 of the remaining 12 (Chi^2-exact test, two-tailed: $Chi^2 = 4.2$, $p = 0.11$). Moreover, there were 10 cases of clutch loss in territories where the clutch of another female had been lost before (in this or in earlier years). In 9 of these 10 cases the decision of the two females was identical, which differs significantly from random (binomial test: $p = 0.011$). However, BSQ, measured as predicted harem size (see Figure 4.2), did not differ significantly between territories where replacements always occurred and territories where they never occurred (T-test, two-tailed: $T_{16} = -1.23$, $p = 0.24$).

Table 4.4. Return rates of ringed females.

Female group	Ringed 1997	Returned 1998	Ringed 1998	Returned 1999	Returned 1997-98	Returned 1998-99	Mean rate
P1	5	4	8	1	80 %	13 %	46 %
M early arrive	3	2	12	2	67 %	17 %	42 %
M late arrive	3	1	10	3	33 %	30 %	32 %
All but P2	11	7	30	6	64 %	20 %	42 %
P2	6	2	14	0	33 %	0 %	17 %
Chi^2 p-value	*1997-98:*	*0.335*	*1998-99:*	*0.155*	*years combined:*		*0.044*
Early finish	12	9	26	6	75 %	23 %	49 %
Late finish	4	0	21	0	0 %	0 %	0 %
Chi^2 p-value	*1997-98:*	*0.019*	*1998-99:*	*0.027*	*years combined:*		*0.001*
Early finish non-P2	10	7	20	6	70 %	30 %	50 %
Early finish P2	2	2	6	0	100 %	0 %	50 %
Chi^2 p-value	*1997-98:*	*1.000*	*1998-99:*	*0.280*	*years combined:*		*0.646*

Female groups are: primary (P1) and secondary (P2) females of polygynous males, as well as early and late breeding monogamous (M) females. Late finish comprises females that fledged young only after the 25th of July. The first Chi^2-exact test is between P2 and all non-P2 females. The p-value for years combined was calculated by stratified cross-tabulation according to Robins et al. (1986).

The weights of nestlings at 11 days of age (and also wing and tail length; data not shown) produced by secondary females did not differ from those of young from late monogamous broods, indicating that secondary females compensated for the lack of paternal assistance by working harder. Even though high food densities in polygynous territories may have facilitated this, secondary females tended to suffer higher winter mortality (Table 4.3 and Table 4.4). Survival data for late monogamous females are scanty, making comparisons with secondary females unreliable (Chi^2-exact test, two-tailed: $p = 0.164$; years combined). In a comparison with all other females, secondary females had significantly lower return rates (Chi^2-exact test, two-tailed: $p = 0.044$; years combined). The main reason for this appeared to be their tendency to delay postnuptial moult when doing a replacement clutch. Females, that still had to feed their offspring late in the season, delayed the onset of moult until the independence of young. At the extreme, such females started to moult only at a time when most other females had already left the study area. I therefore looked at the return rates of females whose young fledged later than the normal date of onset of moult (25th of July). None of 25 females with late fledging young returned (Chi^2-exact test, two-tailed: $p < 0.001$; years combined). Secondary females with early fledging young showed no reduction in winter survival as compared to non-secondary, early-finishing females (Chi^2-exact test, two-tailed: $p = 0.646$; years combined).

In conclusion, females face a clear trade-off between current and future reproduction. Those that decide to replace a lost clutch will have a very low chance of survival to the next breeding season. Whether or not females replaced lost clutches was correlated with both female status and also to unidentified territory properties.

DISCUSSION

Testing between polygyny models

I followed the stepwise procedure proposed by Searcy & Yasukawa (1989) to test between alternative models possibly explaining the occurrence of territorial polygyny in the dusky warbler.

Firstly, my data show that, contrary to the skewed-sex-ratio hypothesis (Skutch 1935), there were unmated males available at the time when females decided to mate polygynously. The study site was chosen to comprise the areas of highest breeding densities. This makes it likely that more unmated males could have been present in the surrounding habitats, as harem size and breeding density tended to be positively correlated (see e.g. Petit 1991, Kempenaers 1994).
Secondly, I found that being a secondary female is costly in terms of greatly reduced male assistance, and that these costs are unlikely to be outweighed by direct benefits. Strictly seen, I would need experimental evidence that the lack of male help negatively affects female fitness (Searcy & Yasukawa 1989, Bensch 1997). However, this has been demonstrated for several bird species with comparable amounts of male assistance (reviewed by Bart & Tornes 1989) and the review by Searcy & Yasukawa (1995) indicates that no-cost models apply only to those species with little male help and very large harems. It is, therefore, highly unlikely that the no-cost models could explain polygyny in the dusky warbler.

Thirdly, secondary females settled in territories of high quality, with low predator density, high food abundance and a large number of potential nest sites. The direction of correlation between territory characteristics and harem size suggests that secondary females are choosing the territory in such a way as to maximise their chances of breeding success. The negative influence of high Siberian chipmunk densities on reproductive success was shown by Weiß (2000), and the positive effects of high food abundances and a high number of nest sites to choose from are intuitive. Other studies have found that food availability is a prime factor in territory selection by secondary females (e.g. Verner & Engelsen 1970, Ewald & Rohwer 1982). Differences between monogamous and polygynous territories in nest-predation pressure were found to be important in compensating the costs of polygyny in many studies (Knapton 1988, Temrin & Jakobsson 1988, Askenmo & Neergaard 1989, Bell et al. 1997, Hansson et al. 2000). With regard to the dusky warbler, it may be concluded that secondary females are compensated, at least to some degree by high BSQ.

Whether benefits from high territory quality are large enough to outweigh the cost of polygyny is difficult to answer. Reproductive success of secondary females did at least equal that of simultaneously settling monogamous females. This might be the result of both high BSQ and high female quality. I found that secondary females were more experienced individuals than simultaneous monogamous females, and reproductive success is often age-dependent (Gustafsson 1989, Dhondt 1989, Newton 1989, Saether 1990). In addition, secondary and late monogamous females may differ in other respects as is suggested by the differences in relaying behaviour. This will be discussed in more detail below.

Despite of these difficulties, it still should be possible to rule out the major no-compensation models. The correlation between harem size and BSQ and the temporal patterns of female settlement are consistent with the predictions of the PTM, but not so easy to explain by the deception hypothesis. Moreover, I observed primary and secondary females simultaneously building nests as close as 15 metres from each other. This also contradicts the deception hypothesis, where females are unaware of the presence of other females. The clearest evidence comes from annual variation. In years of low population density the range of used habitat is restricted to the optimal sites and differences in territory qualities do not reach the polygyny threshold. Neither the female deception hypothesis, nor the search-cost models (Searcy & Yasukawa 1989, Slagsvold & Dale 1994) can explain why there should be no or almost no polygyny in years of low population size. If availability of unmated males was the prime factor determining female choice (search-cost models) we would have expected to get the highest, not the lowest rate of polygyny in 1999 (see Table 4.1). The decline of polygyny with population size is consistent only with the PTM.

The role of female age and condition

The data indicate that a female's decision to mate monogamously or as a secondary female is not independent of her age. I can envisage three reasons why this might be:

(1) Older females might be better able to bear the costs of raising a brood without male assistance. There is an extensive literature indicating that breeding performance improves with increasing age (reviewed in Newton 1989, Saether 1990) and increased foraging ability is certainly one of the main factors leading to this relationship (Desrochers 1992, Martin 1995, Forslund & Pärt 1995).

(2) A female's ability to estimate BSQ may increase with age (see the "experience-based-choice hypothesis" of Wootton et al. 1986), so the benefits a female can gain from mating as a secondary female may also be age-dependent. Earlier studies have suggested that individuals may use the breeding success of birds in previous years to evaluate territory quality (e.g. Boulinier & Danchin 1997).

(3) If the residual reproductive value of a female decreases with age (Williams 1966, Pianka & Parker 1975), the cost of polygyny, in terms of a reduction in female condition should decrease with age as well. There is accumulating evidence that, even in short-lived passerines, annual mortality increases with age after the first breeding season (Newton 1989, Ricklefs 1998). Old females should therefore be more ready to concentrate all reproductive effort in the current breeding season, in what is sometimes termed 'big-bang reproduction' (the residual reproductive value hypothesis, Williams 1966, Pianka & Parker 1975, Pugesek 1981, Curio 1983).

The last point indicates that not only age, but also female body condition might influence mating decisions. It may be that females in very good condition are able to bear the costs of polygyny without seriously impacting their residual reproductive value, or that only such females are able to compensate for the lack of male assistance. Females in good condition might therefore more often decide to breed in a secondary position. Under certain ecological conditions, however, the opposite might also occur. Given that body condition is crucial for chances of winter survival, but does not seriously affect a female's ability to raise nestlings, females returning from winter quarters in poor physical condition may do best by going for 'big-bang reproduction'. As such a female will not benefit much from investing in her own condition, she might raise higher quality offspring as a secondary female than she could have done with the help of a male in a low quality territory. The nature of the relationship between female quality and the readiness to raise broods without male help depends on the actual selective regime.

In the case of dusky warblers, all secondary females replaced their clutches if these were lost before the 13th of July. An apparent consequence of this was that none of them returned the next breeding season. We can therefore reject the hypothesis that secondary females chose this mating option because they could tolerate the lack of male help without impacting their winter survival. Rather the readiness of secondary females to go for 'big-bang reproduction' suggests that females of low residual reproductive value decided to mate as secondary females. The willingness of secondary female dusky warblers to increase the fitness of their offspring at the expense of their own survival may be further supported by the fact that females do not overlap reproduction with moult. The trade-off between these two activities has been demonstrated before (Nilsson & Svensson 1996, Svensson & Nilsson 1997) and overlapping may greatly reduce offspring fitness (Hemborg & Lundberg 1998).

Secondary female dusky warblers seem ready to reproduce in the current breeding season at any cost.

There is no way of estimating the residual reproductive value of females when they arrive in the study area. Nevertheless, it may be speculated that condition played a part in female reproductive decision-making. During the short period of female settlement, old females arrived an average of three days earlier than first-year females (T-test, $T_{43} = 3.48$, $p = 0.001$). While it is normal for a first-year female to arrive rather late, late arrival in old females may be indicative of poor condition. Differences in body condition and future reproductive expectations may therefore lead late arriving, old females to prefer good territories, while young females mate monogamously to maximise their chances of survival.

Evidence from other studies

While most earlier studies did not account for variation in females, three papers provide at least some data on qualities of secondary and simultaneous breeding monogamous females. Firstly, Simmons et al. (1986) found 81% of 16 secondary female hen harriers (*Circus cyaneus*) to be older than two years, while only 58% of monogamous females were as old (Chi^2-exact test, two-tailed: $Chi^2 = 2.57$, $p = 0.129$). Secondly, the data published by Bensch (1996) show that significantly fewer secondary female great reed warblers (*Acrocephalus arudinaceus*) were first-year birds (24% of 71 females) than were simultaneous monogamous females (42% of 55 females; Chi^2-exact test, two-tailed: $Chi^2 = 4.57$, $p = 0.036$). Thirdly, Alatalo et al. (1982) mention that in the pied flycatcher (*Ficedula hypoleuca*), wing length of secondary females was non-significantly longer (+0.4 mm) than that of simultaneous monogamous females (n = 24 secondary females, T = 1.20, $p > 0.10$). As wing length is known to increase with age (Alatalo et al. 1984) there might well have been an age difference between these groups. In my data, wing lengths differ also only marginally (57.27 mm vs. 56.92 mm; T-test, two-tailed: $T_{42} = 0.84$, $p = 0.403$), despite a certain age difference.

To test for a relationship between age and mating status once more, I used data on a German population of great reed warblers (data only partially published in Leisler et al. 1995). In contrast to the findings of the Swedish study (Bensch 1996, see above), the group of secondary females contained only non-significantly less first-year birds than the group of simultaneously breeding monogamous females (Chi^2-exact test, two-tailed: $Chi^2 = 0.89$, $p = 0.430$). However, in this study, significantly more secondary females were older than three years (21% of 57 females), compared to simultaneous monogamous females (9% of 163 females; Chi^2-exact test, two-tailed: $Chi^2 = 5.51$, $p = 0.023$).

In summary, all four studies that provide data on age show that secondary females tend to be older than simultaneous monogamous females (dusky warbler $p = 0.072$; hen harrier $p = 0.129$; great reed warbler, Sweden $p = 0.036$; great reed warbler, Germany $p = 0.023$; all Chi^2-exact tests, two-tailed).

Conclusion

The study suggests that individuals might behave in a more sophisticated way than allowed for in traditional models of polygyny. On the one hand, the finding that individual variation in females may also affect mating decisions, renders tests of the PTM even more complicated than previously suggested (e.g. Davies 1989). On the other hand, if we were able to show that the costs and/or benefits of polygyny differ between first-year and older females, and that females make their choices accordingly, the general idea behind the PTM could also be supported in this way. Costs could be measured experimentally be widowing monogamous females of different age classes. Whether older females make better choices than inexperienced females could be studied by forcing females to mate polygynously using removal of unmated males. The idea that some females may depend less than others on male assistance (Gowaty 1996) opens a whole field of challenging questions, as age is certainly not the only candidate feature possibly related to female independence from the male.

Further analysis of female mating behaviour indicates that, besides the effects of female age shown here, there may be also heritable components contributing to the variation observed between individual females (Chapter 5). All the findings shown in this chapter remain valid despite such possible additional effects, as both, heritable and non-heritable components appear to contribute to female behaviour independently of each other.

5. Morphological adaptation to female mating strategies

The study of territorial polygyny in birds has been influential in the development of the theory of social mating systems. Alternative female mating options have been studied within the framework of the polygyny-threshold model and later as the outcome of conflicts of interests between individuals. However, little attention has been given to variation among individual females, and how this affects their mating behaviour. Here I test the hypothesis that some females are better adapted to raise nestlings without male assistance, and thus to mate polygynously. Specifically, I investigate whether intraspecific variation in female bill morphology is related to their mating behaviour. This hypothesis is derived from earlier studies showing that in both intra- and interspecific comparisons, uniparental care by females correlates with catching larger prey items as compared to when both parents together provision the young. Using the polygynous dusky warbler (*Phylloscopus fuscatus*) as a model species, I found that, in accordance with the prediction, females with deep bills were more likely to mate as a secondary female. Moreover, independently of mating status, females with deep bills settled in territories with more food and they received less male assistance in feeding the offspring. I argue that females with stronger bills are better adapted to exploit the abundance of large food items in rich territories and thus to raise young on their own. This study demonstrates the importance of studying individual variation in females, and provides evidence for an extended version of the ‘constrained-female hypothesis’. As bill depth is a highly heritable trait, this study strongly suggests that variation in female mating behaviour is not only related to ecological factors and female condition (Chapter 4), but also to heritable morphological traits.

INTRODUCTION

The study of territorial polygyny in birds has been influential in the development of the theory of social mating systems and individual reproductive strategies (Searcy & Yasukawa 1989, Slagsvold & Lifjeld 1994, Ligon 1999). Because females usually suffer from having to share resources such as male parental care, the main question has been why females mate with already paired males if other breeding options are available. The polygyny-threshold model (PTM; Verner 1964, Verner & Willson 1966, Orians 1969) provides an answer: it suggests that females would do better (in terms of fitness) by mating with an already paired male in a high quality breeding situation (e.g. territory) compared to settling with an unpaired male in a low quality breeding situation. The PTM and its derivatives have been used to explain most social mating systems in passerine birds (Wittenberger 1979, Ligon 1999), even though the assumptions of these models have rarely been tested and may be unrealistic (Davies 1989). Davies’ (1989) paper and subsequent studies led to a new conceptual framework in which variable mating systems are considered the outcome of sexual conflicts among individuals. However, little attention has been given to variation among individual females and how this affects their reproductive options (see Gross 1996).

Many studies of social polygyny have shown that secondary females differ from primary females in that they arrive later on the breeding grounds, and/or are younger (Slagsvold & Lifjeld 1994). However, to date no field study has focussed on differences between females that mate with an already paired male (secondary females) versus simultaneously settling monogamous females. In socially polygynous systems, the decision of where to settle is often characterised by a trade-off between food abundance in a territory and the amount of male assistance that can be expected (Whittingham & Robertson 1994, Hoi-Leitner et al. 1999). The importance of this trade-off clearly depends on the importance of male parental assistance for a female’s reproductive success. The latter is known to vary geographically (e.g. Dunn & Robertson 1992), but may also depend on the quality of the female. Thus, some females might be more ‘emancipated’ from male help than others (Gowaty 1996, see also Gowaty 1997). The general hypothesis I test here is that some females are better adapted to raise nestlings without male help, and that those are more likely to settle with an already paired male. This hypothesis is an extension of the ‘constrained female hypothesis’ (Gowaty 1996), which predicts that females should seek extra-pair copulations when they can rear offspring with little help from their mate, because the cost of the (possible) reduced male care would be lower.

A specific hypothesis can be derived based on a comparative study by Leisler & Catchpole (1992) who investigated the evolution of mating systems in *Acrocephalus* warblers. Six closely related species of similar ecology display a variety of mating systems with monogamous pair-bond and biparental care at one end and promiscuity without pair-bonds and uniparental care by females at the other end. Between these extremes, there are species with facultative polygyny, where a variable proportion of secondary females raise their broods without or with very little male assistance. The higher the food abundance in a species’ habitat, the smaller the contribution of males to the care of the offspring and the higher the frequency of unassisted females. Species with uniparental care feed their nestlings with larger prey items than species where biparental care is the rule. Moreover, these species have stronger bills, presumably as adaptation for catching larger prey (Leisler & Catchpole 1992). Recently, Sejberg et al. (2000) showed that in polygynous great reed warblers (*Acrocephalus arudinaceus*; which were also included in the study of Leisler & Catchpole, 1992) secondary females feed larger prey items to their nestlings than monogamous and primary females, which receive a much larger amount of male assistance. This means that in both inter- and intraspecific comparisons female emancipation from male assistance was correlated with catching larger prey.

Based on these two studies, I investigated whether intraspecific variation in bill morphology is related to female mating behaviour. I predict that, in insectivorous passerines, females choosing uniparental care in optimal habitats (i.e. secondary females) should have bills adapted to catch larger prey compared to simultaneously settling monogamous females in lower quality habitat. To test this, I studied the dusky warbler (*Phylloscopus fuscatus*), a species with a variable social mating system where on average 17% of the males mate polygynously. The foraging behaviour of dusky warblers is similar to that of *Acrocephalus* warblers (Forstmeier & Keßler 2001), and the two genera are closely related to each other (Sibley & Ahlquist 1990). Here I test the hypothesis that bill morphology correlates with intraspecific variation in female emancipation from male parental care. Firstly, I compare bill depth of secondary females with that of simultaneously settling monogamous females. Secondly, I test whether female bill depth correlates with a continuous variable describing female independence from male assistance.

MATERIAL AND METHODS

The study was conducted at the mouth of the Malkachan river, 190 km east of Magadan, in the Russian Far East (154° 14’ E; 59° 51’ N). The area is characterised by bushlands of *Pinus pumila* with some mixture of *Betula middendorffii* and *Alnaster fruticosus*, typically 1-2 m in height. On rich soils in close proximity of the Malkachan river, these bushes are replaced by faster growing *Salix sp.* and *Alnus hirsuta* bushes. These low bushes are the habitat occupied by the dusky warbler.

I studied the mating system of this dusky warbler population in the breeding seasons of 1997 to 1999. Males and females were captured using mist-nets as soon as possible after their arrival, and were marked with a unique combination of plastic colour rings. From all birds, I measured bill depth at the proximal margin of the nostrils to the nearest 0.1 mm using callipers (Figure 5.1). I also measured wing, tail, and tarsus length, footspan (including claws) and body mass. A principal component (‘PC body size’) was extracted out of these five measurements reflecting individual variation in body size (Rising & Somers 1989). Measurements were taken blind with regard to the hypotheses tested here. In the analyses, multiple values for the same individual were averaged. Many studies have found significant effects of year and season on bill morphology (e.g. Davis 1954, Gosler 1987, Morton & Morton 1987, Matthysen 1989). To control for these possible confounding effects, I tested for seasonal and annual changes in bill morphology. Bill depth (first measurements from 76 individual females) showed only a non-significant increase over the breeding season ($r = 0.12$, $p = 0.32$). Mean bill depth did not differ significantly among years (ANOVA, $F_{2,73} = 0.84$, $p = 0.44$). Nevertheless, I did all analyses with and without controlling for capture date and year. Since this did not make any difference in the results, I only report the tests without controlling for these factors.

Male age was determined as first year or older partly based on ringing data, partly on a discriminant analysis using morphological characteristics (tail length, wing length and wing shape). The latter analysis classified 91% of males of known age (n = 65) correctly (Figure 7.1). Female age was determined in a similar way, using tail length and patterns of tail moult (Figure 4.3).

Male territories were usually visited every day or second day, and song posts were plotted on a detailed map. For each polygynous male, female mating status (primary or secondary) was determined based on the order in which females laid their first egg. All non-primary females are referred to as "secondary females", including second, third, fourth and fifth females. As I observed almost no individual variation in the time elapsed between female arrival and clutch initiation (7-8 days; Chapter 4), I used the date of the first egg minus eight as equivalent with arrival date. Within each year, monogamous females were divided into early and late settlers, in such a way that the late settlers showed maximal overlap in arrival date with secondary females.

To quantify the amount of paternal investment, feeding behaviour of parents at nests was recorded during the nestling period. For a total of 72 nests data on the number of feeding trips performed by males and females were collected. When young were 1-15 days old, male and female feeding trips were counted during short (5-60 min) observation periods. Observations were done between 05:00-21:00 h (local time) and some nests were observed more than once a day. For each day and each nest, I calculated the proportion of male feeds (on total number of feeds). These values were then averaged over the nestling period to obtain an estimate of male participation in brood care. The proportion of male feeds was independent of time of day (p = 0.23), but declined with mean nestling age at observation (r = -0.25, n = 72, p = 0.036). To control for this effect I took residuals from the above regression (y = 0.433 - 0.0203 x; where y is the proportion of male feeds and x is the mean date of observation measured in days after hatching).

During the nestling period (late July) in 1998 and 1999 the arthropod fauna of bush vegetation was sampled by beating branches (of a standardised volume of vegetation) with a stick and collecting arthropods from a tray held below the branch. The volume sampled was measured relative to the size of the tray. To standardise the volume of sampled vegetation, only branches with dense foliage were selected and the volume was estimated when branches were in their natural position. Foraging activity of dusky warblers is almost exclusively restricted to this vegetation type. Within each of 45 male territories at least 30 samples per year were collected. I summed up the volumes of all arthropods in a sample (measuring individual length, width and depth on millimetre-paper) and calculated mean arthropod volume per sample for each territory and year. As values were highly correlated among the two years ($r^2 = 0.929$) I assumed that average values would reflect food abundance of territories for all three years of the study. The richest and poorest territory varied by a factor 47. Averages were $\log_{10}$-transformed to approach a normal distribution (Kolmogorov-Smirnov-test after transformation: Z = 1.1, p = 0.17). Using a telescope (30x), the food items carried to the nestlings by the parents were observed. This was done to check whether the sampled arthropods were also fed by dusky warblers to their nestlings. I use arthropod densities per volume of bush as a measure of territory food abundance because foraging success of warblers seems to depend more on arthropod abundance than on the amount of bushes in the territory. The latter is not so variable and birds cannot deplete their territory.

Data shown are mean ± SE. Statistical analyses were performed with StatXact 4.0, SPSS 9.0. and SAS 6.12. All tests are two-tailed.

RESULTS

Female mating status (secondary vs. simultaneously settling monogamous) was nearly significantly related to female bill depth (logistic regression: $Chi^2 = 3.60$, p = 0.058). Thus females with deep bills were more likely to settle as secondary females compared to females with shallower bills. Note that this two-tailed test is conservative, because I made a clear one-tailed prediction. Overall, secondary females had deeper bills than simultaneously settling monogamous females (Figure 5.1), but the difference was not significant (T_{38}= 1.86, p = 0.07). Three of the 40 females shown in Figure 5.1 bred in two seasons. These females had the same status in both years, but are included only once. The difference in bill depth between the two female groups was consistent over all three study years (data not shown). When using a statistically more powerful test, i.e. a pair-wise comparison between secondary and monogamous females matched for study year and arrival date, I found that secondary females had significantly deeper bills (paired t-test: T_{15}

= 2.30, p = 0.036). In this test, the sample of 16 pairs of females included the secondary female with the smallest bill depth (2.3 mm; see Figure 5.1).

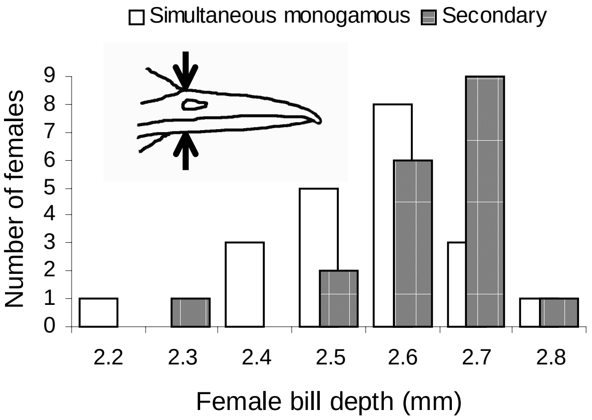


Figure 5.1. Distribution of bill depths of 19 secondary and 21 simultaneously settling monogamous females.

Secondary females received significantly less male assistance in raising nestlings than simultaneously settling monogamous females (percent of feeds by the male, comparing observations at same nestling age: secondary: 2.2 ± 1.2%, monogamous: 40.1 ± 5.0%; Mann-Whitney-test: Z = -4.8, n = 36, p < 0.001). On the other hand, secondary females bred in territories with higher food abundance (mm^3 arthropods per sample: secondary: 254 ± 77 mm^3, monogamous: 117 ± 31 mm^3, T_{34} = -2.28, p = 0.029). As the proportion of male assistance and food abundance are continuous variables, the relationship between these two factors can be investigated for all females irrespective of their social status and the date of arrival at the breeding grounds. In general, females breeding in territories with higher food abundance received less paternal assistance (r = -0.35, n = 61, p = 0.005). Such a pattern of declining male participation in care with increasing food availability, reflects a common trade-off found within populations (Whittingham & Robertson 1994, Hoi-Leitner et al. 1999), between populations (Dunn & Robertson 1992), and between species (Leisler & Catchpole 1992). I therefore decided to summarise this trade-off using a single variable that describes how female independence increases as food becomes more abundant. I calculated the bivariate major axis (BMA; see Sokal & Rohlf 1995) of the variables 'amount of food' and 'proportion of male help'. This is equivalent to performing a principal component analysis (PCA) to summarise a set of correlated variables, but is used when only two variables are to be summarised.

Female bill depth and female emancipation (BMA) are highly significantly correlated (Figure 5.2; r = 0.41, n = 61, p = 0.001) and the correlation is consistent among the three study years (data not shown). This correlation is independent of individual variation in body size. First, bill depth is only weakly correlated with body size (correlation with tarsus length: r = 0.16, n = 75, p = 0.17; correlation with PC body size: r = 0.19, n = 70, p = 0.12). Second, bill depth corrected for body size (using the residuals of bill depth on PC body size) is also strongly correlated with the BMA (r = 0.42, n = 57, p = 0.001). The correlation shown in Figure 5.2 does not only reflect the difference between secondary and monogamous females, because a positive correlation is also present when each group of females is considered separately (secondary females: r = 0.49, n = 18, p = 0.039; primary and monogamous females: r = 0.37, n = 43, p = 0.014). Evaluating each variable of the BMA separately using partial correlation, shows that females with deeper bills tend to settle in territories with more food ($r_{help=const}$ = 0.23, n = 61, p = 0.073) and receive less male help ($r_{food=const}$ = -0.29, n = 61, p = 0.024).

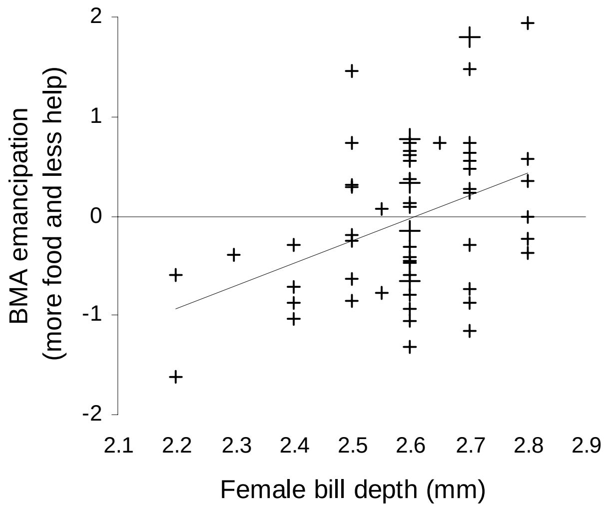


Figure 5.2. Female bill depth in relation to the bivariate major axis (BMA; see text) 'emancipation'. Increasing values indicate territories with increasing food abundance and decreasing male parental assistance (factor loadings: food r = 0.79, help r = -0.79). Increased symbol size refers to two individuals having identical scores.

I investigated various factors that influence how much care a male provides using an ANCOVA with individual nests as the statistical unit (n = 68). Using a step-wise procedure I determined the best subset of factors explaining variance in the amount of male help. This analysis shows that secondary females receive less help than other females, that male help declines over the season, that males with long tails help less than short-tailed males, and that females with deep bills receive less help. Food abundance in the territory did not enter the model (Table 5.1). The effect of female bill depth is significant in any reasonable variant of the presented model and also remains when male characters (age and tail length) are excluded ($F_{1,64} = 7.1$, $p < 0.01$).

Table 5.1. ANCOVA explaining the amount of male assistance in brood provisioning at 68 dusky warbler nests ($r^2 = 0.64$). As male tail length strongly depends on male age, a nested design is used. This means that a separate regression coefficient of tail length is estimated within each level of the factor male age (dichotomised in first-year males and older males). Therefore, the factor male age, although non-significant, cannot be omitted from the model. When "food abundance" is entered as a covariate, its effect is not significant and the p-values for other variables remain basically the same.

factors / covariates	d.f.	sum of squares	F	p
hatching date	1	0.333	16.59	0.0001
female status	1	0.316	15.79	0.0002
female bill depth	1	0.185	9.22	0.0035
male age	1	0.000	0.01	0.9150
male tail length (nested within male age)	2	0.270	6.74	0.0023
food abundance*	1	0.016	0.80	0.3750
(residual)	61	1.223		

* excluded from the presented model

DISCUSSION

The main finding of this paper is that, in the polygynous dusky warbler, females with stronger bills were more likely to breed on territories with high food abundance where they received less paternal care. This result at the intraspecific level corroborates evidence from a comparative study of *Acrocephalus* warblers' mating systems. Leisler & Catchpole (1992) showed that species with strict biparental care had relatively slim bills, bred in unproductive habitats and fed their nestlings with small prey items. Polygynous and promiscuous species with a high degree of uniparental care had stronger bills, bred in habitats with more food and fed their nestlings with larger prey. The presented results suggest that female emancipation from male help in raising the brood, through female bill morphology and territory quality, is an important factor determining the mating system of this species. Thus, the 'decision' to become polygynous cannot be seen independently from the ability of the female to raise her young without male assistance. The present study thus supports the 'constrained female hypothesis' (Gowaty 1996). However, I do not claim that female mating behaviour in the dusky warbler can be reliably predicted from bill measurements. Other factors, such as the availability of unmated males will also determine the outcome of a female's mating decision. This renders it less likely to observe a significant effect of bill morphology on mating status within a limited sample of females (see the effect of a single outlier in Figure 5.1). I now discuss possible mechanisms of why deeper bills may facilitate uniparental care by the female. I then consider how the intraspecific correlation between bill morphology and mating behaviour may be caused.

There is little doubt that intraspecific variation in bill morphology correlates with individual prey size preferences (e.g. Grant et al. 1976, Herrera 1978, Grant 1985, Gosler 1987, Price 1987, Smith 1987, own data not shown). There are three possible explanations of why females in rich habitats with little male help may on average catch larger prey items than other females.

(1) Birds in rich habitats may specialise on large prey. Small prey items are always much more abundant than large prey (e.g. Leisler & Catchpole 1992, own data not shown). It is likely that in poor habitats all sizes of prey have to be utilised, whereas in rich habitats the absolute abundance of large prey may be high enough to allow the birds to specialise on it (Leisler & Catchpole 1992).

(2) Unassisted females may catch larger prey further away from the nest. Sejberg et al. (2000) found that female great reed warblers with no or little male assistance feed their young with larger prey items than assisted females. The authors hypothesised that unassisted females may be forced to travel longer distances than assisted females, in order to compensate for the lack of male help. According to the central place foraging theory (Orians & Pearson 1979), prey size should increase with travelling distance. Consequently, unassisted females should catch larger prey. However, this hypothesis is weakened by contradicting results from studies where widowed females foraged closer to the nest (Sasvári 1986, Aho et al. 1997). A combination of different mechanisms is probably required to fully explain the findings of Sejberg et al. (2000) with regard to prey size choice of males and females.

(3) Prey size may increase with time constraints. Unassisted females need to catch prey at a higher rate than assisted females (Sasvári 1986, Pinxten & Eens 1994, Aho et al. 1997) and they may achieve this by increasing search speed (Sasvári 1986, Aho et al. 1997, own data not shown) and by using more energy-consuming foraging manoeuvres (Nyström 1990). Interspecific comparisons suggests that in small foliage-gleaning passerines, increased speed of search should result in capturing predominantly large prey items (e.g. *Regulus ignicapillus* vs. *R. regulus*, see Leisler & Thaler 1982, Thaler & Thaler 1982; *Parus cristatus* vs. *P. ater*, see Mattes et al. 1996, Pollheimer & Leisler unpublished data). Brood-size manipulations in starlings and pied flycatchers produced equivocal results with regard to effects of increased work load on prey size (Lifjeld 1988, Wright & Cuthill 1990, Siikamäki et al. 1998, Wright et al. 1998). However, these results do not necessarily contradict the presented hypothesis, as much depends on the foraging techniques used by the respective species and neither starlings nor pied flycatchers are foliage-gleaners like the dusky warbler. For any of the above reasons, unassisted females in rich territories may catch larger prey items than assisted females in poor territories (as in the study of Sejberg et al. 2000), and females with stronger bills may be better adapted to do this.

The observed correlation between female bill morphology and her decision where to breed (Figure 5.2) is unlikely to be due by chance (p = 0.001). It is also unlikely to be explained by confounding variables such as female body size (see the analyses above), age (bill depth is independent of age; data not shown; see also Gosler 1987), competitive ability (females do not compete aggressively for breeding sites; Chapter 4), or timing of arrival (bill depth does not correlate with arrival date; not shown). Therefore, the correlation between bill morphology and mating strategy is most likely explained in one of the following ways.

(1) Behavioural differences may induce morphological change. Numerous studies have shown that seasonal variation in bill morphology is associated with dietary changes (e.g. Davis 1954, Gosler 1987, Morton & Morton 1987, Matthysen 1989) apparently caused by differences in wear of the constantly growing bill (Lüdicke 1933). However, in contrast to the pattern I found, bill depth in females catching larger prey should become smaller rather than larger, because larger items are harder and require extended handling times. Thus, this explanation can be rejected.

(2) Individuals might adjust their behaviour dependent on their morphology. I suggest that females with deep bills settle in richer habitats than shallow-billed females. This may be a consequence of between-female differences in estimates of habitat quality. A shallow-billed female would gain less from moving to rich habitats and suffer more from a lack of male assistance than a deep-billed female, because it cannot utilise the abundance of large prey items with the same efficiency. On the other hand, a deep-billed female would suffer more from moving to poor habitats, as its bill might not be optimised for collecting small prey items. The observation that females with deep bills receive less male assistance than shallow-billed females, may be the result of deep-billed females being better able to compensate for lack of male help. Males may adjust their paternal effort to the female's ability to feed nestlings alone.

(3) Morphology and behaviour may be genetically correlated. Pleiotropic effects of genes on both the morphological and the behavioural trait could cause such genetic correlations (Falconer 1989).

In most bird species heritability of bill depth is high ($h^2 > 0.5$ in four of five species; Smith & Zach 1979, Grant 1983, Gosler 1987). Females inheriting a relatively deep bill should (either through learning from experience or through inherited behavioural differences) show a higher disposition to mate as a secondary female than others. Demonstrating that female mating strategy is heritable is, however, a virtually impossible task. I agree with Dominey (1984) that the vast majority of alternative mating tactics are due neither to a simple genetic polymorphism of alternative strategies, nor to a single conditional strategy with genetic uniformity of all individuals. Ecological circumstances, condition-dependence and heritable components may all simultaneously influence a female's mating decision. In conclusion, the polygyny-threshold might differ for two females of the same age and condition and arriving at the same time, but differing in heritable components of bill morphology.

6. A test of the ‘constrained-female hypothesis’

The Constrained-Female Hypothesis (CFH) states that females risk losing their social partner’s assistance in brood care when they have extra-pair copulations. Thus intraspecific variation in female faithfulness may depend on (1) the amount of male care that females expect to receive (2) the ability of females to raise offspring without male help, (3) food availability, facilitating uni-parental care. I test these predictions looking at the dusky warbler (*Phylloscopus fuscatus*), a species with a polygynous mating system and a very high rate of extra-pair paternity (45% of offspring). In accordance with prediction (1) I find that females are more likely to have extra-pair young when they cannot expect to receive male assistance in brood care (i.e. secondary females of polygynous males and females breeding late in the season). This pattern is neither confounded by variation in male quality nor in male mate-guarding behaviour. Using female age and morphology as predictors for their ability to raise nestlings alone, there is only very limited support for prediction (2). Finally, variation in food availability (3) appears to have no influence on female extra-pair matings. Overall, the findings do support the CFH, but the explanatory power is low compared with the apparent role of variation in male quality. An alternative explanation, stating that female faithfulness is affected by the accuracy with which females can assess the quality of males, is unable to explain the observed patterns as well as the CFH does.

INTRODUCTION

Extra-pair paternity, i.e. when a female copulates with a male other than her social partner, is both frequent and widespread among monogamous birds (Petrie & Kempenaers 1998). However, despite much study it is still controversial why females have extra-pair copulations (Ligon 1999). Researchers have typically looked at qualities of males to understand why some individuals have higher success in obtaining paternity than others (e.g. Hasselquist et al. 1996, Kempenaers et al. 1997). A new promising approach is to analyse variation in female emancipation, to explain why some females remain faithful while others do not (Gowaty 1996, 1997, Hoi-Leitner et al. 1999, Ligon 1999). The Constrained-Female Hypothesis (CFH; Gowaty 1996, 1997) states that females having extra-pair copulations risk losing their social partner’s assistance in brood care (Dixon et al. 1994, Westneat & Sargent 1996, Møller & Tegelström 1997, Møller & Cuervo 2000). As some females may depend more than others on their partner’s help, they may also be more constrained in their choice of with whom they copulate. The CFH predicts that three kinds of females can afford to be unfaithful: (1) females that cannot expect to receive much male help already for other reasons, (2) females with the ability to raise their young alone, and (3) females in territories with high food availability, facilitating uni-parental brood care.

In polygynous mating systems males typically help their primary female in raising the offspring, while secondary females often cannot expect much assistance (Slagsvold & Lifjeld 1994 and references therein). According to the CFH, secondary females should therefore have more extra-pair matings than primary females (prediction 1). However, when this pattern is found, it may alternatively be explained by the fact that males cannot guard their secondary females sufficiently well (Dunn & Robertson 1993, Freeland et al. 1995, Soukup & Thompson 1997, Møller & Ninni 1998). Moreover, patterns may be confounded by variation in male quality. If polygynous males are of higher quality than others, then secondary females may have little reason for unfaithfulness (e.g. Freeman-Gallant 1997). The second prediction of the CFH is difficult to test as we usually lack information about which female characters can be used as a measure of their ability to provision the brood unassisted (but note that there is support at the level of interspecific comparison; Møller 2000). Finally, the third prediction suffers from the same difficulty as the first. Females breeding in territories with much food may be mated to the best males, as reflected by their success in competition for the best breeding sites. Again these females may be unable to find extra-pair mates better than their social partner. Experimental manipulation of food availability is one promising way out of this dilemma (as successfully done by Hoi-Leitner et al. 1999).

The dusky warbler (*Phylloscopus fuscatus*) offers an excellent system, allowing the circumvention of all the above mentioned difficulties. In Chapter 10, I show that a male's ability to obtain extra-pair paternity depends on his singing performance. The aim of the present chapter is to analyse whether variation in female emancipation from the male can explain the occurrence of extra-pair paternity independently of male qualities. Singing performance was unrelated to both male mating status and food availability (Table 10.1). Thus females did not prefer to copulate with polygynous males or with owners of high quality territories (Figure 7.6). In addition, male dusky warblers do not guard any fertile female (Chapter 9). Consequently, neither variation in male attractiveness nor in mate guarding intensity should confound the patterns predicted by the CFH.

Moreover, it was shown that polygyny in the dusky warbler is explained best by the polygyny-threshold model (Orians 1969), where females actively choose whether they prefer to mate monogamously in low-quality habitat or to become secondary females in territories with a good food supply (Chapter 4). I found that old females and females with deep bills preferred secondary status over monogamy. I interpret these findings on female age and bill morphology as reflecting the ability of females to raise a brood unassisted (Chapters 4 and 5). Thus I have already identified female traits that are likely to reflect female independence from male brood care.

This study system, where 45% of the offspring are sired by extra-pair fathers, allows the testing of all of the above predictions made by the CFH. I predict that the occurrence of extra-pair paternity will depend on (1) the expected amount of male care, (2) female characteristics and (3) territory quality. As male participation in brood care is typically restricted to females of primary status, but also strongly declines as the season proceeds (Chapter 4), it is predicted that (1) nests of secondary females and late hatching broods will contain more extra-pair young. (2) Nests of old females and of females with deep bills will have more extra-pair offspring as compared to nests of young and shallow-billed females. (3) The probability of female unfaithfulness will increase with food availability.

All these factors were shown to be correlated with each other. Secondary females more often than others replace lost clutches and thus tend to breed late in the season (Chapter 4). Secondary females are older and deeper billed than others and also breed in territories with better food supply (Chapters 4 and 5). Thus I use principal component analysis (PCA) to test whether a combination of all these factors can best explain the occurrence of female unfaithfulness.

MATERIAL AND METHODS

The study was conducted in pristine landscape at the mouth of the Malkachan river, 219 km east of Magadan, in the Russian Far East (154° 14' E; 59° 51' N). Here dusky warblers breed in high density in bushlands located in the transition from inland taiga forests to coastal tundra. I studied this population over three consecutive breeding seasons between 1997 and 1999. The dusky warbler is an insectivorous long-distance migrant passerine and has a sexually monomorphic dull brown plumage (Glutz von Blotzheim & Bauer 1991). The species is present in the study area from the last days of May to the first days of September. I followed the birds for the duration of the summer season, which comprises a single brood (replacement clutches do occur) and a complete postnuptial, pre-migratory moult.

This population shows a variable mating system with 11% of males unmated, 70% monogamous, 17% polygynous and one case of polyandry (n = 95 males). The social partner of a female can unambiguously be defined as the owner of the territory where she builds the nest. Nests were checked frequently in order to obtain dates of egg-laying and hatching. Female ranks in polygynous relationships were determined by the order of female settlement. All non-primary females are referred to as "secondary females", including the third, fourth and fifth females.

Males and females were captured using mist-nets and were marked with a unique combination of plastic colour rings. I measured bill depth at the proximal margin of the nostrils to the nearest 0.1 mm using callipers. In the analyses, multiple values for the same individual were averaged. Female age was determined as first year or older partly based on ringing data, partly on a discriminant analysis using tail length and the number of tail feathers moulted during winter (Figure 4.3). The latter analysis classified 94% of females of known age (n = 16) correctly.

Male participation in brood care is restricted to feeding of nestlings and, to a minor extent, of fledglings. To quantify the amount of paternal investment, data on the number of feeding trips performed by males and females were collected during the nestling period. For each day and each nest I calculated the proportion of male feeds (on total number of feeds). These values were then averaged over the nestling period to obtain an estimate of male participation in brood care (for details see Chapter 5).

During the nestling period (late July) in 1998 and 1999, the arthropod fauna of bush vegetation was surveyed by beating branches (of a standardised volume of vegetation) with a stick and collecting arthropods from a tray held below the branch. Foraging activity of dusky warblers is almost exclusively restricted to this vegetation type. Within each of 45 male territories, at least 30 samples per year were taken. I summed up the volumes of all arthropods in a sample (measuring individual length, width and depth on millimetre-paper) and calculated mean arthropod volume per sample for each territory and year. Averages were $\log_{10}$-transformed to approach a normal distribution (for details see Chapter 5).

In 1998 and 1999 I studied paternity for 195 nestlings from 46 different nests using the microsatellite markers Phtr1, Phtr2, Phtr3 (Fridolfsson et al. 1997), Pocc5 (Bensch et al. 1997), FhU2 (Primmer et al. 1996), HrU7 (Primmer et al. 1995) and Gf05 (Petren 1998). I took blood samples from 43 of 58 territorial males in 1998 and from all of 28 territorial males in 1999. Samples of maternal DNA were available for 24 of 46 nests. I extracted the DNA from blood samples using the QIAamp Blood Kit. PCR's were done with fluorescence-labelled primers (otherwise following Bensch et al. 1997), and products were scored on an ABI 377 sequencer. The seven markers allowed to assign offspring to potential fathers with an average error probability (see Kempenaers et al. 1999) of $p = 0.016$ (range: 0.00002-0.117, n = 195, 17 cases with $p > 0.05$). For details see Chapter 10.

RESULTS

Comparing microsatellite alleles of mothers with those of their offspring, none of 601 locus-comparisons produced a mismatch, suggesting that mutations were very rare. However, 88 of 195 nestlings (45%) showed at least one mismatch (9x1, 22x2, 29x3, 21x4, 6x5, 1x6 mismatches) with the social father. These I consider to be extra-pair young. I identified the genetic fathers of all but 16 extra-pair young, all from 1998, the year where I failed to collect blood samples from 26% of the territorial males. For all analyses presented below I exclude the single case of social polyandry (where one of the two males sired all five young). From the remaining 45 nests, 18 (40%) contained no extra-pair young, 12 nests (27%) contained a mixture of both within-pair and extra-pair young and 15 nests (33%) held only extra-pair offspring. Nests of monogamous females and primary females of polygynous males showed similar rates of extra-pair paternity (41% of 122 young vs. 48% of 33 young). As these two groups of females can expect similar intensity of male brood care (Figure 4.1), they are treated together and are from here onwards referred to as "primary females". Nests of secondary females contained a somewhat higher proportion of extra-pair young (63% of 35 young). There was no difference in the rate of extra-pair paternity between the two years (primary females: 1998: 44% of 91 young; 1999: 41% of 64 young).

Figure 6.1 shows the rates of extra-pair paternity for all 45 nests (36 primary and 9 secondary) plotted against the date of hatching. Female unfaithfulness was more frequent late in the season (logistic regression, primary and secondary females pooled, faithful n = 18 vs. unfaithful n = 27, $\text{Chi}^2 = 5.50$, $p = 0.019$). This increase in female unfaithfulness was paralleled by a decrease in male participation in brood care over the season (Spearman-rank correlation, $r_s = -0.504$, $n = 72$, $p < 0.0001$; data from 1997-1999; Figure 6.2). Secondary females received greatly reduced male assistance as compared with primary females (Mann-Whitney-U-Test, $Z = -5.24$, $p < 0.0001$).

The sample of 45 nests shown in Figure 6.1 includes data from 41 different females. Two primary females had two nests within one season (first and replacement clutches of 1999) and two other primary females had nests in both 1998 and 1999 (with different partners). All four of them showed the same rate of extra-pair paternity in both nests (binomial test, $n = 4$, $p = 0.073$), despite differences in hatching dates (1, 3, 11 and 16 days respectively), possibly suggesting that females may also vary intrinsically in their mating behaviour. To avoid pseudo-replication I included only the first nests of these four females in the further analyses. Moreover, two cases where I lack information on female age and female bill morphology were excluded. Thus 39 females (15 faithful and 24 unfaithful; 30 primary and 9 secondary) entered the logistic regression analyses shown in Table 6.1.

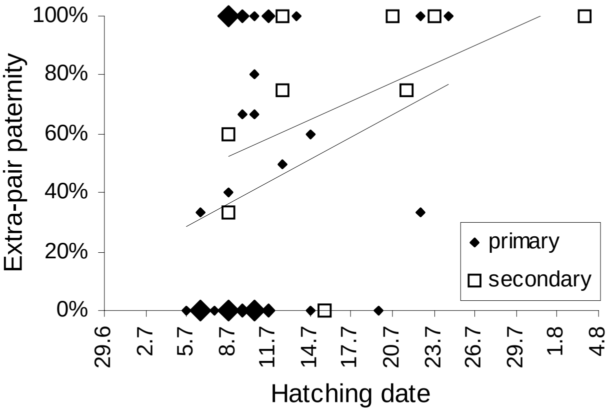


Figure 6.1. Seasonal effect on extra-pair paternity (n = 45 nests; data from 1998 and 1999). Different symbol sizes refer to one, two or three nests, respectively. Linear regression lines are indicated for nests of primary (i.e. monogamous and primary females of polygynous males) and secondary females separately.

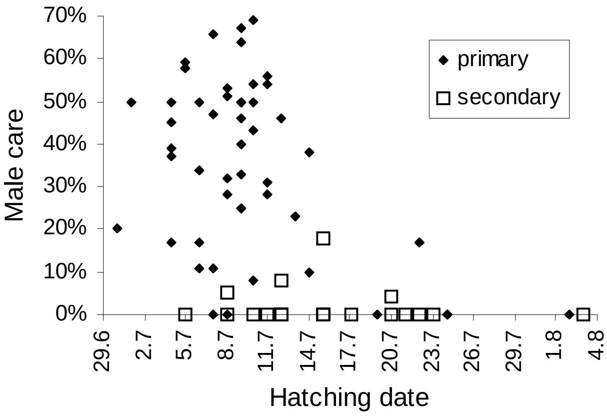


Figure 6.2. Seasonal effect on male participation in brood care (percentage of feedings of nestlings done by the male; n = 72 nests; data from 1997 to 1999). Primary nests include both nests of monogamous females and nests of primary females of polygynous males.

Table 6.1. Logistic regressions explaining faithfulness vs. unfaithfulness of 39 individual females.

	Factor alone[a]		Factor after accounting for Date[b]		Factor vs. Date[c]	
Factor	Chi^2	p	Chi^2	p	Wald Factor	Wald Date
Date	5.52	0.019	-	-	-	-
Status[d]	4.24	0.040	1.35	0.245	1.16	1.99
Age[e]	2.68	0.102	1.46	0.228	1.43	2.80
Bill depth	2.79	0.095	1.36	0.243	1.24	2.60
Food	0.01	0.911	0.29[f]	0.591[f]	0.29[f]	3.60
PC_{1-5}[g]	6.08	0.014	-	-	-	-
PC_{1-4}[g]	8.64	0.003	-	-	-	-
PC_{2-4}[g]	6.86	0.009	3.18	0.075	2.72	1.44

[a] uni-variate regressions using the respective factor as independent variable

[b] stepwise bi-variate regression reflecting the significance of entering the respective factor after accounting for Date as the first factor

[c] bi-variate regression contrasting the relative effects (Wald statistic) of the respective factor and Date as the other factor

[d] primary vs. secondary females

[e] first-year vs. older females

[f] correlation opposite to the prediction derived from the CFH

[g] principal components, see Table 6.2

Four out of five proposed factors showed some correlation with female unfaithfulness. Females that can expect only very limited male help (secondary females and late breeders) more often had extra-pair young. Female age and bill morphology, presumably reflecting independence from male assistance, also showed the predicted tendency to influence female faithfulness. Food availability, however, was unrelated to extra-pair paternity (assuming an effect size such as the factor 'Date' has (d = 0.67) the power of this test is

0.64). Principal components (see Table 6.2), reflecting a combination of factors, generally showed stronger correlations with extra-pair paternity as compared with single factors. A principal component summarising the first four variables (PC_{1-4}) gave the best fit. This principal component did not differ significantly between females with mixed paternity and those with only extra-pair offspring in their nests (T-test, $T_{22} = -0.15$, p = 0.88), justifying their combined treatment.

Table 6.2. Factor loadings on three principal components (PC), extracted from five, four and three variables, respectively.

Factor	PC_{1-5}	PC_{1-4}	PC_{2-4}
Date	0.762	0.793	
Status	0.851	0.835	0.853
Age	0.394	0.574	0.721
Bill depth	0.465	0.422	0.395
Food	0.615		
Explained variance	41.1%	45.8%	46.8%

The seasonal increase in extra-pair paternity (Figure 6.1) with declining male assistance (Figure 6.2) is consistent with the CFH, but is open to alternative explanations (see Discussion). It is therefore of interest whether other factors of female independence are still correlated with extra-pair paternity when the seasonal effect is controlled for. Neither female status, nor female age, nor female bill depth significantly improve the regression model once the factor 'Date' is included (Table 6.1). Although these factors still show weak trends in the direction predicted by the CFH, Date is the better predictor in bi-variate regression models (see Wald statistics in Table 6.1). However, a principal component summarising the effect of these three variables (PC_{2-4}) explains more of the total variation in female faithfulness than does the factor Date. This indicates that other parameters such as female status, age or bill morphology have some influence on female faithfulness beyond that which is explicable by seasonal effects. There is no combination of two factors that both significantly contributes to variation in extra-pair paternity (in a bi-variate logistic regression model). This is due to (1) positive correlations between these factors (see Table 6.2) and (2) rather small effect sizes combined with a small sample size. The proportion of variation in female faithfulness that can be explained by all the four variables together (Date, Status, Age, Bill depth) is rather low (multiple logistic regression, $Chi^2 = 9.01$, df = 4, p = 0.061, Cox and Snell $r^2 = 0.206$).

DISCUSSION

In accordance with the predictions derived from the CFH (Gowaty 1996, 1997), I found that (1) females that cannot expect to receive much male help in brood care (late breeding females and secondary females of polygynous males) are more likely to have extra-pair young. This finding is unlikely to be confounded by variation in male quality or mate-guarding intensity. (2) Females that appear better adapted to raise offspring without male assistance (old females and females with deep bills; see Chapters 4 and 5) also tend to be less faithful to their social partners. However, given the fact that females of the latter type are often found in situations where they will receive no male help (see Chapters 4 and 5), the statistical power is not sufficient to significantly confirm both effects independently of each other. Generally, the amount of variation in extra-pair paternity explicable by variation in female independence was rather low. Noticeably, variation in food availability did not affect female faithfulness (but see Hoi-Leitner et al. 1999), despite a nearly 50-fold difference in arthropod density between the richest and the poorest territory (see Chapter 5).

The difficulties arising from weak effects and interrelated factors were partly solved by means of principal component analysis. A combination of factors contributing to female independence shows a highly significant covariation with extra-pair paternity. Moreover, the fact that single factors are positively correlated with each other, i.e. that secondary females are older and have deeper bills, provides additional support for the CFH (see Chapters 4 and 5).

Nevertheless, disentangling the contributions from several factors remains difficult. The strongest correlation is between hatching date and likelihood of extra-pair paternity. Late broods received no, or virtually no, male care and also contained most extra-pair young. Reduced male care could result from female unfaithfulness and vice versa. However, there is support for the idea that males should reduce their parental effort late in the season irrespective of variation in extra-pair paternity. In the dusky warbler, brood care late in the season appears to be costly in terms of greatly increased winter mortality due to a trade off between care and postnuptial moult (Chapter 4; see also Nilsson & Svensson 1996, Svensson & Nilsson 1997, Hemborg & Lundberg 1998). As late breeding females are able to fledge offspring of normal body condition even without male assistance (Chapter 4), it should pay males to invest in their own feather moult rather than in brood care. Given that late breeding females cannot expect to receive male assistance for this reason, it appears plausible to explain the increased rate of extra-pair paternity as resulting from a “nothing-to-lose situation”.

However, there may be alternative explanations for the seasonal increase in the rate of extra-pair paternity. Assuming that female knowledge about male quality is limited, but increases with duration of the breeding season, it has been hypothesised that female unfaithfulness will increase with improving knowledge (incomplete-knowledge hypothesis; Slagsvold & Lifjeld 1997). As this alternative scenario cannot be disproved by the data available, it is of interest to know whether there is support for the CFH beyond what is attributable to seasonal effects. After accounting for seasonal effects on extra-pair paternity by stepwise logistic regression, a principal component summarising the remaining variation in female independence (PC_{2-4}: Status, Age, Bill depth) is still correlated with female faithfulness. Although this residual correlation is significant only in a one-tailed test (two-tailed: $p = 0.075$), PC_{2-4} is a better predictor for female behaviour than is the factor Date.

Two recent reviews have analysed the relationship between social and genetic mating systems (Møller & Ninni 1998, Hasselquist & Sherman in press). Møller & Ninni (1998) found that polygynous males suffer from higher rates of cuckoldry as compared to monogamous males. This is consistent with the CFH, but also with the “male trade-off hypothesis” stating that polygynous males cannot guard their females sufficiently well. The dusky warbler offers the rare opportunity to reject the latter hypothesis in favour of the CFH, as males of this species are unusual (see Birkhead & Møller 1992) with regard to the fact that they do not guard their fertile females (Chapter 9). In contrast to these patterns, Hasselquist & Sherman (in press) found that polygynous species show lower rates of extra-pair paternity as compared to monogamous species. Thus they rejected the “male trade-off hypothesis” in favour of the “female choice hypothesis” stating that in polygynous species a higher proportion of females can pair with the male of their choice and therefore refrain from extra-pair copulations. However, this interpretation does not account for the fact that females typically base their social mating decision on territory quality but not on male quality (Alatalo et al. 1986) and that these two quality parameters are not necessarily positively correlated (Chapter 10; Quarnström & Forsgren 1998). Moreover, the “female choice hypothesis” is incompatible with the above findings of Møller & Ninni (1998). Finally, inclusion of the polygynous dusky warbler, with its extraordinarily high rate of extra-pair paternity, into the data set used by Hasselquist & Sherman (in press) would considerably change the outcome of the analysis (roughly a reduction of effect size by one third).

In summary, the present study provides support for the CFH while being incompatible with both the “male trade-off hypothesis” and the “female choice hypothesis”. Factors describing how much help a female can expect to receive from her social partner, show the strongest correlation with female faithfulness. In addition, females that are presumably better at raising offspring without male assistance show a weak tendency to have extra-pair young more often. To resolve these patterns in more detail, both a larger sample and incorporation of male attractiveness as another main factor would be required. I was unable to include variation in male quality in the present study due to the lack of male data for about half of the sample. However, existing data suggest that variation in male quality may be of greater importance than variation in female independence (see Chapter 10).

7. Polygyny from the male perspective

In the polygynous mating system of the dusky warbler (*Phylloscopus fuscatus*), male-male competition over the most preferred territories largely decides social pairing success. Old males and males with high body mass had a greater chance of mating polygynously, while first-year males and males of low body weight more often remained unmated. This is consistent with the idea that prior residence and fighting abilities determine the outcome of territorial conflicts. In addition, males with long tails were more likely to stay unmated, and at the same time, mated males with long tails contributed less to offspring care than did short-tailed males. This suggests that the social mating decision of primary females also depended on the readiness of males to provision the young. Analysis of extra-pair paternity showed that a male's success in social pairing was only a weak predictor of real reproductive success. Nevertheless, polygynous males, on average, sired 3.4 times more offspring than monogamous males and socially unmated males sired 0.7 times as many. In general, competitive ability and attractiveness as a copulation partner have major effects on male reproductive success, while parental qualities appear to be of minor importance.

INTRODUCTION

The phenomenon that some individuals have higher reproductive success than others resulting from differences in mating success, is what is known as 'sexual selection'. Two components of sexual selection contribute to variation in male mating success (Andersson 1994). (1) Males typically compete with each other over access to females (intra-sexual selection), and (2) females, typically the choosy sex, prefer some males over others as partners for mating (inter-sexual selection). From paternity studies it is well known that, in birds, there can be substantial differences between social and genetic mating systems (Ligon 1999). Females may try to pair socially with the owner of a high-quality territory (providing good resources) or with a male that is particularly good in provisioning the offspring (good parent; Hoelzer 1989), but at the same time copulate with another male that is for instance of high genetic quality (good genes). Females may face trade-offs, e.g. when extra-pair copulations lead to reduced parental investment by the social partner (Dixon et al. 1994, Møller & Cuervo 2000, Møller & Tegelström 1997, Westneat & Sargent 1996), thus females will unlikely succeed in obtaining good resources, a good parent and good genes all at once. This leaves varying options to males that individually differ in competitive abilities, parenting abilities and phenotypic attractiveness. The aim of the present study is to investigate the relative importance of these factors in contributing to male mating success.

The dusky warbler *Phylloscopus fuscatus* offers an excellent opportunity to study this topic, as there is considerable variation in male mating success at both the social and the genetic level. The species has a facultatively polygynous social mating system, where some males pair with several females (up to five), while other males stay unmated. The occurrence of polygyny in this species is best explained by the polygyny-threshold model (Verner 1964, Orians 1969), where secondary females are compensated for the lack of male assistance by high territory quality (Chapter 4). It is therefore expected that male-male competition over the possession of high-quality territories will largely decide about which males become polygynous and which males remain monogamous or unmated.

Paternity analysis has shown that the rate of extra-pair paternity in the dusky warbler is among the highest found in birds (see Petrie & Kempenaers 1998). Forty-five percent of all nestlings were not sired by the females' social partners (Chapter 10). Thus, the social mating decision of females (choice of territory and social partner) is largely independent of the decision with whom to copulate. This raises the question, to what extent males do still profit from being mated polygynously and to what extent unmated males obtain reproductive success (see Lubjuhn et al. 2000).

More specifically, I address the following questions:
(1) Which individual characteristics influence male success in competition over the most preferred territories, where secondary females are likely to settle? (2) Is male mating success also influenced by a

female preference for a good parent? (3) How strongly are social and genetic mating success correlated?

MATERIAL AND METHODS

The study was conducted in pristine landscape at the mouth of the Malkachan river, 190 km east of Magadan, in the Russian Far East (154° 14’ E; 59° 51’ N). The area is characterised by a transition from inland taiga forests to coastal tundra along the shoreline of the Okhotsk Sea. At this transition there are extensive bushlands of *Pinus pumila* with some admixture of *Betula middendorffii* and *Alnaster fruticosus*, typically 1-2m in height. These bushlands are the habitat occupied by the dusky warbler.

The dusky warbler is an insectivorous long-distance migrant passerine with a sexually monomorphic dull brown plumage. Dusky warblers winter in south-eastern Asia (Glutz von Blotzheim & Bauer 1991) and are present in the study area from the end of May to the beginning of September. The breeding season consists of a single brood (replacement clutches do occur), followed by a complete postnuptial, pre-migratory moult. This dusky warbler population was studied over three consecutive breeding seasons between June 1997 and August 1999. In 1997, investigations only started at the end of the spring arrival period, thus arrival data are available only for 1998 and 1999. During the first season, studies were restricted to the central part of the study area, but were extended to the north and south in the following years (Figure 8.1). Breeding populations in 1997 and 1998 were similar in size (17 vs. 16 territorial males in the central part of the study area), while there was a tremendous decline between 1998 and 1999 (58 vs. 28 territorial males in the overall area). Evidently, this decline was caused by an unusually high winter mortality (see Chapters 3 and 8). Polygyny was frequent in the years before the population decline, but was rare in 1999 when only territories in high-quality habitats were occupied (1997: 3 unmated, 9 monogamous, 5 polygynous males; 1998: 6 unmated, 35 monogamous, 9 polygynous males; 1999: 2 unmated, 24 monogamous, 2 polygynous males). For more details see Chapter 4.

Dates of spring arrival were measured as the number of days after the arrival of the first male of the respective season, and the mean of these values did not differ between 1998 and 1999 (10.2 vs. 10.3). Male territories were usually visited every day or second day, and song posts were plotted on a detailed map drawn from a 1 : 5000 satellite photograph of the area. ‘Harem size’ is defined as the number of different females breeding within the area of a male’s territory.

Male dusky warblers were captured using mist-nets and fitted with a unique combination of plastic colour rings. The following morphological measurements were taken: wing length, wing formula, tail length, tarsus length (as shown in Schmid & Spitznagel), footspan including claws, bill depth, bill width and body mass. To obtain a measurement of body size that is independent of changes in body mass (reflecting body condition) and of changes in feather lengths (reflecting age; see below), one principal component (‘PC body size’) was extracted from tarsus length (factor loading: $r = 0.81$), footspan ($r = 0.78$), bill depth ($r = 0.46$) and bill width ($r = 0.35$). Multiple measures for the same male were averaged.

As it was impossible to capture all males at a fixed stage of the season and at a fixed time of day, body mass measurements had to be adjusted according to the level of visible fat deposition which varied greatly throughout the season (quadratic regression, $r^2 = 0.16$), and time of day (linear regression, $r^2 = 0.34$). Fat-deposition, estimated in nine distinct classes (according to Kaiser 1993), strongly influenced variation in body mass (ANOVA, $F_{5,158} = 15.3$, $p < 0.0001$; only six of nine fat-classes occurred). Lean body weights were calculated by applying correction factors to individuals that showed visible fat deposition. In addition, birds that were caught during the postnuptial moult showed a 5.3% higher body weight as compared to non-moulting birds ($T_{163} = -4.6$, $p < 0.0001$). Measures from moulting birds were brought into line with non-moulting birds by using a correction factor. Obtained lean mass estimates showed a much higher within-individual repeatability (calculated following Lessells & Boag 1987) as compared to uncorrected weight measurements (repeatability = 0.56, $F_{40,62} = 4.1$, $p < 0.0001$, vs. repeatability = 0.38, $F_{40,62} = 2.5$, $p = 0.0005$), while there was no individual repeatability for the amount of fat-deposition (repeatability = 0.09, $F_{40,62} = 1.3$, $p = 0.20$). Body condition was estimated by taking the residuals from a linear regression of lean body mass on PC body size.

Full-grown juvenile birds can reliably be sexed using morphological measurements (confirmed by molecular sexing following Griffith et al. 1998). To allow a morphological comparison between juvenile birds trapped in autumn (wearing fresh feathers) and adult birds trapped in spring (having worn feathers), I tried to estimate the decrease in feather length that was caused by wear. The length that a feather had when it was fresh was extrapolated from existing feather fringes. Individuals with heavily worn wingtips (more than 1.5 mm lacking) were very rare (6%).

Adults may moult a variable amount of tail feathers in winter (23% did not moult, 64% moulted some tail feathers, 13% moulted all 12 tail feathers), and these fresh feathers can easily be recognised (Chapter 4). Two different tail measures were used: 'tail length moulted' is the actual length of the tail after the winter, irrespective of whether it consists of old or fresh feathers. 'Tail length unmoulted' is the length that the tail had before winter moult. In both cases, lengths of fresh feathers were estimated. The measure 'tail length unmoulted' is needed for age determination, as the increase in tail length between the juvenile and the adult plumage can already happen during the winter moult. On average, however, winter-moulted tails were 0.44 mm (± 0.32 SE; non-significantly different from zero, p = 0.17) shorter than preceding summer-moulted tails (using males where partial moult allowed direct within-individual comparison). The fact that outer tail feathers are shorter than central feathers was taken into account, trying to get the most realistic estimate of the length that a tail had just after summer moult. For the males that moulted all 12 tail feathers during winter (13%), I assume that 'tail length unmoulted' was the same as 'tail length moulted'.

To allow the calculation of sexual dimorphisms the same morphological measurements were taken of females (for treatment of measurements see Chapter 4).

In 1998 and 1999 I studied paternity for 195 nestlings from 46 different nests using the microsatellite markers Phtr1, Phtr2, Phtr3 (Fridolfsson et al. 1997), Pocc5 (Bensch et al. 1997), FhU2 (Primmer et al 1996), HrU7 (Primmer et al. 1995) and Gf05 (Petren 1998). I took blood samples from 43 of 58 territorial males in 1998 and from all of 28 territorial males in 1999. Samples of maternal DNA were available for 24 of 46 nests. I extracted the DNA from blood samples using the QIAamp Blood Kit. PCR's were done with fluorescence-labeled primers (otherwise following Bensch et al. 1997), and products were scored on an ABI 377 sequencer. The seven markers allowed to assign offspring to potential fathers with an average error probability (see Kempenaers et al. 1999) of p = 0.016 (range: 0.00002-0.117, n = 195, 17 cases with p > 0.05). For details see Chapter 10.

Table 7.1. Morphological measurements from males of known age. Data from 6 first-year males are pooled with data from up to 41 juvenile males. Estimates of lean body mass are from 7 first-year birds. Measurements on feathers reflect (partly estimated) lengths in fresh, unworn condition. Tarsus length was measured as shown in Schmid & Spitznagel (1985).

Trait	First-year and juvenile	Older than first-year	T-test
Wing length	63.0 (n = 47)	65.1 (n = 20)	p < 0.0001
Tail length (unmoulted)	51.4 (n = 47)	53.9 (n = 20)	p < 0.0001
Second primary to tip	8.31 (n = 45)	10.28 (n = 20)	p < 0.0001
First primary	36.0 (n = 47)	35.9 (n = 21)	p = 0.74
Tarsus length	25.4 (n = 47)	25.3 (n = 21)	p = 0.56
Footspan with claws	30.0 (n = 42)	30.1 (n = 21)	p = 0.50
Bill depth	2.59 (n = 24)	2.64 (n = 21)	p = 0.07
Bill width	3.22 (n = 24)	3.27 (n = 21)	p = 0.22
Lean mass	9.76 (n = 7)	9.80 (n = 21)	p = 0.79

RESULTS

Table 7.1 shows morphological measurements of males of known age. Males that are older than in their first year, have significantly longer tails, wings and a relatively shorter second primary as compared to males wearing their first plumage (i.e. juveniles in autumn and returning first-year males in spring). Other morphological traits showed no significant variation with age. As males may moult a variable number of tail feathers during the winter, I here refer to measurements on unmoulted tail feathers. To allow the pooling of data from juvenile birds having fresh feathers with those of first-year males having more worn feathers, I use estimated lengths of fresh feathers. The estimated decrease in feather lengths by wear (birds in spring compared to when fresh) was 0.8 mm for the tip of the wing and 0.3 mm for the tail. The tip of the second primary was not affected by wear. Body mass data from juvenile and first-year males were not pooled to avoid bias by seasonal effects.

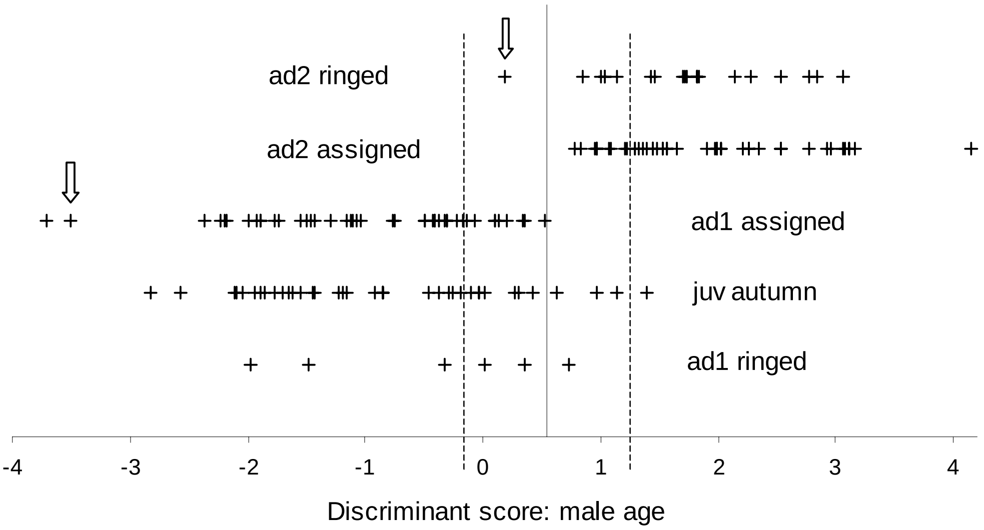


Figure 7.1. Discriminant analysis separating males in their first plumage (full grown juveniles measured in autumn and first-year males ‘ad1’ measured in spring) vs. subsequent plumages (males older than in their first year ‘ad2’, measured in spring). Individuals of unknown age were assigned to either of these groups. The solid line marks the threshold for assignment, dotted lines mark the 90% confidence interval for assigning individual birds. Fifty-nine of 65 males of known age (91%) would have been classified correctly (5 of 6 ad1, 35 of 39 juv and 19 of 20 ad2). The only misclassified ad2 male was already measured the year before (indicated by arrow). Factor scores on the discriminant axis are as follows: tail length of unmoulted feathers (r = 0.84), wing length (r = 0.75) and distance from the tip of the second primary to the tip of the wing (r = 0.53).

These age-related changes in wing and tail measurements can be used to determine the age of individuals of unknown age (Figure 7.1). The obtained discriminant analysis (standardised canonical coefficients of discriminant function: tail 0.67, second primary 0.37, wing 0.32) would have misclassified only 6 of 65 males of known age. Forty-four males of unknown age were classified as first-year males (36 of them at $p < 0.1$) and 45 males were classified as older males (35 of them at $p < 0.1$). Eleven males that were aged as first-year birds when captured for the first time had increased their ‘agescore’ when re-trapped the following year (mean increase = 2.00, range 3.7 to 0.9; paired t-test, $T_{10} = 6.3$, $p < 0.0001$). One of them (marked by arrows in Figure 7.1) would have been misclassified by the discriminant analysis in his second year. Eight males that were aged as older when captured for the first time still increased their ‘agescore’ to the next season (mean increase = 0.56, range 1.5 to -0.7; paired t-test, $T_{10} = 2.3$, $p = 0.053$).

In order to analyse which male traits correlate with success in competition over territories, I test whether males that occupied the same territory (one after the other in different years) are more similar to each other than expected by chance. The results are shown in Table 7.2. Male age and morphological characters that reflect male age show significant ‘repeatabilities’. This means that some territories are typically occupied by first-year males, while others are mostly taken by older males. This suggests that older males would have preferential access to high-quality territories where males have good chances to mate polygynously. In 1999, when the population size was greatly reduced, low-quality territories remained unoccupied. Sixty-one percent of the territories that had been held by a first-year male in 1998 stayed vacant in the following year. In contrast, only 13% of the territories of older males remained unoccupied (Chi^2 = 11.3, p = 0.0018). Thus in years of high population size the majority of first-year males has to settle in low-quality habitat.

The relationship between male age and male mating status is shown in Figure 7.2. Except for one first-year male that was mated with five females, there is a clear correlation between male age and male mating success (using a Spearman rank correlation to reduce the 'pull' by this outlier: r_s = 0.24, n = 86, p = 0.026).

Table 7.2. Univariate ANOVAs testing for associations between male traits and territories. Over the course of the study, 22 territories were occupied by 2 different males and 7 territories by 3 males (n = 65 males). The dichtomised character male age was tested by a Chi^2-exact test in an unordered 2x29 table.

Trait	Statistics	p
Wing length	F = 1.96	0.030
Tail length (moulted)	F = 1.72	0.065
Tail length (unmoulted)	F = 2.46	0.009
Second primary to tip	F = 1.89	0.040
PC body size	F = 0.74	0.792
Lean body mass	F = 1.41	0.165
Body condition	F = 1.19	0.311
Discriminant score age	F = 2.34	0.011
Age (first-year vs. older)	Chi^2 = 44.4	0.003

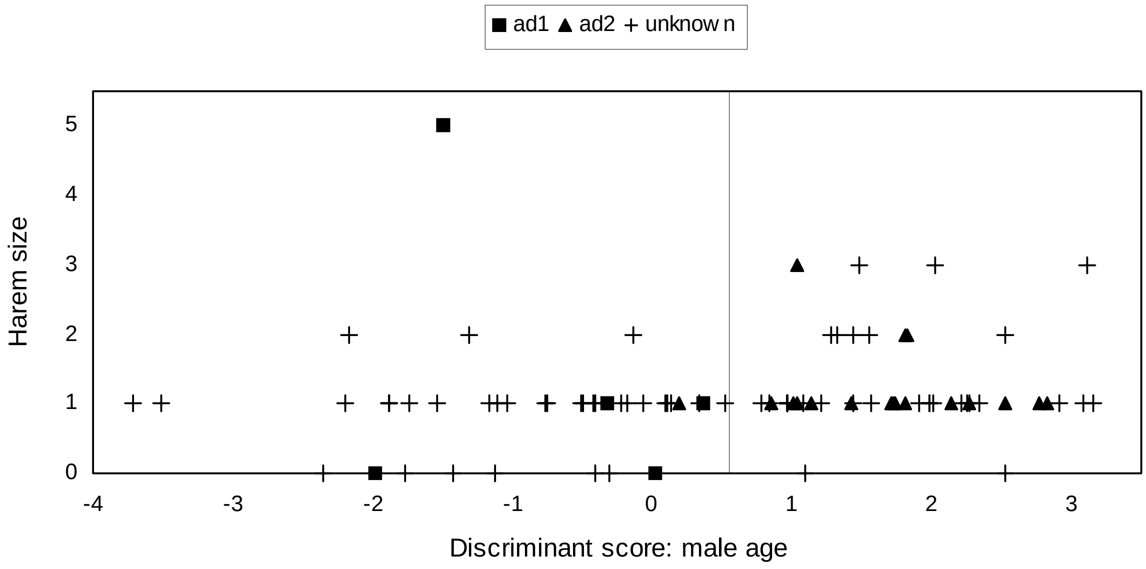


Figure 7.2. Relationship between male age and number of females breeding in a male's territory. The vertical line marks the threshold for assigning males of unknown age to either first-year (left) or older males (right).

For a more detailed analysis of which factors influence male status, I use a stepwise backwards logistic regression, entering up to eight explanatory factors (year, age, wing length, tail length moulted, PC body size, lean mass, condition, arrival date). The best fitting models are presented in Table 7.3. These are given in two variants: once using the full sample of males and once excluding all males that were aged by discriminant analysis with an error probability of p > 0.1. As the rate of polygyny declined over the course of the study, the factor 'year' had to be included in two of the models. As expected, polygynous males were older than non-polygynous males, and unmated males were younger than mated males. Moreover, there was a significant effect of male body mass, with heavier males being polygynous and the lightest males being unmated. The relationship between male body mass and harem size is highly significant (r_s = 0.27, n = 90, p = 0.01; Figure 7.3). However, I found no support for the idea that body mass correlated with success in aggressive fighting. In long-lasting fights over the possession of a territory, there was only a non-significant tendency for the heavier male to win the conflict (paired t-test, $T_7 = 0.8$, $p = 0.47$). To understand the relationship between male mating status and body mass better, I split body mass into two components, namely PC body size and body condition (residual mass on PC body size). In a multinomial logistic regression, male mating status (unmated vs. monogamous vs. polygynous) is significantly influenced by male body mass ($Chi^2 = 10.0$, $p = 0.007$). Replacing body mass by PC body size and condition (both factors entering together), shows that body condition explains most of the variation (PC body size: $Chi^2 = 2.9$, $p = 0.24$; condition: $Chi^2 = 8.0$, $p = 0.018$).

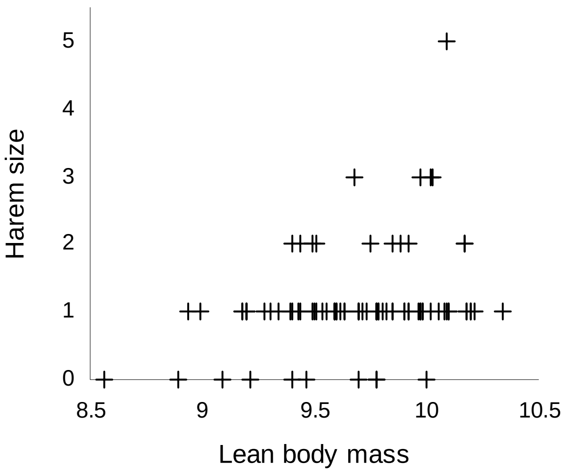


Figure 7.3. Correlation between male body mass and harem size.

Table 7.3. Logistic regression models explaining male mating status. The coefficient of regression B indicates the direction of correlation. Positive values of B mean that larger values of the respective factor increase the probability that a male belongs to the first named test group (i.e. polygynous or unmated, respectively).

Test groups	Total Chi^2	Total p	Factor	B	p
Polygynous (n = 15) vs. non-polygynous (n = 75)	10.7	0.014	Year Male age Lean body mass	-1.1 1.1 1.7	0.018 0.095 0.102
Polygynous (n = 14) vs. non-polygynous (n = 61), males aged with p > 0.1 excluded	18.9	0.0003	Year Male age Lean body mass	-1.9 2.0 3.2	0.002 0.022 0.020
Unmated (n = 10) vs. mated (n = 78)	17.8	0.0005	Male age Lean body mass Tail length (moulted)	-3.1 -3.5 0.5	0.009 0.006 0.041
Unmated (n = 9) vs. mated (n = 64), males aged with p > 0.1 excluded	26.9	<0.0001	Male age Lean body mass Tail length (moulted)	-5.4 -5.5 0.8	0.004 0.005 0.018

Only one result was really surprising. Males with longer tails had a significantly higher probability of staying unmated (Table 7.3). This is interesting in the light of the fact that males with longer tails contributed significantly less to the feeding of the offspring as compared to males with shorter tails (Table 5.1). At the same time, tail length shows the strongest sexual dimorphism of all characters measured (Figure 7.4), and it is the trait with the largest dimorphism between age classes (Table 7.1).

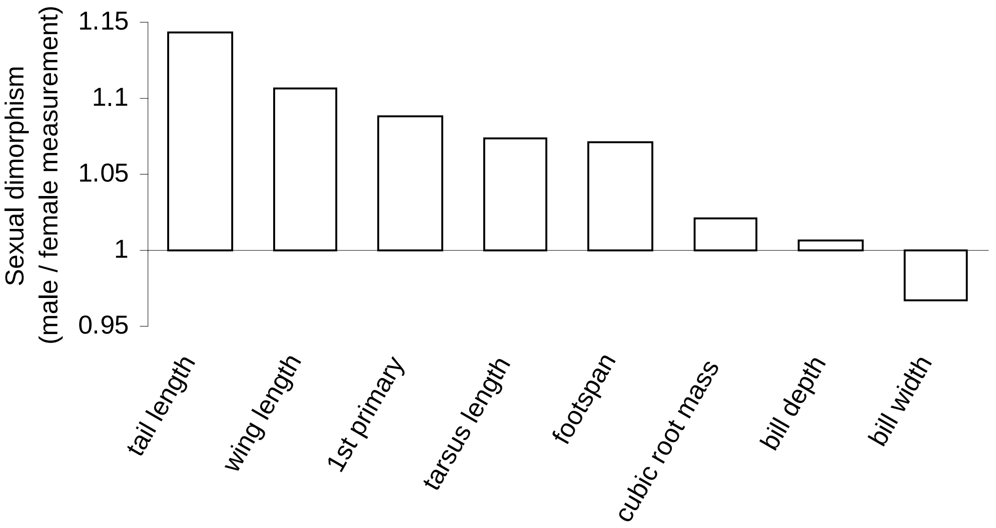


Figure 7.4. Sexual dimorphism of eight morphological characters.

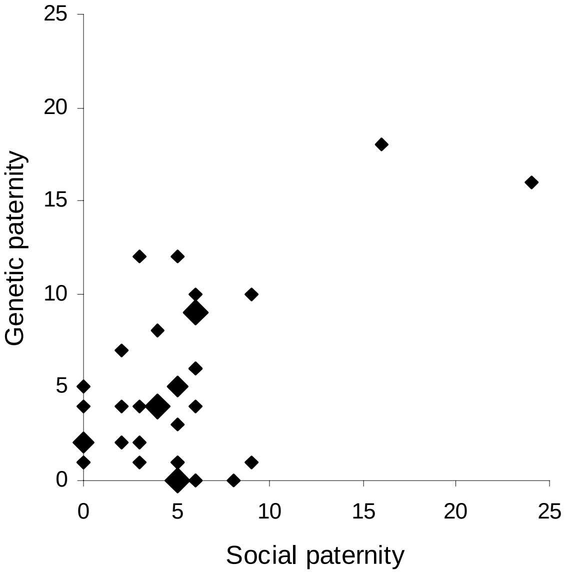


Figure 7.5. Correlation between apparent and real reproductive success for 39 males. 'Social paternity' is the number of young stemming from the nests in a male's territory (n = 195 young, all those for which genotypes are known). 'Genetic paternity' is the total number of offspring sired by a male (n = 179 young, all those for which the genetic father could be identified). Males that had neither social nor genetic paternity are omitted. Different symbol sizes refer to one, two and three males, respectively.

The date of arrival at breeding grounds showed no correlation with mating status, once the other factors (see Table 7.3) were controlled for. Entering arrival date in a logistic regression model (in a second block after accounting for the other factors) neither improved the model for polygynous vs. non-polygynous males (n = 8 vs. n = 60, $Chi^2 = 0.3$, p = 0.56), nor the model for unmated vs. mated males (n = 7 vs. n = 59, $Chi^2 = 0.7$, p = 0.41). Note that these analyses were done on a more limited set of data, as arrival data are available only for two of the three seasons of study.

Paternity analysis revealed that 88 of 195 young (45%) from 27 of 46 nests (59%) were not sired by their social father. I was able to identify the genetic father of all but 16 nestlings. For more details see Chapter 10. As a result of the high rate of extra-pair paternity, there was only a weak correlation between social and genetic paternity, i.e. the number of offspring coming from a male's territory vs. the number of offspring that were actually sired by a male (Figure 7.5). Note that the statistical unit used in this figure is the individual male, thus for males breeding in both 1998 and 1999, I summed up the number of young. Males that had neither social nor any genetic paternity were omitted from this figure. The fact that the number of young that fledge from a male's territory is a weak predictor for that male's reproductive success, rises the question whether males still profit from being mated polygynously.

Social and genetic paternity in dependence on male mating status are shown in Figure 7.6. Note that in this figure the reproductive season of a male is the statistical unit and that males without any paternity are included in the sample. Thirty-one males had no social paternity, a result of a high rate of nest predation. The figure shows how 195 offspring were socially distributed among 66 territorial males and how many of 179 offspring (the father of 16 young was unknown) were sired by these 66 potential genetic fathers (i.e. all males for which genotype and social paternity were known). Note that these figures do not exactly reflect the realised reproductive success, as 33 of 195 young, for which DNA was available, did not survive until fledging. Omitting these non-surviving young did not alter the general patterns (not shown). Polygynous males had significantly higher social (Mann-Whitney-U, Z = -2.8, p = 0.005) and genetic paternity (Mann-Whitney-U, Z = -3.0, p = 0.003) as compared to monogamous males. There was no difference between monogamous and polygynous males in how large the difference between social and genetic paternity was (Mann-Whitney-U, Z = -0.1, p = 0.95). The number of young sired by unmated males was only non-significantly lower as compared to monogamous males (Mann-Whitney-U, Z = -0.4, p = 0.69).

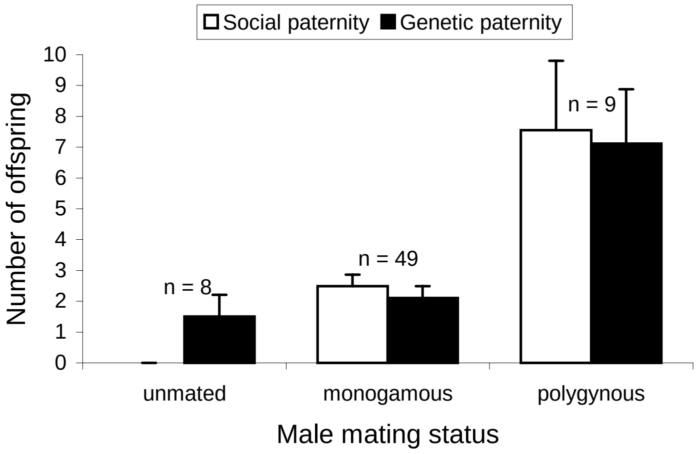


Figure 7.6. Social and genetic paternity in relation to male mating status. Polygynous males (mean harem size 2.67 females) sired on average 3.38 times more young than did monogamous males, while reproductive success of the average unmated male was 0.71 times that of the average monogamous male. Ranges for individual variation in genetic paternity were 0-5 offspring for unmated males, 0-10 offspring for monogamous males and 0-16 offspring for polygynous males.

DISCUSSION

Of seven male characteristics analysed (age, arrival date, wing length, tail length, lean body mass, structural body size, body condition), two showed a strong correlation with social pairing success. Older males more often mated polygynously than did first-year males, and the latter more often remained unmated. In addition, independently of male age, body mass was positively correlated with pairing success. Due to a high frequency of extra-pair paternity, success in social pairing was only a weak predictor for the actually realised reproductive success of an individual male. Nevertheless, as female choice of EPC-partners was independent of a male's social status (see Chapter 10), polygynous males had, on average, much higher reproductive success than monogamous males. Males that were socially unmated sired only little fewer young than did monogamously mated males.

The high rate of extra-pair paternity suggests that a female's social pairing decision should depend on direct benefits rather than on the genetic quality of the potential partners. This is firstly because direct benefits typically appear to be of greater importance than indirect benefits (Andersson 1994), and secondly, females paired with males of low genetic quality can adjust their mating decision by having extra-pair copulations with high quality males (see Chapter 10). Direct benefits can be divided into two types, namely territory quality and male assistance in brood care. As secondary females of polygynous males normally do not receive any male help, territory quality mostly decides whether a male has a chance to mate polygynously. Consequently, polygyny depends on male success in competition over territories. In contrast, success in attraction of a primary female might depend on both, territory quality and male parental qualities. In Chapter 5 I have shown that male participation in brood care was strongly negatively correlated with male tail length (p = 0.0023; controlling for hatching date, male age, female status and female bill morphology; see Table 5.1). The finding that mated males had shorter tails than unmated males (Table 7.3), therefore strongly suggests that females prefer to pair with short-tailed males (i.e. good parents). Interestingly, early in the season, when social pairing takes place, males were sometimes seen to cock their tails during display.

How might the correlation between tail length (controlled for age) and participation in brood care be explained?

(1) The ‘differential investment hypothesis’ (Burley 1986, Møller & Thornhill 1998, Sheldon 2000) suggests that females that are mated to highly attractive males would be ready to increase their investment in parental care. It is argued that the costs of increased efforts would be balanced by benefits in terms of more attractive and / or more viable offspring (‘sexy-son’ or ‘good genes’ process). In the dusky warbler, male attractiveness was strongly correlated with singing performance (see Chapter 10), but not with tail length. In a pair-wise comparison between males that lost paternity in their own nest and the males that cuckolded them, the winners of paternity had only non-significantly longer tails ($T_{13} = 1.1$, $p = 0.30$). Thus, it appears unlikely that variation in male attractiveness was the reason for the fact that females paired to long-tailed males took a greater share in offspring provisioning.

(2) Alternatively, males may be trading investment in parental care against energy allocated for other purposes, such as mate attraction or territory defence. A great number of studies has investigated the role of testosterone in mediating this trade-off (summarised in Ketterson & Nolan 1999). Experimentally elevated plasma levels of testosterone almost invariably resulted in a suppression of parental effort, but enhanced mating behaviour and aggressiveness (Raouf et al. 1997, De Ridder et al. 2000, Ketterson & Nolan 1999 and references therein). In the barn swallow, *Hirundo rustica*, individuals with high testosterone levels had longer tails than males with low testosterone levels (Saino & Møller 1994). In both species, the barn swallow and the dusky warbler, tail length is the most sexually dimorphic trait and also shows the most pronounced increase from the juvenile plumage to the adult male plumage. Potentially, androgen levels might affect this morphological trait (Saino et al. 1995). Thus it might be speculated that male dusky warblers with longer tails had naturally higher androgen levels than short-tailed males, and consequently they invested more in sexual display and territorial defence than in parental care. Females may prefer to mate socially with short-tailed males, but it appears very unlikely that short-tailed males would have higher overall fitness than long-tailed males (see Raouf et al. 1997). The data also indicate that tail length (controlled for age) is unrelated to the number of offspring sired (ANCOVA, $F_{1,61} = 0.01$, $p = 0.91$). As the wing and tail morphology of short-tailed males is not very different from that of females, it is unrealistic to assume that short-tailedness could be a honest signal for parenting abilities, mediated by condition-dependent trait-expression (i.e. the good-parent process; see Hoelzer 1989, Linville et al. 1998).

The observed correlation between male age and success in competition over the best territories is not surprising. Prior residence appears to be the most important factor in determining the outcome of competition over territories in birds (Krebs 1982, Beletsky & Orians 1987, Jakobsson 1988, Tobias 1997), and this also appears to apply to the dusky warbler (Chapter 8). The fact that body mass correlated with success in competition, was attributable to differences in body condition rather than in structural body size. Fights over the possession of territories were observed only rarely, but they involve energy-consuming mutual chasing and this can last over long periods of time (up to two days) before one of the contestants gives up. Thus a good body condition is a prerequisite of wining such conflicts. There were no indications that these differences in body conditions were the result of rather than the condition for occupying a high quality territory. At least, I found no correlation between male body condition and arthropod density in the territory (data not shown; for methods see Chapter 5). The absence of a body-size effect may be explicable by the fact that smaller males tend to invest more in gaining prior residence to compensate for their possible disadvantages in physical conflicts (Chapter 8). Unexpectedly, there was no effect of arrival date on male mating status, once age and body mass were controlled for. In principal, such an effect should be expected (Chapter 8; see also Hasselquist 1998). The data suggest that this might have been due to a small sample size in combination with chance events, such as a late arriving male taking over a vacant polygynous territory, after the owner had been killed by a sparrowhawk.

In conclusion, the fact that females (especially secondary females) base their social mating decision mostly on territory quality, leads to intense male-male competition for high-quality territories. Old and heavy males were particularly successful in such competition. In addition, there is some evidence that females preferred those males as social partners that were likely to contribute more than others to offspring care.

8. Competition for early arrival in males

It is often assumed that, in migratory birds, males of highest phenotypic quality are the first to arrive at breeding grounds, as only males in good body condition can afford the costs of early arrival. Here I argue that variation in how much an individual can gain from being early may sometimes override these patterns of condition dependence. Benefits from early arrival will depend on how good the chances of an individual are of successfully occupying and defending a high-quality territory. Other studies have shown that these chances depend on male resource-holding power (RHP) and on value asymmetries (VE), as resulting from prior ownership. Patterns of spring arrival were studied in a polygynous population of the dusky warbler *Phylloscopus fuscatus*, a species with high breeding-site tenacity. During the period of postnuptial moult, just before departure to winter quarters, about half of the males preoccupied and vigorously defended high-quality territories. Apparently these males enhanced their success in competition over these territories in the following breeding season by taking advantage of having prior ownership. Males with good chances of obtaining a high-quality territory (i.e. males that had occupied such territories before) were the first to arrive in spring, suggesting that high motivation drives early arrival. In contrast, there was no indication for male quality or body condition to affect arrival patterns. Interestingly, males of small body size, possibly reflecting low RHP, invested more in gaining prior ownership than did large males. The present study suggests that, in some species, individual variation in benefits rather than in costs resulting from early arrival determine which males are the first to arrive.

INTRODUCTION

In migratory birds, males that arrive earliest on breeding grounds typically occupy the best territories and consequently have the highest reproductive success (Brooke 1979, Arvidsson & Neergaard 1991, Bensch & Hasselquist 1991, Lundberg & Alatalo 1992, Wiggins et al. 1994, Aebischer et al. 1996, Lozano et al. 1996, Hasselquist 1998, Potti 1998, Currie et al. 2000, Gil & Slater 2000, Weggler 2000). Competition for early arrival is most intense in species with polygynous mating systems, where some males mate with several females while others stay unmated (e.g. Hasselquist 1998). For some species there is evidence that males of highest phenotypic quality are the first to arrive (Møller 1990, 1994a, 2001, Møller & De Lope 1999, Rätti et al. 1993, Marra & Holberton 1998, Marra et al. 1998). As it can be argued that the *costs* of advancing arrival time would always be larger for individuals in lower condition (Møller 1994a, Kokko 1999), it is tempting to assume that arrival time will generally reflect male quality. However, this neglects the fact that the potential *benefits* from arriving early may not be the same to all individuals for reasons outlined below.

Experimental studies on male-male competition over territories (Krebs 1982, Beletsky & Orians 1987, Jakobsson 1988, Tobias 1997) have investigated how the outcomes of territorial conflicts depend on male fighting ability (resource holding power, RHP, Parker 1974) vs. asymmetry in territory value to contestants (value asymmetry, VA). The RHP-hypothesis, which states that males with highest RHP will win territorial conflicts, has received only limited support as far as birds are concerned (e.g. Petrie 1984, Marra 2000). The VA-hypothesis helps to explain why males that had occupied a territory previously, enjoy a ‘home advantage’. This advantage results from an asymmetry in the value that a given territory has to a previous owner versus a newcomer. The greater familiarity with the territory (Metzgar 1967, Davies & Houston 1981, Krebs 1982, Stamps 1987) and the advantage of having the relationships with competing neighbours settled (Krebs 1982), result in a greater value of the territory to the previous owner than to a newcomer. Thus the male which has the greatest interest in owning a territory will win the conflict over its possession. The great majority of studies addressing this topic found support for the VA-hypothesis (Nolan 1978, Krebs 1982, Beletsky & Orians 1987, 1993, Jakobsson 1988, Tobias 1997).

With this in mind, it becomes clear why some males may profit more than others from arriving early. (1) If both, RHP and VA play a role, then smaller males, with presumably lower RHP, may be more inclined to pay the costs of early arrival, while larger males may partly rely on their ability to evict smaller competitors. (2) In species with high site tenacity, a first-time breeder may not gain much from arriving early, if he risks being evicted from the territory of his choice by the last-year owner of that territory. This argument has already been used by Hinde (1956) to explain why old males typically arrive in advance of first-year males (see also Jakobsson 1988). (3) Variation in the value of territories is not restricted to this dichotomy between previous owners and first-year males. Males that owned a high quality territory in the previous year would have more to gain from early arrival than a male that occupied a low-quality territory. The higher the value of a territory, the more a male will have to invest to succeed in competition. It is therefore very suggestive to argue that a male should adjust his timing of spring arrival to the value of the resource he can defend (here: the value of his last-year territory). It is important to note that the ability to defend this territory would not necessarily result from the male's RHP, but rather from the fact that competitors would know about his readiness to engage in escalated fight because of the great value the territory has to him (Krebs 1982).

The idea that males should adjust their timing of arrival in response to the benefits they can obtain from being early, has received very little attention besides explaining age-dependent arrival. Here I argue that males may invest differentially in regaining the territory they owned the previous year, depending on the quality of their territory rather than on their own quality or condition.

The dusky warbler (*Phylloscopus fuscatus*), a long-distance migrant passerine with a polygynous mating system, offers an excellent opportunity to study this question. The occurrence of polygyny in this species results from heterogeneity in habitat quality (Chapter 4). Male-male competition over the possession of high-quality territories therefore largely decides which males become polygynous and which males remain monogamous or unmated (Chapter 7). At the end of the breeding season, dusky warblers have a complete postnuptial moult, just before their departure to their winter quarters. In contrast to the great majority of other bird species, male dusky warblers often engage in territorial conflicts during this moulting period. Some of the males leave their low-quality territories and try to establish a new territory in the midst of other males, which in turn endeavour not to lose part of their own high-quality territories to the intruders. As aggression is only directed towards territorial males, and not to females or juveniles, I assume that males do not defend food resources for moult, but breeding territories in anticipation of the next breeding season (as found in *Phylloscopus trochilus* and *Phoenicurus ochruros*; Lawn 1994, Weggler 2000). Such preoccupation of resources in late summer or autumn is more widespread than commonly thought, but has received only limited attention (see Schüz 1942, Morley 1943, Kalela 1958, Falls 1969, Haukioja 1971, Hegner & Wingfield 1986, Logan & Carlin 1991, Logan & Hyatt 1991, Yamagishi 1991, Lawn 1994, Weggler 2000).

In the dusky warbler, only about half of the males continue to defend their territories after the breeding season, namely during the period of postnuptial moult. Thus there is variation in how much males invest in claiming territorial interests towards their neighbours, just as there is differential investment in early spring arrival. Apparently, both mechanisms are used to take advantage of prior ownership. It may be predicted that:

(1) For reasons outlined above, investment in prior ownership (preoccupation during moult and spring arrival time) should be related to the value of the defended resource.

(2) Males that do not invest in territorial preoccupation should not pay the costs of early spring arrival either, as they can opt only for low-quality territories.

(3) If differences in RHP have additional effects, then smaller males, with presumably lower RHP, should invest more in gaining prior ownership, while larger males may rely stronger on their ability to evict smaller competitors.

If, in contrast, the costs of advancing arrival time overrule these differences in benefits, one would predict to find a correlation between the date of arrival and male body condition (Kokko 1999).

MATERIAL AND METHODS

The study was conducted in pristine landscape at the mouth of the Malkachan river, 190 km east of Magadan, in the Russian Far East (154° 14' E; 59° 51' N). The area is characterised by a transition from inland taiga forests to coastal tundra along the shoreline of the Okhotsk Sea. At this transition there are extensive bushlands of *Pinus pumila* with some admixture of *Betula middendorffii* and *Alnaster fruticosus*, typically 1-2m in height. The dusky warbler avoids closed forest as well as open tundra, but occupies virtually all areas where coverage by bushes exceeds roughly 10%.

The dusky warbler is an insectivorous long-distance migrant passerine. It has a sexually monomorphic dull brown plumage and sexual dimorphism in body size is not very pronounced (males: mean = 10.0 g, n = 128; females: mean = 9.4 g, n = 78). Dusky warblers winter in south-eastern Asia (Glutz von Blotzheim & Bauer 1991) and are present in the study area from the end of May to the beginning of September. The breeding season consists of a single brood (replacement clutches do occur), followed by a complete postnuptial, pre-migratory moult, which lasts from the end of July to the beginning of September.

This dusky warbler population was studied over three consecutive breeding seasons between June 1997 and August 1999. In 1997, investigations only started at the end of the spring arrival period, thus arrival data are available only for 1998 and 1999. Birds were observed during the period of postnuptial moult in 1997 and 1998, but not in 1999. During the first season, studies were restricted to the central part of the study area (see Figure 8.1), but were later extended to the north and south. Breeding populations in 1997 and 1998 were similar in size (17 vs. 16 territorial males in the central part of the study area), while there was a tremendous decline between 1998 and 1999 (58 vs. 28 territorial males in the overall area). Evidently, this decline was caused by an unusually high winter mortality. Return rates, based on colour-ringed males that held a territory in the study area for at least one month, were 43% between 1997 and 1998 (6 of 14), but only 25% between 1998 and 1999 (12 of 48). Theses values are similar to the return rates observed in females (53% in 1998 vs. 14% in 1999; Chi^2-exact test for common odds ratio, p = 0.006; for details see Chapter 4). Dates of spring arrival were measured as the number of days after the arrival of the first male of the respective season, and the mean of these values did not differ between years (10.2 vs. 10.3). Seven of the 58 territories in 1998 were not observed because of difficulty of access and these were left out of the analyses.

Male dusky warblers were captured using mist-nets and fitted with a unique combination of plastic colour rings. The following morphological measurements were taken: wing length, wing formula, tail length, tarsus length, footspan including claws, bill depth, bill width and body mass. To obtain a measurement of body size that is independent of changes in body mass (reflecting body condition) and of changes in feather lengths (reflecting age; see below), one principal component (“PC body size”) was extracted from tarsus length (factor loading: r = 0.81), footspan (r = 0.78), bill depth (r = 0.46) and bill width (r = 0.35). Multiple measures for the same male were averaged.

As it was impossible to capture all males at a fixed stage of the season and at a fixed time of day, body mass measurements had to be adjusted according to the level of visible fat deposition which varied greatly throughout the season (quadratic regression, $r^2 = 0.16$), and time of day (linear regression, $r^2 = 0.34$). Fat-deposition, estimated in nine distinct classes (according to Kaiser 1993), strongly influenced variation in body mass (ANOVA, $F_{5,158} = 15.3$, $p < 0.0001$; only six of nine fat-classes occurred). Lean body weights were calculated by applying correction factors to individuals that showed visible fat deposition. In addition, birds that were caught during the postnuptial moult showed a 5.3% higher body weight as compared to non-moulting birds ($T_{163} = -4.6$, $p < 0.0001$). Measures from moulting birds were brought into line with non-moulting birds by using a correction factor. Obtained lean mass estimates showed a much higher within-individual repeatability (calculated following Lessells & Boag 1987) as compared to uncorrected weight measurements (repeatability = 0.56, $F_{40,62} = 4.1$, $p < 0.0001$, vs. repeatability = 0.38, $F_{40,62} = 2.5$, $p = 0.0005$), while there was no individual repeatability for the amount of fat-deposition (repeatability = 0.09, $F_{40,62} = 1.3$, $p = 0.20$). Body condition was estimated by taking the residuals from a linear regression of lean body mass on PC body size.

Male age was determined as first year or older partly based on ringing data, partly on a discriminant analysis using feather measurements (tail length, wing length and wing shape). The latter analysis classified 91% of males of known age (*n* = 65) correctly (see Figure 7.1). As this ageing technique implies some uncertainties, important results are presented in two variants, once including all individuals and once including only individuals where age was known by ringing.

Male territories were usually visited every day or second day, and song posts were plotted on a detailed map drawn from a 1 : 5000 satellite photograph of the area. ‘Harem size’ is defined as the number of different females breeding within the area of a male’s territory. For each territory ‘vegetation cover’ was estimated as the percentage of the territory area (minimum-polygon method) covered by bushes or trees. During the moulting period of 1998, food availability was estimated for each of 51 male territories. The arthropod fauna of bush vegetation was sampled by shaking the content of branches into an umbrella. Foraging activity of dusky warblers is almost exclusively restricted to this vegetation type, and as a typical gleaning species it mostly catches prey of low mobility (Forstmeier & Keßler 2001). Observations at the nest were carried out to ensure that the most abundant food items (prey species and prey size) that were sampled were also fed by the dusky warblers to their nestlings (unpublished data). Within each territory 10 samples were collected, each being taken from an approximately constant volume of bush vegetation. Sampling locations were spread more or less equally over the entire territory area. The volumes of all arthropods in a sample (measuring length, breadth and height on millimetre-paper) were summed and mean arthropod volume per sample was calculated for each territory. The resulting values were log-transformed to approach a normal distribution.

To measure the readiness of males to defend their breeding territories against other males, territorial intrusions were simulated using playback of song. Each of 68 territory owners (17 in 1997 and 51 in 1998) was challenged on four different days (typically once per five days) between August 4th and 19th of 1997, and August 6th and 23rd of 1998, respectively. Playbacks were done during late afternoon to minimise the background level of spontaneous singing. Using a Sony TCM-459V recorder and a Sony SRS-A21 active loudspeaker, one minute of song (recorded elsewhere) was played from the centre of a male’s territory. It was recorded whether or not the territory owner responded with song within the five minutes following playback. As males may not have been present at their territory when the playback was performed, this procedure was repeated four times. For the analyses only the dichotomy between males that responded at least once and those that never reacted, is used.

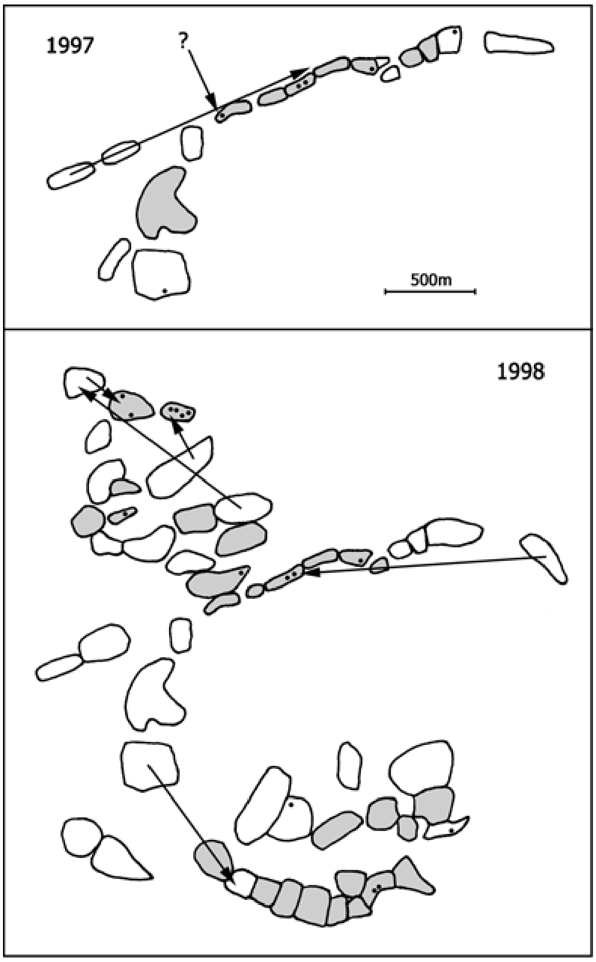


Figure 8.1. Map of breeding territories: the central part of the study area in 1997 and the whole study area in 1998. Shading indicates which territories were still defended by their primary owner when challenged by playback during the period of postnuptial moult. Arrows represent movements of males (during the moulting period) either replacing a primary owner of a vacant territory or trying to take over part of a still-defended territory. The question-mark indicates the unknown origin of a moving male. Dots indicate the nesting site of secondary (i.e. second, third, fourth and fifth) females of polygynous males.

RESULTS

Thirty-five of 69 males (47% in 1997 and 52% in 1998) showed their readiness to defend their breeding territories when challenged with playback during the period of postnuptial moult (Figure 8.1). In the remaining breeding territories playbacks did not provoke any aggressive response, either because males were not present or because males were reluctant to engage in conflicts. Seven males (two in 1997 and five in 1998) left their territories to establish a new territory, mostly in the close vicinity of males that had been mated with three or more females (Figure 8.1). Two of them replaced males that left their territories undefended, and five managed to occupy a small fraction of a still defended territory. Four out of these seven moving males survived to the next breeding season and successfully established a breeding territory at the site they had preoccupied in autumn. The tendency to move from monogamous to polygynous territories was also obvious when looking at the movements of all returning individuals. All of five returning polygynous males tried to reoccupy their last-year territory (four of them succeeded). In contrast, 12 of 14 returning monogamous males moved to another territory (significantly different from polygynous males: $Chi^2 = 11.6$, $p = 0.002$), namely eight tried to take over a previously polygynous territory (six of them succeeded). These 12 territory switches can be divided into six long-distance movements (>500 m) and six cases where directly adjacent territories were taken over. Most interestingly, at least four of these six long-distance movements had already taken place during late summer of the previous season (see Figure 8.1). In the fifth case, there was only an uncertain observation of the male at its later breeding territory.

To avoid pseudo-replication, the following analysis is restricted to the data from 1998 (n = 51 territories). Territories that were defended during the period of postnuptial moult had a significantly higher coverage by bushes or trees ($T_{49} = -4.4$, $p < 0.0001$) and a larger harem size ($Z_{49} = -2.1$, $p = 0.034$) than non-defended territories (Figure 8.2). However, defended territories had only non-significantly higher food densities (i.e. arthropod mass per volume of vegetation) as measured during the moulting period ($T_{49} = -1.1$, $p = 0.28$). Vegetation coverage may be interpreted as reflecting territory attractiveness, as there was a strong correlation with the date of first occupation during spring arrival ($r = -0.43$, $n = 43$, $p = 0.004$).

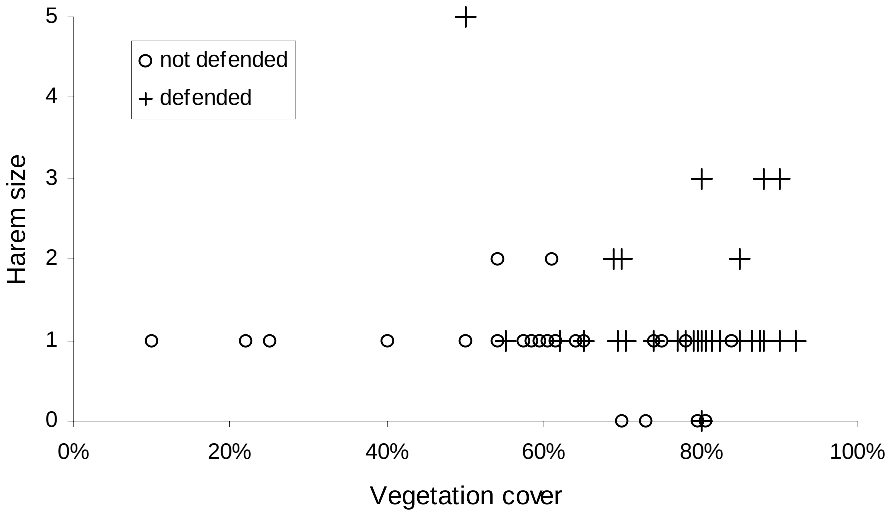


Figure 8.2. Characteristics of territories that were defended by their owners when challenged by playback during postnuptial moult vs. not defended territories. Vegetation cover is the percentage of the territory area covered by bushes and trees. Harem size is the number of different females nesting in a male's territory.

To test whether male characteristics also affected the probability of response to playback, a stepwise logistic regression was used. For this purpose the five males that moved their territory (Figure 8.1) had to be excluded. For another five males some morphological data were lacking (leaving n = 41 males). In the first step, territory characteristics were entered into the logistic regression model (coverage: $B = 0.13$, $p = 0.005$; harem size: $B = 2.1$, $p = 0.022$; full model: $Chi^2 = 19.7$, $p < 0.0001$). Adding male traits in a second step, revealed a negative correlation with male body size ($Chi^2 = 6.6$, $B = -1.44$, $n = 41$, $p = 0.01$; Figure 8.3). Interestingly, body size had almost no effect when it was looked at without accounting for territory quality ($Chi^2 = 2.0$, $B = -0.49$, $p = 0.16$). This means that the effect of body size was only strong when considered relative to territory quality. Thus small males defended their territories even if it was of low quality, while large males tended to leave even high-quality territories undefended. Body size was neither strongly correlated with vegetation coverage (r = 0.06, n = 41, p = 0.71) nor with harem size (r_s = 0.16, n = 41, p = 0.31). Entering male body condition did not significantly improve the above logistic regression model (Chi^2 = 1.3, B = 2.0, p = 0.26), but there was a higher probability for older males as compared to first-year males to react on the playback (Chi^2 = 3.7, B = 2.1, p = 0.054).

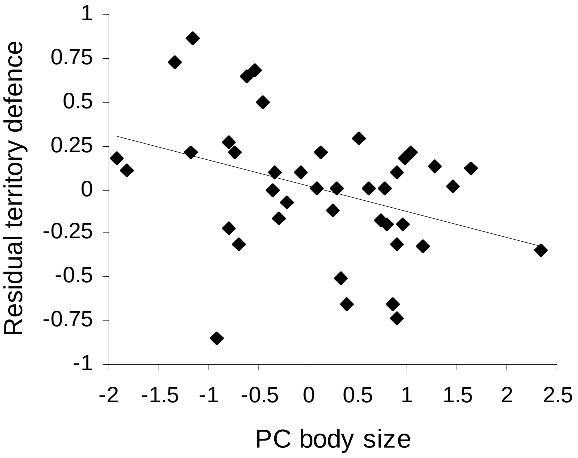


Figure 8.3. Residuals of male response to playback in relation to male body size. The y-axis shows residuals from a logistic regression (reaction vs. no reaction) after accounting for the effects of vegetation cover and harem size (see Figure 8.2). PC body size is a principal component extracted from hind-limb and bill measurements. The correlation is significant (r = -0.37, n = 41, p = 0.017). Note that the outlier (left hand bottom corner) is a male that possibly tried to establish a new territory elsewhere (uncertain observation near the place where it settled the following year). In that case it had to be excluded as were the other males that moved their territories (r = -0.47, n = 40, p = 0.002).

For the analysis of spring arrival patterns the full data set is used, i.e. males from 1997 and 1998, arriving in 1998 and 1999 (n = 74 males). First-year males (n = 30), which never preoccupy territories, arrived on average 12.2 days after the first male of the season. Males that were at least two years old (n = 44) arrived on average at day 8.9 (i.e. 3.4 days earlier; T_{72} = 3.4, p = 0.001). For 27 of these males (mean arrival at day 9.2), it was known whether they had defended a territory near the place of settlement during the previous autumn or not. Individuals that had preoccupied a territory arrived on average 5.5 days in advance of those that had not (day 6.2, n = 12 vs. day 11.7, n = 15; T_{25} = 3.9, p = 0.0006). The latter arrived almost simultaneously with the first-year males (Figure 8.4). This difference in arrival date between preoccupying and non-preoccupying males was not explicable by morphological differences, as the early arriving group tended to have shorter wings (T_{24} = 2.0, p = 0.059). Mistakes in age determination (7 of 15 non-preoccupying males arrived unringed) also cannot be responsible, as the difference in arrival remained (difference 5.8 days) when these uncertainly aged individuals were excluded (T_{18} = 3.3, p = 0.004).

When plotting arrival dates of preoccupying and non-preoccupying males against their body size (Figure 8.4) an interesting interaction is revealed. Non-preoccupying males arrived early when they were large (r = -0.62, n = 15, p = 0.015; excluding unringed arriving males: r = -0.78, n = 8, p = 0.021), while the trend was in the opposite direction for preoccupying males (r = 0.30, n = 12, p = 0.30).

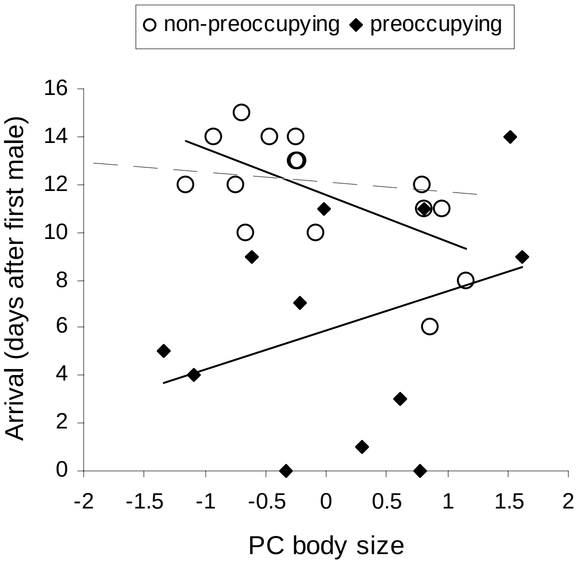


Figure 8.4. Arrival dates of males that had preoccupied a territory in the previous autumn (i.e. males that reacted to playback; n = 15) and of those that had not preoccupied a territory (n = 12) in relation to their body size. The solid lines show regressions for these two groups, the hatched line indicates the relationship between arrival date and body size for first-year males (n = 41) that are not shown in the scatter plot. The effect of preoccupation and the interaction with body size is significant (GLM: total r^2 = 0.49; preoccupy: $F_{1,23}$ = 17.9, p = 0.0003; size: $F_{1,23}$ = 0.04, p = 0.85; preoccupy x size: $F_{1,23}$ = 5.0, p = 0.036).

The strong difference in spring arrival between preoccupying and non-preoccupying males raises the question whether this is due to (1) intrinsic differences in male quality, (2) differences in body condition, or (3) differences in motivation reflecting the chances of owning a high-quality territory.

(1) A subset of 12 males from whom arrival data was available for two seasons, showed only little individual consistency in arrival date (individual repeatability = 0.34, calculated following Lessells & Boag (1987); $F_{11,12} = 2.1$, $p = 0.12$). More specifically, in 1999, seven preoccupying males arrived on average 4.9 days in advance of four non-preoccupying males. However, in the previous year these seven individuals had arrived 0.8 days later than the four others, and this change was not attributable to age-related effects.

(2) There was no indication that body condition affected arrival date, neither when looking at all individuals (ANCOVA, effect of age: $F_{1,70} = 10.7$, $p = 0.0017$; effect of condition: $F_{1,70} = 1.4$, $p = 0.24$), nor when restricting to the males that were known from ringing to be older than one year ($r = -0.01$, $n = 19$, $p = 0.96$), nor when analysing preoccupying ($r = 0.17$, $n = 12$, $p = 0.61$) and non-preoccupying ($r = 0.11$, $n = 15$, $p = 0.69$) males separately. For the given sample size of $n = 73$ males, a power of 0.80 is reached for effect sizes larger than $r = 0.28$.

(3) Males which had bred in, or adjacent to, highly polygynous territories (three to five females) arrived significantly earlier during the following spring compared with monogamous males who had no polygynous neighbours (day 4.4, $n = 7$ vs. day 11.0, $n = 9$; $T_{14} = 3.4$, $p = 0.004$; effect size $d = 1.74$).

DISCUSSION

The observed patterns of male territoriality and spring arrival indicate that timing of arrival is strongly influenced by a male's chances to succeed in competition over the best territories, rather than by intrinsic male qualities or body condition. Male dusky warblers breeding in low-quality habitat tended to leave their territories during postnuptial moult and establish a new territory in close vicinity of highly polygynous territories. Similar patterns have been found in other species that show territoriality during late summer or autumn (Lawn 1994, Weggler 2000). About half of the males preoccupied high-quality territories during the moulting period, apparently in anticipation of the next breeding season. Eighty-nine percent of the returning males occupied the territory they had defended the previous season or a directly bordering vacant territory. Most interestingly, the amount of competition experienced during autumn appeared to affect the timing of spring arrival. Males that defended highly polygynous territories and males in territories directly bordering these were among the first to arrive the following spring. In contrast, individuals that had not preoccupied a territory during the previous moulting period, arrived as late as did first-time breeders. Since there is not much competition for the low-quality territories available to these males, the benefits of advancing spring arrival are limited. The idea that the amount of competition between individuals influences arrival patterns has already been used to explain why males typically arrive in advance of females (Ketterson & Nolan 1976, Myers 1981, Francis & Cooke 1986, 1990).

Alternative explanations for the observed patterns were not supported. Principally it might be argued that (1) males occupying the best territories could have experienced the best moulting conditions, resulting in a good body condition and consequently in early spring arrival, or that (2) only the males of highest intrinsic quality could afford to be territorial during autumn. Thus they could take the best territories and their early arrival might be a consequence of their intrinsic qualities. These alternative explanations are unlikely for the following reasons. (1) Preoccupied territories differed from non-preoccupied ones in ultimate qualities (harem size) rather than in proximate qualities (food density during the moulting period). Thus it appears unlikely that preoccupying males experienced better moulting conditions than others. (2) There were no measurable effects of body condition on the date of male arrival, although this might partly result from the fact that male condition was not measured at arrival, but mostly later in the season (see Methods). (3) If non-measurable differences in male qualities played an important role one would have expected to find a larger within-male consistency in arrival dates than was found. Males from whom arrival data from two seasons were available showed that the effect of having preoccupied a high-quality territory was much larger than possible intrinsic male effects.

How can a male increase his future success in competition by investing in late-summer territoriality? The value-asymmetry (VA) hypothesis states that the male having the strongest interest in owning a given territory will win the conflicts over its possession (Krebs 1982). The larger the value of a territory to a given male, the more likely this male is ready to engage in escalated fighting. Neighbouring males are unlikely to challenge a male that has held a territory successfully already for a long time. This is because long-lasting ownership may reflect a male's ability to defend his territory. Thus the longer a male owns a territory, the less often he will be challenged, i.e. the less he will have to invest in territorial defence. Consequently, this territory will be of greatest value to this individual male, for it becomes inexpensive to defend (Krebs 1982). To be successful in such competition a male has to 'convince' his neighbours of his territorial interests. The fact that dusky warbler males sing intensively to defend their territories during the period of postnuptial moult, suggests that convincing neighbours is important for success in competition. It also shows that value asymmetries do not result from differences in familiarity with the territory alone, as this familiarity could also be gained without any singing. In Chapter 9 I show that male dusky warblers are capable of recognising the individual songs of their neighbours from the previous season. Such abilities are a necessary precondition for the above outlined scenario.

A surprising finding of the present study is that investment in gaining prior ownership varied with male body size. Smaller males tended to defend their territories during moult even when territories were of low quality, while large males tended to leave even high-quality territories undefended. This finding could be interpreted in two different ways. (1) There may be body-size related energetic constraints on territoriality when simultaneously engaging in moult. The fact that virtually all passerines with late-summer or autumn territoriality abort aggressiveness during moult (Schüz 1942, Haukioja 1971, Hegner & Wingfield 1986, Logan & Carlin 1991, Logan & Hyatt 1991, Yamagishi 1991, Lawn 1994, Weggler 2000) may indicate energetic constraints, but could also reflect incompatibility in hormonal control (e.g. Wingfield & Monk 1992). (2) Larger males may rely on their ability to evict smaller males from their territories, while smaller males could compensate for physical inferiority by investing more in gaining prior ownership. Some bird studies support the idea that body size is related to RHP (Petrie 1984, Marra 2000). Note that several other studies have claimed such a relationship (Ebenman & Nielsson 1981, Lundberg et al. 1981, Ulfstrand et al. 1981, Tiainen 1982, Michalak 1995), but these were probably confounded by age-dependent morphological changes (Norman 1983, Alatalo et al. 1984, Gezelius et al. 1984, Hogstad 1985). On the other hand, there are studies that found no relationship between RHP and body size (Arcese & Smith 1985, Robinson 1986, Lemel 1989, Beletsky & Orians 1993, Silverin 1998). With regard to the dusky warbler, I found no additional direct support for the importance of body size for winning territorial fights (data not shown), but this may have been due to small sample size in combination with only limited effect size.

Patterns of spring arrival (Figure 8.4) provide additional support for the idea that body size does influence RHP in the dusky warbler. Males that had not preoccupied a territory during moult arrived only late in spring. Within this late arriving group, larger males arrived significantly earlier than smaller ones. The latter may have given up competing for high-quality territories (low RHP, no preoccupation, late arrival), while larger males with increased RHP may still opt for better territories by advancing their arrival by a few days. In contrast, the opposite pattern is found within preoccupying males (though non-significantly). In this group of males, that try to compete for the best territories, the small ones may aim at arriving first, to compensate for their lower RHP. Larger individuals may still succeed in competition for the best territories without paying the costs of arriving very early.

The dusky warbler may seem to be a special case considering its unusual behaviour of late summer territoriality. However, the issue raised here is not restricted to species where males compete for high quality territories, but may even apply to non-territorial species. A well studied example of the latter type is the barn swallow, *Hirundo rustica* (Møller 1994b). Although Møller put most emphasis on the fact that the costs of early arrival vary with male phenotypic quality (Møller 1994a), he also stated that low-quality males would gain less than high quality males from being early (see figure 7.6 in Møller 1994b). As there is assortative mating with respect to phenotypic quality (Møller 1993), an early arriving low-quality male may not be accepted by the high-quality females available at that time, and it may have to wait until the arrival of low-quality females (Møller 1988b, 1993, 1994b). The critical distinction between territorial and non-territorial systems, lies in the factors that promote male mating success. In the barn swallow the attractive male has more to gain from arriving early than the unattractive one. In the dusky warbler, males having high VA and low RHP should invest in advancing their arrival.

This distinction has implications for the often assumed relationship between male phenotypic quality and arrival date. In the barn swallow, there is one male characteristic (tail length) that correlates well with both, the ability to survive harsh weather (thus to meet the costs of early arrival; Møller 1994a) and with attractiveness to females (thus with the benefits from arriving simultaneously with high-quality females). It is therefore not surprising that male tail length and date of arrival are highly correlated (r = 0.59; Møller 1994a) and that there is a high within-male consistency in arrival date (R = 0.51; Møller 2001). It is intriguing that, in this species, first-year males arrive simultaneously with older males (Møller 1994a), as there is neither competition for high-quality territories (Møller 1994a), nor a female preference for older males (Møller 1992). In territorial systems the correlation between male phenotypic quality and the date of spring arrival may often be blurred by value asymmetries. Potti (1998) failed to detect any individual consistency in spring arrival dates in the pied flycatcher, *Ficedula hypoleuca* (R = 0.04), a system of resource-defence polygyny.

The fact that costs of advancing arrival should be larger for individuals of lower quality or in worse condition (Kokko 1999) should apply to all systems, but this relation may be weak if these costs vary stochastically between years. Condition-dependent selection may act only when early arriving males face unfavourable circumstances (see Whitmore et al. 1977). Males in poor body condition have less chance of surviving extremely bad weather (Møller 1994a), but they may actually have to pay this cost only say once every ten years (Møller 1994a). Such an unpredictable selective regime may favour benefit-dependent arrival times, given that potential benefits vary between individuals.

9. Why mated males sing so much

The fertility announcement hypothesis states that males sing most intensively during the period of female fertility in order to ensure their paternity, as females would prefer to sexually mate with males singing at a high rate. The dusky warbler (*Phylloscopus fuscatus*) is one of the few species in which singing intensity clearly peaks when females are fertile. As a test of the fertility announcement hypothesis, I study why males of this species sing so much after pairing. Dusky warblers have two distinct kinds of song, an individually specific, stereotype song type (S-song) and a highly variable song type (V-song). S-song is used as an individually recognisable signature to mark the claimed territory area. Playback experiments indicate that males can even memorise their neighbours from the previous breeding season. S-song is used while patrolling over the territory area, presumably to ward off intruding males. Males do not guard fertile females, but intensity of S-song peaks when a male's partner is fertile. In contrast, V-song appears to advertise male quality, functioning to attract females for copulation. This song type is used at the highest rate when any female, the own or the neighbouring, is fertile. The present study clearly supports the idea that song can function as a paternity guard. However, analysis of extra-pair paternity in this species found that females choose copulation partners on the basis of the quality of their V-song, but not on the quantity of song (Chapter 10). This means that the fertility announcement hypothesis does not apply to the dusky warbler, as the presumed mechanism – selection on song rate – is not given. I discuss what selective pressures may favour and maintain such ways of paternity insurance.

INTRODUCTION

It is generally accepted that male birds sing in order to acquire a mate and to defend a territory and its resources (Searcy & Andersson 1986, Catchpole & Slater 1995). In some species males cease from singing once they are paired with a female (e.g. Catchpole 1973), while in some other species males also sing intensively after pairing (e.g. Møller 1988a). Greig-Smith (1982) suggested that song after social pairing might function to ensure within-pair paternity ('mate retention') and/or to attract neighbouring females to perform extra-pair copulations. Mace (1987) first demonstrated that singing was most intense during the period when females were laying eggs, supporting the idea that song may function as a paternity guard. Møller (1991) carried this field one step further by suggesting a mechanism that could allow song to act as a paternity guard. If the rate of singing was a condition dependent trait, and thereby a reliable indicator of male quality, females might prefer to copulate with males singing at high rate. Given this female preference, intensive singing could, on the one hand, prevent the own female from being unfaithful, and, on the other hand, attract neighbouring females for extra-pair copulations. Simultaneously, singing at high rate would help to discourage neighbouring males from intruding into the territory, as females paired to males singing at a high rate would tend to remain faithful to their mates. Møller claimed that for these reasons a majority of bird species would reach a peak of singing intensity during the period of female fertility. As neighbouring males may use male singing intensity as a cue to recognise the period of female fertility, this hypothesis was named the fertility announcement hypothesis.

Over the past decade quite a few studies have challenged Møllers hypothesis by analysing temporal patterns of singing intensity (reviewed by Gil et al. 1999). In most species males sang more intensively before pairing than during the period of female fertility, thus leading to a rejection of the fertility announcement hypothesis (Gil et al. 1999). Some studies described puzzling cases, where singing was most intense in the fertile and especially in the post-fertile period (Rodrigues 1996b, Currie et al. 1998). Finally, there were a few studies showing a clear temporal relationship between male singing activity and female fertility (Mace 1987, Welling et al. 1997, Pinxten & Eens 1998). It can be summarised that the fertility announcement hypothesis may apply at best to a restricted number of species. However, the question of why males of some species still sing intensively after pairing, has not yet been answered satisfactorily. Most seriously, the mechanism underlying Møllers model (i.e. a female preference for high song rates) remains to be tested.

Preliminary observations on the dusky warbler (*Phylloscopus fuscatus*) suggest that this species might be a potential candidate for the fertility announcement hypothesis, as dusky warbler males sing intensively after pairing (e.g. Johansen 1954). Looking at this species, I pick up on Møllers question of why mated males sing so much. I investigate to what extent the fertility announcement hypothesis provides a likely explanation. Interestingly, the dusky warbler has two distinct kinds of song, an individually specific, stereotype song type (S-song) and a variable song type (V-song). These song types are so distinct that Bergmann (1996) initially thought they belonged to different species. In several passerine species stereotype songs appear to be territorial signals directed towards males, while more complex songs often address females (Catchpole 1980, 1982, Slater 1981, Groschupf 1985, Fessel and Hoi 1996). It might be suggested that, in the dusky warbler, stereotype song functions as a territory defence, while variable song advertises for copulations to both, the own and neighbouring females. This produces testable predictions on temporal patterns of song-type use: S-song should be used most intensively during fertility of the own female, to prevent other males from intruding the territory. V-song should be used at a high rate as long as any female in the neighbourhood, including the own, is receptive.

To develop an understanding of song functions in this candidate model species for the fertility announcement hypothesis, I take the following steps. I firstly describe and characterise the two song types of the dusky warbler, as this is still to be done (see Bergmann 1996). Dybowski (in Taczanowski 1872) mentioned only the monotonous S-song, while Beick (in Stresemann et al. 1937), referring to V-song, even made comparisons to the song of the nightingale. Later authors were partly confused by such discrepancies (see Glutz von Blotzheim and Bauer 1991, Cramp 1992). I investigate patterns of both, temporal and spatial use of these two song types to test hypotheses concerning their function in male-male and male-female communication. A playback experiment is used to determine whether the individual distinctiveness of S-song may serve to facilitate individual recognition. I also analyse V-song repertoire size and syllable-type sharing between neighbours to shed some light on possible functions of V-song.

MATERIAL AND METHODS

The study was conducted in pristine landscape at the mouth of the Malkachan river, 190 km east of Magadan, in the Russian Far East (154° 14’ E; 59° 51’ N). Here dusky warblers breed in high density in bushlands of varying coverage and height, located in the transition from inland taiga forests to coastal tundra. I studied this population over three consecutive breeding seasons between 1997 and 1999. The dusky warbler is an insectivorous long-distance migrant passerine and it has a sexually monomorphic dull brown plumage. The species is present in the study area from the last days of May to the first days of September. I followed the birds for the duration of the summer season, which comprises a single brood (replacement clutches do occur) and a postnuptial, pre-migratory moult.

All territorial males and most of the females (84%) were colour ringed. The birds were observed daily and nests were checked frequently in order to obtain dates of settlement, pairing, egg-laying and hatching. The exact date of pairing proved to be difficult to determine. In all cases where I managed to do this, the first egg was laid either 7 or 8 days later (n = 1 and n = 5 respectively). As a result of brevity of the breeding season females are constrained to start the clutch as soon as possible, and I assume that an interval of 7 or 8 days is the minimal time span required for nest building (only the female builds) and egg formation. I therefore define the date of female settlement as being 8 days before deposition of the first egg of the first clutch.

The song of dusky warblers consists of short strophes (typically of 1-2s duration) with pauses of typically 5s between strophes (Figure 9.1). There are two distinct kinds of song type (stereotype song type = “S-song“ and a variable song type = “V-song“), that can easily be distinguished in the field. In 1997 I observed the use of song posts and song types for 14 territorial males nearly every day and plotted them to the nearest 5m on a detailed map (scale 1 : 1000) that was obtained from own distance measurements. To illustrate spatial and temporal patterns of song-type use on a typical example, a 18h focal observation of a territorial male was conducted. This male had been selected for its territory being spatially isolated from other territories, in order to minimise direct influences from neighbouring males. Each minute song type and singing location of the male was recorded to the nearest 10m.

For each of 14 territorial males of 1997 I took measurements of vegetation structure at the five or six most frequently used song perches. Within a 20m x 20m square area around the perch I estimated cover of bush vegetation in five layers (0m-0.5m, 0.5m-1m, 1m-1.5m, 1.5m-2m, >2m above the ground). Using 0m height for parts of the square without any bush cover I calculated a value of mean vegetation height for the square area around a perch. This measurement reflects both, the average height of bushes and the total coverage of the area by bushes.

In 1998 song rate was measured for 16 males holding a territory in the same area as studied in 1997. For each male 10 min focal observations were performed once per day between 04:30-10:00 h. These observations were carried out almost daily between male settlement and hatching of nestlings and sporadically after that period. Focal observations were started at predetermined times, irrespective of whether the male was singing or not. In order to decrease systematic biases caused by between-male differences in time of day at observation male observation order was randomised to the extent allowed by constraints of observers travelling distances. During this 10 min period the number of strophes of each song type was recorded for each minute separately. For most of the analyses I used song rates per minute (mean number of strophes per minute). To quantify the relative share of the two song types (irrespective of song rate) I discarded all minutes without song (38% of 6,240 min) and those during which both song types have been recorded (3%). From the remainder I calculated the share of minutes with only S-song and only V-song.

For statistical analysis I defined three discrete phases to allow pair-wise testing: (1) The nest-building phase is from day –8 to –2, with day 0 being the day when the first egg is laid. (2) The peak-fertility phase comprises all those days after which an egg was laid, reflecting the period with highest chances of fertilising eggs (Howarth 1974, Colegrave et al. 1996). (3) The post-fertility phase is from the day of deposition of the last egg to day +12. Note that other authors have defined the fertile period differently, partly because they could use a pre-fertile period as a reference (e.g. days –39 to –9 in non-migratory European robins, *Erithacus rubecula*; Tobias & Seddon 2000). An increasing intensity of sperm competition over the course of the nest-building phase can be expected, but sperm competition should be strongest in the second phase, when the chances of fertilisation are highest. For each male I calculated mean song rates for each phase.

Tape recordings of songs were made with a Nagra SN recorder and a Sennheiser MKH 815T directional microphone in 1997, a Sony TCM-459V recorder and a Shure Prologue 16AM microphone in 1998, a Sony TC-D5 PRO II recorder and a Sennheiser K6-M67 microphone in 1999. Recordings of S-songs were obtained from a total of 85 males (including 18 individuals recorded in more than one season). A small sample of S-song strophes per individual was sufficient to obtain the full repertoire of syllable types used (maximally three syllable types). I sampled a small number of V-song recordings from most of the males in each breeding season. Recordings of 100 continuous strophes (approx. 10 min) were often difficult to obtain, so most analyses are based on recordings of 30 strophes. All song recordings were analysed with Avisoft SASLab Pro (sampling frequency 22,050 Hz, 16 bit, time resolution 5.8 ms, bandwidth 111 Hz). Syllable types were categorised by visual inspection of printed spectrograms, (see Figures 9.1 and 10.1).

Getting a precise measure of the full V-song repertoire of an individual dusky warbler male proved a virtually impossible task, as new syllable types (rarely used types) continue to turn up throughout even the longest recordings. I used the computer program EstimateS (Version 5.0.1, R. K. Colwell, http://viceroy.eeb.uconn.edu/estimates), to make extrapolations on the full repertoire sizes. Although this program is designed to obtain statistical estimators of true species richness from repeated censuses, it is highly suitable for my purposes. Simple capture-recapture techniques (mentioned by Catchpole and Slater 1995) assume that all syllable types are used at equal rate. This leads to an underestimation of repertoire size if some syllable types are much more frequently used than others. This problem is analogous to the fact that species communities contain both, abundant and rare species, and EstimateS is designed to cope with this. Note that this program is inappropriate for species with strong sequentiality of syllable-type delivery. Recordings of 25 continuous strophes were used as the unit of survey (like one census of a species community), with syllable types representing the species. Abundances were defined as the number of strophes in which a syllable type was found (theoretically varying from 0 to 25). I always entered data from four recordings for each male (4x25 strophes), and let the program calculate several different estimators of the true number of syllable types, i.e. what is expected to be found in an infinite number of recordings of that male. In this paper I present mean estimates, averaged among eight different estimators (namely ACE, ICE, Chao 1, Chao 2, Jack 1, Jack 2, MMRuns, MMMean), all of which produced fairly similar results.

In order to make comparisons between two repertoires (obtained from 30 strophes) I calculated a coefficient of syllable type sharing (Sörensen index; see McGregor and Krebs 1982) as $2*C/(R_1+R_2)$, where R_1 and R_2 are the numbers of syllable types found in repertoire 1 and repertoire 2, respectively, and C is the number of syllable types that the two repertoires have in common. I used this measure to determine whether neighbouring males shared more syllable types than males located 0.5-3km apart from each other.

In 1999 I performed a playback experiment to determine whether males discriminate between S-songs of individuals they are familiar with and S-songs of presumably unfamiliar males. Males that had just established territories in early spring of 1999 at the same site they had occupied the previous year, received playback of the S-song of the nearest neighbour from the previous year (given that this individual had not yet arrived) and, as a control, the S-song of a randomly selected other male, that had bred at least 1km apart in 1998.

The two playbacks (presentation of familiar and unfamiliar song) took place at least 24h apart and the order of treatment was randomised. Playbacks were done with a Sony TCM-459V recorder and a Sony SRS-A60 active loudspeaker. Tapes used for playback were prepared from recordings obtained in 1998 and were standardised for song rate (8 strophes per min), duration (1min) and volume using the Avisoft SASLab Pro. In the field, sound pressure was adjusted and fixed at a natural output level. I made sure that bush vegetation allowed a more or less continuous approach by birds, not being hindered by gaps in the vegetation. I measured the intensity of male response to playback as the minimal distance of approach to the loudspeaker while singing. I decided to use this as the sole measure of aggressive response to playback, as previous playback experiments in 1997 and 1998 showed a high repeatability and a strong relationship between closest approach and male age reflecting confidence of territory ownership (unpubl. data). Additional parameters of male reaction were not recorded to avoid the problem of multiple testing.

RESULTS

Song type characteristics

Spectrograms of ten consecutive V-song strophes and ten consecutive S-song strophes of a single male are shown in Figure 9.1. The main differences between the two song types are summarised in Table 9.1, based on V-songs recorded from 30 males and S-songs from 85 males.

Table 9.1. Characteristics of stereotype song type (S-song) and variable song type (V-song). All differences in means and standard deviations are highly significant ($p < 0.0001$).

	S-song mean ± SD (range)	sample size	V-song mean ± SD (range)	sample size
Song rate (strophes / min)	4.74 ± 2.33 (1-16)	1937 min (16 males)	7.81 ± 4.25 (1-19)	1350 min (16 males)
Number of syllables per strophe	3.69 ± 0.66 (3-6)	120 strophes (85 males)	6.01 ± 1.84 (1-13)	120 strophes (30 males)
Versatility (syllable types per strophe)	1.00 ± 0.00 (1)	120 strophes (85 males)	1.63 ± 0.83 (1-5)	120 strophes (30 males)
Individual repertoire (30 strophes)	1.41 ± 0.62 (1-3)	85 males	18.62 ± 3.87 (9-27)	30 males
Population repertoire (32 males, 60 strophes each)	30		205	

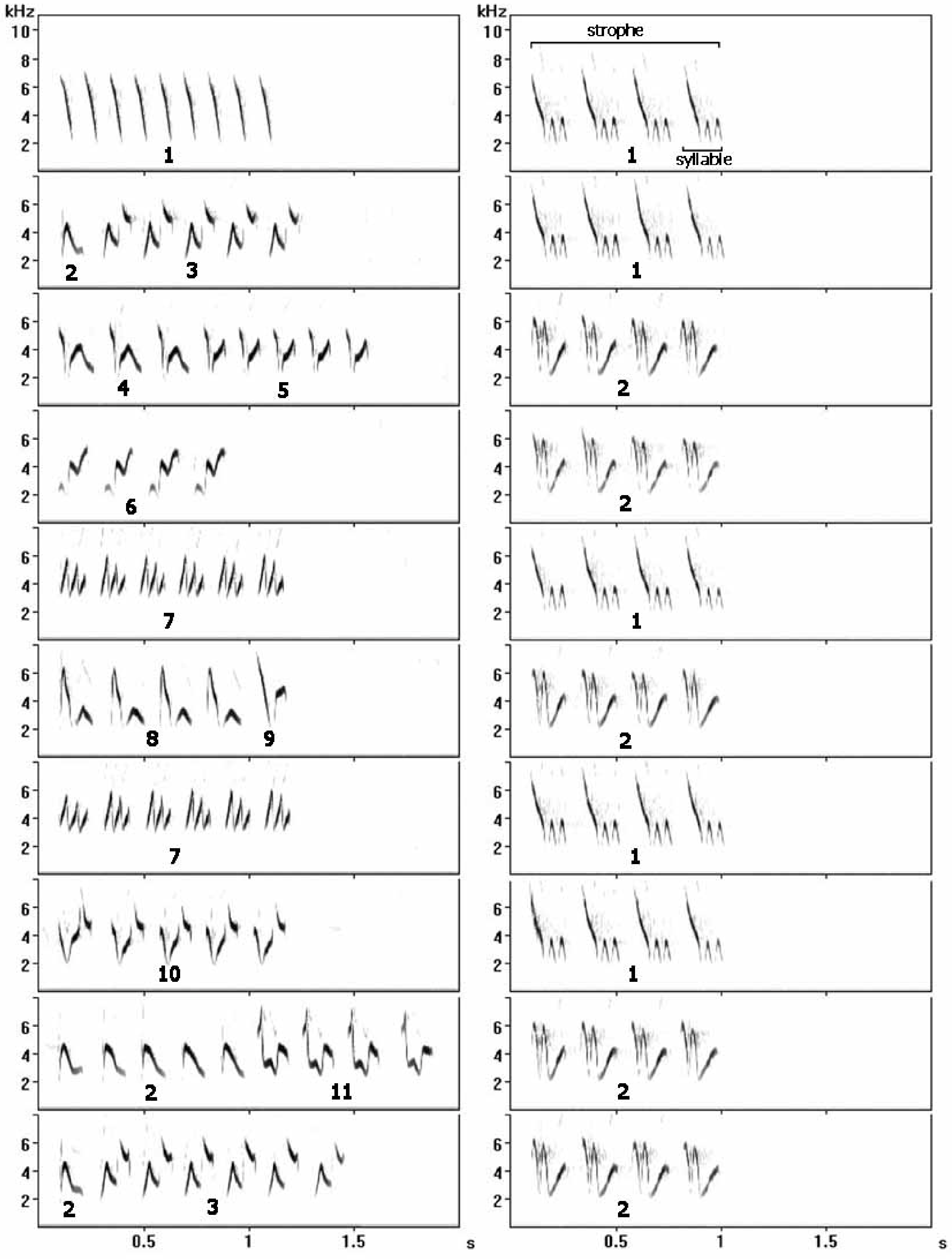


Figure 9.1. Spectrograms of 10 continuous strophes of variable song-type (V-song, left side) and 10 continuous strophes of stereotype song-type (S-song, right side) of a single male (Bandwidth 111Hz, time resolution 5.8ms). The total duration, including pauses, of the 10 V-song strophes was 54s, of the 10 S-song strophes 74s. Numbers reflect the classification of different syllable types (1-11 in V-song and 1-2 in S-song).

S-songs are characterised by a small individual but a large population repertoire. Of the 85 males analysed, 56 used only one syllable type, 23 males used two syllable types (as the example in Figure 9.1) and 6 males used three different types. This population of 85 males used 40 different syllable types altogether, allowing to recognise most males individually by their S-song syllable type. All males using two or three syllable types had a unique combination of syllable types. I estimated that an average male using only one syllable type will, statistically speaking, find exactly one twin male (using the same syllable type) within a sample of 42 males. Experienced human listeners can learn to recognise individual males by their S-songs with reasonable confidence, suggesting that S-songs may signal individual identity. Circumstantial evidence suggests that young males learn the S-song from tutors other than the social father, and that they may compile their individual S-song repertoire from different tutors. As a rule, individual S-song repertoires are kept throughout an individual's live. Only one out of 18 males observed in more than one season had exchanged one of his two syllable types to a new one between his very first and the following breeding season.

V-song differs from S-song by the following characteristics (see Table 9.1 and Figure 9.1): (1) V-song is, on average, produced at a higher rate per minute compared to S-song. (2) In V-song, pauses between strophes may contain series of short calls (the “drrr“-call depicted in Glutz von Blotzheim and Bauer 1991). These calls were present in 50% of 107 V-song recordings, but were never heard in S-song. (3) V-song strophes, on average, are longer than S-song strophes, and contain more and a more variable number of syllables. (4) V-song regularly shows syllable-type switches within strophes, that do not occur in S-song. (5) V-song comprises large individual repertoires.

Individual V-song repertoires found in 100 continuous strophes comprised an average of mean ± SD = 33.9 ± 7.1 (range: 22 - 42, n = 10 males) syllable types. I split these recordings into 4 parts, each of 25 strophes. From these 4 samples I calculated estimates of full repertoire sizes of males, using the EstimateS program: mean ± SD = 44.9 ± 12.0 (range: 28 – 61). For comparison, I did the same for 10 other males where I had 4 different recordings (each of 25 strophes) that had been taken over the whole breeding season (one recording per week). The repertoires found in these samples of 100 strophes were not significantly larger (mean ± SD = 38.5 ± 6.5, range: 22 - 46) than those mentioned above (T-test, T_{18} = 1.5, p = 0.15), but the estimates of full repertoire sizes were considerably higher (mean ± SD = 61.4 ± 13.1, range: 30 – 75; T-test, T_{18} = 3.0, p = 0.009). The fact that this latter method yielded higher estimates of full repertoire size is a result of a higher turn-over of syllable types between recordings when these are taken at one-week intervals. The repertoire sizes found within 25-strophe bouts did not differ between the two groups of males (18.7 vs. 19.0, T-test, T_{18} = 0.2, p = 0.81).

This indicates that males do not make use of their full repertoire at a given time and / or continuously learn new syllable types from their neighbours. The latter hypothesis is confirmed by the finding that males have a significantly higher coefficient of syllable-type sharing with their nearest neighbour (mean ± SE = 0.35 ± 0.05, n = 13) than with a randomly selected male from 0.5-3km distance (mean ± SE = 0.15 ± 0.02, paired t-test, T_{12} = 4.0, p = 0.002). Part of the variation in syllable-type sharing between neighbours is explicable by the seasonal changes. Repeated measurements of syllable-type sharing on the same pairs of neighbours (n = 8 pairs) show that repertoire sharing increases with duration of neighbourhood (ANCOVA; effect of pair: $F_{7,16}$ = 7.5, p = 0.0004; effect of date: $F_{1,16}$ = 7.3, p = 0.016; effect of number of days between the paired recordings: $F_{1,16}$ = 3.9, p = 0.067; the latter variable varied between 0-5 days, mean = 1.7). Single cases indicate that males may rebuild nearly their whole repertoire within a few weeks, and may adopt new syllable types that were present in the repertoires of their neighbours already at the beginning of the season.

Spatial use of song types

The great majority of males defending established territories use only one or sometimes two selected bushes or groups of bushes from which they exclusively display their V-song (“V-song perch“). All the remaining territory area is covered with S-song. Figure 9.2 illustrates this pattern on the example of a typically behaving male observed over a full day period. Only 1.7% of 1,937 observations of song-type and perch use from 14 males in 1997 did not comply with the rule of spatial separation. There are two main sources of deviation: (1) Males moving through their territory area and singing S-song, will generally switch to V-song if they encounter and evict an intruding male. (2) Males intending to leave the V-song perch rarely anticipate a single S-song strophe just before leaving. In contrast to these rules, males that have no established territory or are just starting to establish one, often do not show a clear distinction between a V-song perch and the territory area.

Birds select the location of the V-song perch on the basis of vegetation structure (Figure 9.3). In all of 14 territories studied in 1997, V-song perches showed a greater mean vegetation height than the four most frequently used S-song perches in the territories (paired t-test of means, $T_{13} = 9.7$; $p < 0.0001$). As the measure of vegetation height shown in Figure 9.3 reflects both, the coverage and height of bushes, males appear to seek to have a maximally large volume of dense bush vegetation underneath, when singing V-song. If males face the choice between dense bushes and a tall tree lacking bushes below, they prefer the bushes. Therefore, not the height of the singing perch, but the volume of bush appears to be of importance. New males settling in this area in 1998 and 1999 (n = 14) chose identical V-song perches as their predecessors, with one minor exception.

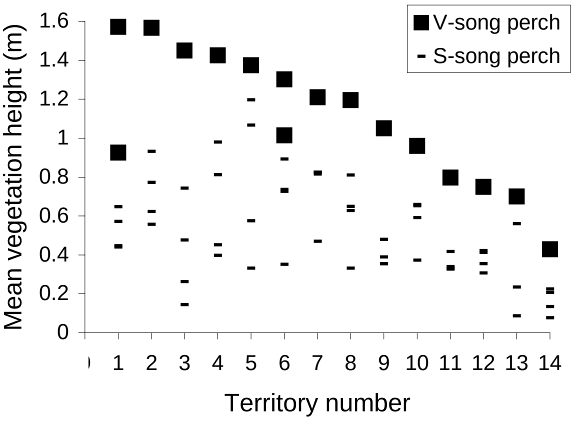


Figure 9.3. Vegetation height at song perches for each of 14 territories. Measurements were taken at all perches regularly used for V-song (12x1 and 2x2) and the four most frequently used perches for S-song. Mean vegetation height is estimated within a square of 20m x 20m around the centre of the perch and reflects both the height and coverage of bush vegetation (as height of 0 was entered for the proportion of area lacking bush cover).

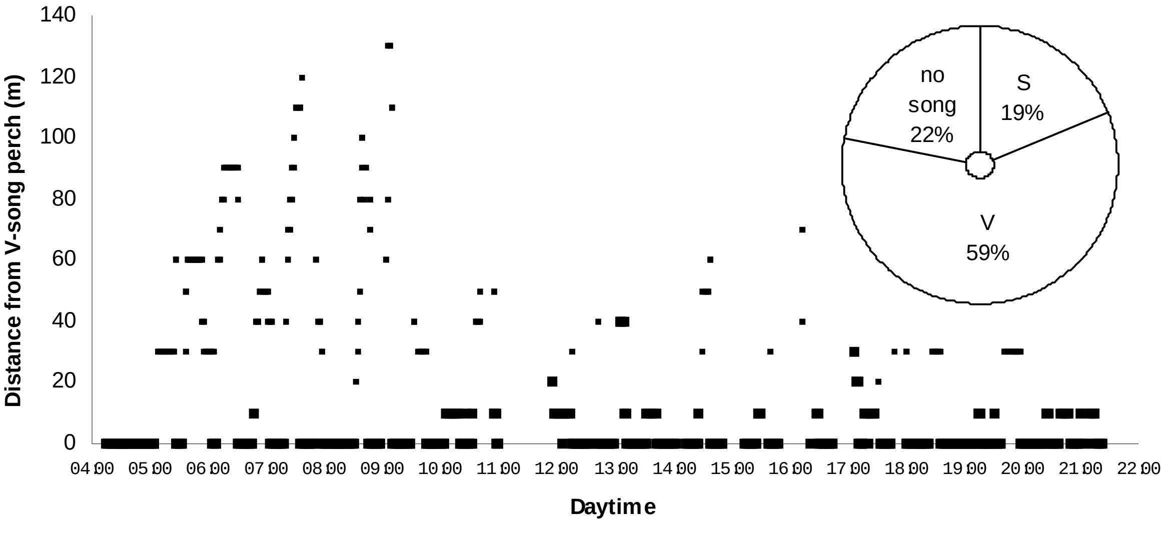


Figure 9.2. Spatial and diurnal use of two different song types (V-song in bold squares, S-song in dots) by an individual male. The male was observed on 20th of June 1997, the day when its own female laid the fifth of six eggs. As a rule, S-song was used all over the territory area, more than 20m away from the V-song perch, whereas V-song was used close to that perch. Each of 1,029 minutes was assigned to either V-song, S-song or pause (lack of any symbol indicates a pause). The pie-chart shows the proportions of minutes assigned to either category.

Temporal use of song types

The population-wide amount of V-song and S-song use varied greatly throughout the season (Figure 9.4). Daily means of the proportion of V-song relative to total song (derived from song rate measurements on 16 males) are shown for 1998. Very similar overall patterns were observed in 1997 and 1999 (not shown).

During times when only males but no females are present in the study area (before female arrival in early June and after female departure in late August, when males are still defending territories) both song types are used in approximately equal proportion. When females start to arrive in the breeding area, males use S-song almost exclusively. As soon as females start to lay eggs, the proportion of V-song increases and remains very high until the start of incubation of the latest replacement clutches. Notice that the arrival of females (n = 35) and deposition of eggs (n = 245) indicated in Figure 9.4 reflect patterns from the overall study area, while song rate data are from 16 males from the central part of the study area. This is justified by the fact that arriving females were seen to move through the whole area.

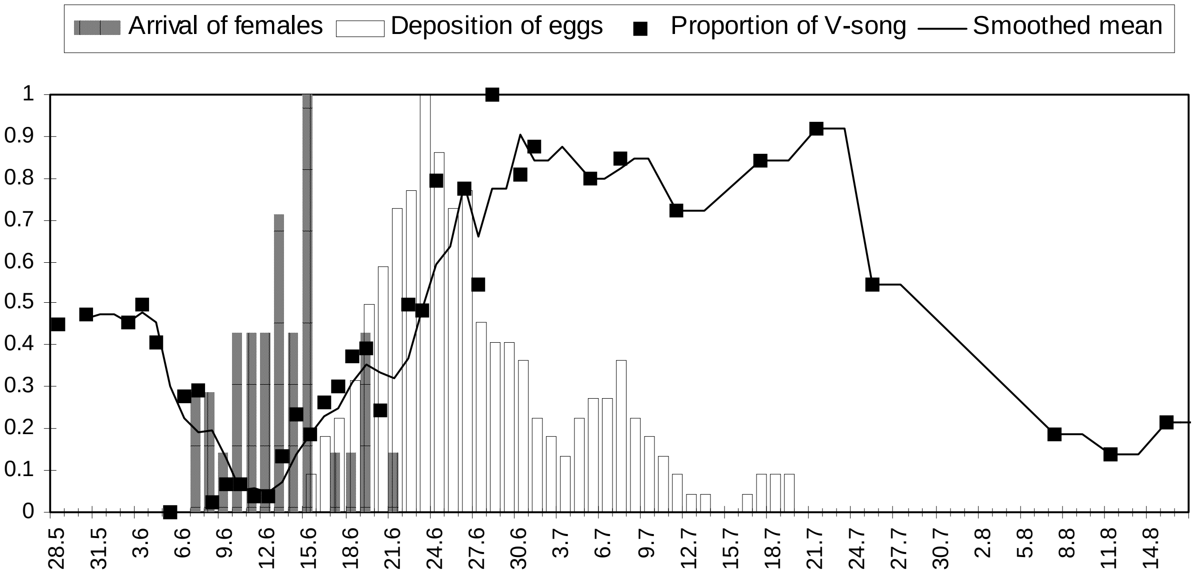


Figure 9.4. Seasonal patterns of population-wide song-type use, arrival of females and egg-laying. Squares indicate the proportion of V-song use relative to total song, measured for 16 males in the centre of the study area. The solid line shows the smoothed mean of the proportion of V-song (3-day averages). Bars indicate daily numbers of newly arriving females (n = 35) in the whole study area (the highest value of seven females was set to 1 on the y-axis) and daily numbers of eggs laid (n = 245) in the whole population (the highest value of 21 eggs was set to 1 on the y-axis). All eggs laid after July 2^{nd} were from replacement clutches.

A finer temporal resolution of singing patterns is reached when looking at singing intensity of individual males (Figure 9.5). Three of the 16 males surveyed in 1998 remained unmated, another one lost its female probably due to predation. Ten of the remaining 12 were mated monogamously, two males were polygynous. Singing intensity of these 12 males is shown in relation to season, measured in days before and after the monogamous or primary female laid the first egg (Figure 9.5). As mentioned in the Methods, pairing takes place roughly eight days before the start of egg-laying. The last egg was laid 3-6 days after the first. Total singing intensity clearly peaks during the egg-laying period, fitting with the expectations derived from the fertility announcement hypothesis. S-song is used at a constantly high level from mate attraction to the end of egg-laying but hardly thereafter. The intensity of V-song increases during the period of female fertility and remains very high during incubation.

Overall singing intensity in the peak-fertility phase was significantly higher than in the nest-building phase (paired t-test: $T_{11} = 7.1$, $p < 0.0001$) and almost significantly higher than in the post-fertility phase (paired t-test: $T_{11} = 2.2$, $p = 0.051$). Intensity of S-song in the peak-fertility phase tended to be higher than in the nest-building phase (paired t-test: $T_{11} = 2.0$, $p = 0.076$) and was significantly higher than in the post-fertility phase (paired t-test: $T_{11} = 5.7$, $p = 0.0001$).

Intensity of V-song was significantly higher in the peak-fertility phase than in the nest-building phase (paired t-test: $T_{11} = 4.2$, $p = 0.002$) and was even higher, but not significantly, in the post-fertility phase (paired t-test: $T_{11} = 1.0$, $p = 0.35$). The three males that remained unmated showed very similar patterns. Singing intensity (S-song and V-song considered separately) averaged among these three males differed by less than one SD (measuring between-individual variation) from the mean of the 12 mated males for the two first phases. During period 3, however, S-song was more frequent in unmated than in mated males ($T_{13} = 2.4$, $p = 0.034$).

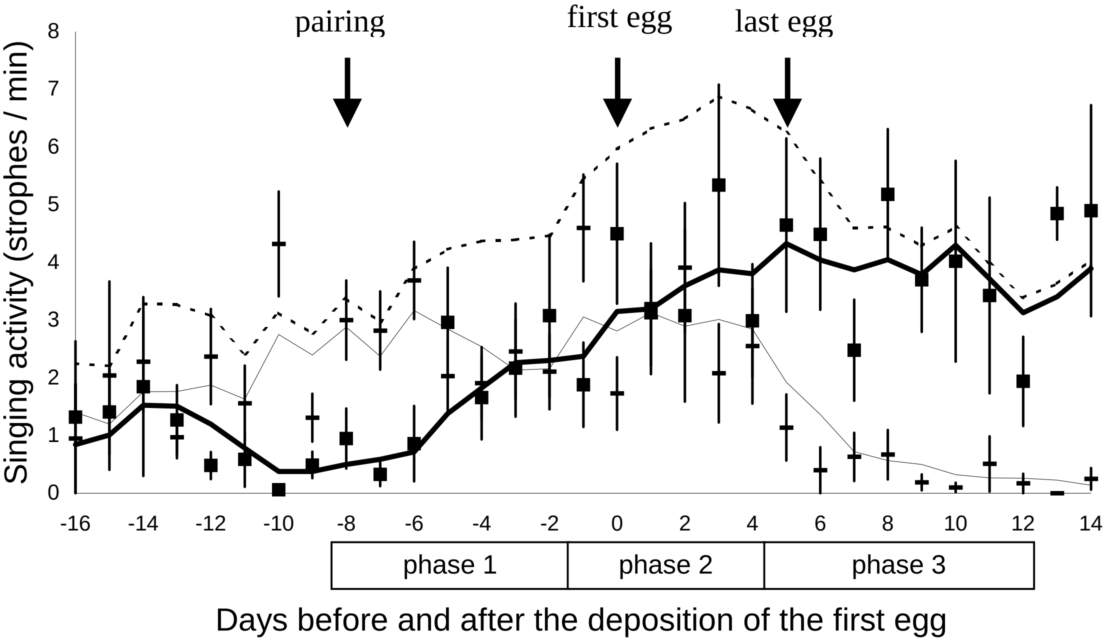


Figure 9.5. Mean song activity (mean ± SE; averaged among 12 males) of V-song (bold squares) and S-song (bars) in relation to the reproductive cycle. Curves show smoothed means (3-day averages) of V-song (bold line), S-song (tiny line) and total song (sum of S-song and V-song; hatched line). The date of the last egg varied between 3-6 days after the first egg (2x3, 3x4, 6x5, 1x6 days), whereas the date of pairing almost invariably occurred 8 days prior to the start of egg-laying. For statistical analyses I use a division into three phases (see text).

During the phase of highest female fertility males spend most of the daytime singing. The 12 males sang during 497 of 620 minutes of observation (80%) between 4:30–10:00h in phase 2. The male shown in Figure 9.2 sang 78% of the 1,029min it was observed, while no single encounter between this male and its female was witnessed during that day. Mate guarding, in the sense of a male following its fertile social female, was hardly ever witnessed in any breeding pair. Conservatively speaking, males spend much less than 10% of the time during the fertile period in close vicinity (<20m) of the female.

Playback experiment

All seven experimental males reacted to playback by approaching and singing V-song, as this is typically observed in aggressive male encounters. Playbacks of S-song of nearest neighbours from the previous season elicited significantly stronger responses than S-song of males having had no prior ownership in this area (paired t-test on $\log_{10}$-transformed distances of closed approach: $T_6 = 6.2$, $p = 0.001$). This result indicates that: (1) Males discriminate between familiar and unfamiliar S-song types from the previous year, supporting the idea that S-song may facilitate individual recognition. (2) The territory establishing male may perceive males with prior territory ownership in the area as a greater threat than other males, because the prior territory owner should have strong intentions to settle in this place.

DISCUSSION

Testing the fertility announcement hypothesis

The present study demonstrates that, in the dusky warbler, singing intensity reaches its seasonal peak when females are fertile. This is remarkable, as males of most other passerine species start to sing less once they are mated (Gil et al. 1999). Therefore, the dusky warbler offers a very good system to study the applicability of the fertility announcement hypothesis (Møller 1991) to species which do sing intensively after pairing. The fertility announcement hypothesis states that males should try to sing as much as they can, because this will increase their attractiveness to females. This idea is based on the assumption that females prefer to copulate with males singing at high rate. However, data on extra-pair paternity (Chapter 10) do not support this assumption. The paternity analysis showed that: (1) Nearly half of the offspring were sired by males from nearby territories. (2) Females consistently preferred males with high-quality V-songs as copulation partners. (3) The measure of V-song quality that was strongly correlated with paternity patterns, was unrelated to song rate (Pearson correlation: $r = -0.31$, $n = 15$, $p = 0.27$). As song rate *per se* was not under sexual selection, the fertility announcement hypothesis does not apply to this system.

If females do not prefer males with a high song rate, why should males then sing intensively during female fertility? I suggest that males display their V-song during that period because females base their choice of copulation partners on the quality (not quantity) of that song type. I argue that there is no need to invoke intersexual selection on song rate – female preference for song quality might be sufficient – in order to obtain a peak of singing activity when females are fertile.

Functions of the two song types

Deeper insights into song functions can be gained by looking at the two song types separately. Studies of song-type functions in other passerine species (Catchpole 1980, 1982, Slater 1981, Groschupf 1985, Fessel and Hoi 1996) led us to the hypothesis that the S-song might be used as a territorial signal, while the much more complex V-song might signal male quality towards females.

The first part of this hypothesis is supported by the following findings: (1) As predicted, S-song was used at high intensity when a male's social partner was fertile, the period when it is most crucial to keep out intruding males. (2) S-song is used while the male is patrolling through the territory area. Periods with much S-song are therefore the periods of high patrolling activity and male intruders are best discovered when patrolling. Observations of male intrusions suggest that these may lead to secretive extra-pair copulations. Increased territorial defence by males during female fertility was also found in European robins, *Erithacus rubecula* (Tobias & Seddon 2000). (3) The individuality of S-song strengthens the idea that this song type serves to mark the claimed area by using a kind of individual signature.

Our results also support the idea that V-song may advertise male quality: (1) Males use V-song most intensively when their own female is fertile and also after this period, when neighbouring females are still laying eggs (late females, secondary females and females making replacement clutches). (2) V-song is presented only from a certain group of bushes, the interior of which provides maximal protection from view by others. My observations strongly suggest that females visit males at these song perches and that extra-pair copulations happen inside of these bushes. Although such visits appeared to occur quite regularly (judging from male behaviour), the density of bush vegetation hindered me from witnessing even a single extra-pair copulation. As social males provide substantial parental care, one should expect extra-pair copulations to happen secretively. Alternatively, the selection of V-song perches may be interpreted as an anti-predator behaviour, but I found no behavioural differences between areas with frequent and very infrequent predator encounters (Figure 9.3). (3) Paternity analysis strongly suggests that females choose copulation partners based on the quality of their V-songs (Chapter 10).

Two findings on song-type use may appear counterintuitive: the use of S-song for attraction of females for social pairing (Figure 9.4) and the use of V-song in aggressive male-male interactions. I suggest that the two song types do not primarily differ in whom they address, they differ in their function. S-song marks a territorial area, while V-song reflects male singing abilities. The importance of these messages may differ between male and female receivers and this should also vary throughout the season.

The fact that males are capable of discriminating between familiar and unfamiliar S-song, as shown by the playback experiment, renders it very likely that females may also be able to individually recognise males that they know from the previous breeding season. Even juvenile females potentially have the possibility to look for future social partners in late summer and early autumn when adult males are still defending territories using both, S-song and V-song. It might be hypothesised that females prefer to mate generally with older males, or specifically with certain males of known identity and quality. Although very few studies have actually shown the existence of such long-term memory (e.g. Godard 1991), there are no indications why individual recognition should not be a common phenomenon (Falls 1992).

The fact that males switch from S-song to V-song when they have aggressive encounters is best understood as signalling arousal. Similar phenomena, such as switching to another song type, increasing the rate of switching between song types or singing more variable songs have been described for many other species (Lemon 1968, Dixon 1969, Schroeder & Wiley 1983, Lemon et al. 1987, Staicer 1989, Spector 1991, Luschi and Seppia 1996).

Assuming that females judge male quality by V-songs, what is the significance of large repertoires and syllable-type sharing between neighbours? In the dusky warbler males typically engage in countersinging. Some incidental recordings of countersinging males indicate that syllable-type matching does occur quite regularly. Moreover, the finding that syllable-type sharing is highest between nearest neighbours and even increases with duration of acquaintance (see McGregor & Krebs 1989, Mountjoy & Lemon 1995), suggests an important role of matching. Recent studies indicate that syllable-type matching correlates with aggressiveness of male-male interactions (Beecher et al. 2000) and other studies suggest that females may assess potential extra-pair males by eavesdropping on male-male interactions (Otter et al. 1999). I hypothesise that males compete with each other about the quality of their songs (whatever the criterion for quality is; see Chapter 10) and continuous learning from neighbours is part of this competitive interaction. Such competition would be most intense if females could judge male quality only from direct comparison between males (i.e. when these match their syllable types). By introducing new variation (e.g. syllable type switches within strophes or new syllable types) birds may try to escape from being matched or challenge their neighbours with something they cannot match.

Are there any likely alternative interpretations of the functions of song-type use after pairing? Rodrigues (1996b) studied song in the closely related chiffchaff (*Phylloscopus collybita*) and found a temporal pattern of singing intensity resembling that of the V-song shown in Figure 9.5. Song rates during female fertility were roughly twice those around pairing and became higher still in the post-fertile period. Applying my conclusions to the case of the chiffchaff would mean that males probably advertise their quality to attract females for copulations. However, Rodrigues interpreted the late singing in the chiffchaff as territorial defence and as attracting a new female in anticipation of possible nest predation. I can argue that this at least does not apply to the dusky warbler. The risk to lose a territory is relatively high early in the season as long as new males arrive to the breeding area, but loss of territory never occurred during the breeding period. Similarly the chance of attracting a female strongly declines as soon as there are no more new females arriving. The intensity of song related to these two functions should therefore decline rather than increase over the course of the season.

The lack of mate guarding

Comparing the dusky warbler to congeneric species and other passerines, it is not only very astonishing that paired males sing so much, but also that they do not guard their fertile females. In the well studied European *Phylloscopus* species, males prefer mate guarding over singing in order to maximise their reproductive successes (Arvidsson 1992, Rodrigues 1998, Gil et al. 1999). The fact that all dusky warbler males, irrespective of their individual V-song quality, do not guard their mates, demands a general explanation. There is one striking difference between the dusky warbler and its European counterparts that might hypothetically explain this phenomenon. In my study area, dusky warblers suffer heavily from brood parasitism by the oriental cuckoo (*Cuculus saturatus horsfieldi*). Eight out of 40 nests (20%) found prior to the deposition of the first egg were parasitised by cuckoos. Half of these nests were deserted and in the other four cases the cuckoo egg was accepted. In contrast, European cuckoos (*Cuculus canorus*) hardly ever parasitise on European *Phylloscopus* warblers (Glue & Morgan 1972), and this is probably because these show a very strong and successful rejection behaviour (Moksnes & Röskaft 1992). As the presence of conspicuously behaving males near the nest increases the risk of parasitism (Banks & Martin 2001), I suggest that male dusky warblers avoid parasitism by not accompanying their nest-building females. Other studies suggest that mate guarding is not very efficient in reducing cuckoldry by conspecifics (Kempenaers et al. 1995), and a slight increase in the risk of cuckoldry by heterospecifics may render this behaviour maladaptive. The fact that dusky warbler males guard their territories instead of their mates is unusual, but certainly not unique. Robins (*Erithacus rubecula)* guard their mates not very intensively, but increase their territorial aggressiveness when females are fertile (Tobias and Seddon 2000). Other studies have described such variation in paternity defence strategies in relation to group composition (Langmore 1996) or to the overall operational sex ratio (Currie et al. 1998).

Conclusions

When pairing occurs male singing intensity declines in most passerine species (Gil et al. 1999). Territorial defence can be maintained with little song and paternity can be ensured through mate guarding by following and/or frequent copulation (Birkhead & Møller 1992). However, in some species, such as the dusky warbler, song has achieved the function of a paternity guard. The high risk of parasitism by cuckoos may have contributed to the fact that males guard their territories instead of their fertile females. S-song is used during guarding the territory against male intruders and V-song advertises male quality towards females. Obviously, males can simultaneously advertise for both within-pair and extra-pair copulations. This system may originate from the fact that females select copulation partners on the basis of V-song quality.

I agree with Møller (1991) that song can function as a paternity guard. Theoretically this is most easily explained if there is a direct female preference for males singing at high rate (the basic mechanism underlying the fertility announcement hypothesis). However, in the dusky warbler, reality does not match this theoretical explanation. As there is no female preference for males singing at high rate, I have to conclude that a female preference for high song quality can be sufficient to let mated males sing so much.

10. Singing performance correlates with paternity

Song is one of the most conspicuous aspects of bird behaviour (Catchpole & Slater 1995). Since Darwin (1881) it has been assumed that song is a sexually selected trait which can be seen as the acoustic analogue of the peacock's tail (Catchpole & Slater 1995, Searcy & Yasukawa 1996, Hasselquist et al. 1996). Females often prefer males singing at a high rate or with larger repertoires (Catchpole & Slater 1995, Searcy & Yasukawa 1996, Hasselquist et al. 1996, Buchanan & Catchpole 2000). As these traits are typically correlated with territory quality, females profit directly from this choice (Searcy & Yasukawa 1996), but evidence that they also obtain genetic benefits is very limited (Searcy & Yasukawa 1996, Hasselquist et al. 1996). Recent studies on physiological limitations of sound production (Lambrechts 1996, Suthers & Goller 1997, Podos 1996, 1997, 2001) suggest that more subtle differences in the way males sing might reflect their quality (Suthers & Goller 1997, Vallet et al. 1998, Lambrechts & Dhondt 1986). Here I show that such a measure of singing performance of male dusky warblers *Phylloscopus fuscatus* determines their success in obtaining extra-pair paternity. Paternity assignment reveals that 45% of the offspring were sired by neighbouring males. Males maintaining a high sound amplitude within strophes were consistently preferred as extra-pair fathers. This song parameter correlates with male longevity, but not with any other male or territory trait, indicating that females may obtain 'good genes' for their offspring by choosing high quality singers. The presented data also suggest that attractive males invest less in competition over territories as they can reproduce via extra-pair paternity.

RESULTS AND DISCUSSION

The dusky warbler is a single-brooded, long-distance migrant passerine with a cryptic, sexually monomorphic plumage lacking any obvious sexual ornaments. I studied a population of individually colour-ringed birds breeding near Magadan, Russian Far-East (59° 51' N 154° 14' E), from 1997 to 1999. This population shows a variable mating system with 11% of males unmated, 70% monogamous, 17% polygynous and one case of polyandry (n = 95 males). A female's social partner can unambiguously be defined as the owner of the territory where she builds the nest. In contrast to the majority of passerines (Birkhead & Møller 1992), male dusky warblers do not guard their fertile female, but spend most of the daytime singing. And interestingly, males sing at the highest rate when their social partner is fertile (Chapter 9), which is consistent with the hypothesis that males sing to ensure within-pair paternity and to gain extra-pair paternity (Møller 1991, Gil et al. 1999). Cuckoldry was unusually frequent (Petrie & Kempenaers 1998): extra-pair males sired 45% of 195 nestlings in 27 out of 46 broods (59%, data from 1998-1999, see Appendix). I found the genetic fathers of 82% of the extra-pair young. Twenty-seven out of 31 identified fathers (87%) were among the five nearest neighbours. Hence, this species offers an excellent opportunity to test whether female choice for extra-pair copulation partners depends on differences in male singing abilities.

The variable song type of male dusky warblers consists of on average 27 different syllable types per 60 strophes (range: 10-40; n = 32 males). Neighbouring males share a significantly higher proportion of syllable types than expected by chance (35% vs. 15%; calculated following McGregor & Krebs (1982); paired t-test, $T_{12} = 4.0$, $p = 0.002$), suggesting that males continuously learn new elements by copying other males (Chapter 9). As found in many other species (Catchpole & Slater 1995), counter-singing males often match their syllable types. Thus, males may compete with each other over (1) how many syllable types they can sing (repertoire size), (2) how fast they can repeat them within strophes (syllable rate, see Appendix), or (3) how well they can sing a given syllable type, and females may judge males by listening to these contests ('eavesdropping'; Otter et al. 1999). I assess the quality of singing by measuring the percentage of time within strophes during which sound amplitude exceeds a threshold level ('percentage peak performance', see Appendix; in short 'performance'). This reveals a male's ability to maintain a high sound amplitude during rapid frequency modulations and to sing with short pauses between syllables (Figure 10.1).

Note that this measure reflects subtle differences in sound production, but has nothing to do with song rate (i.e. the number of strophes sung per unit of time). To compare males, I use residuals from the population mean (see Figure 10.1 and Appendix).

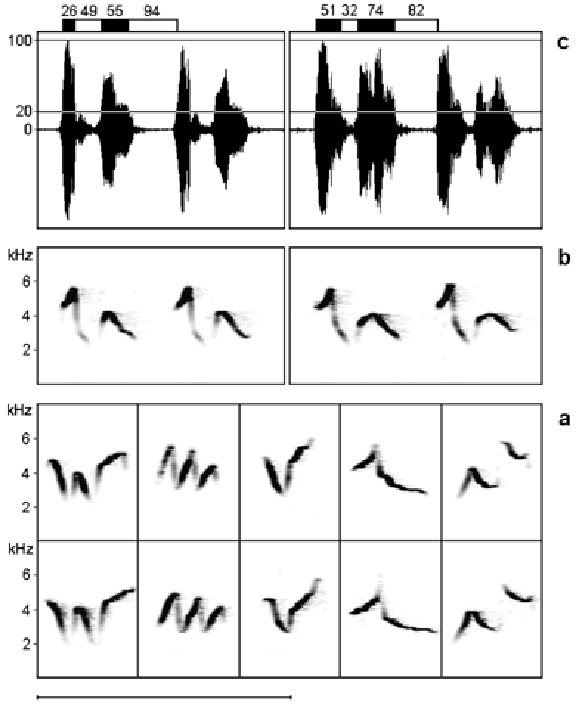


Figure 10.1. Measuring singing performance. (a) Spectrograms (frequency over time; scale bar, 0.5 s) showing examples of five different syllable types (syllables taken out of the strophes) sung by two neighbouring males (top vs. bottom). Note the diversity of syllable types and the precision of syllable-type matching. (b) Spectrograms showing the same syllable type sung by two males differing in performance. (c) Corresponding oscillograms (amplitude over time) showing how to measure 'percentage peak performance'. I measured the time when the amplitude exceeds a threshold value of 20% of the maximum value. The bars and numbers on top of the figure indicate the time intervals (in milliseconds) when song above (filled) or below (open) the threshold value is produced. The male on the left reaches peak performance during 36% of the time, the male on the right during 52%. From these measurements, 'population performance' would be calculated as 44% (average among all males), and 'residual performances' as –8% and +8%, respectively.

To test whether females preferred particular males as extra-pair fathers, I compared song characteristics of the social partner with those of the extra-pair fathers within broods (i.e. pair-wise comparisons, data on song and paternity available for n = 7 broods). Extra-pair males did not differ from cuckolded males in repertoire size (paired T_6 = -0.4, p = 0.68), nor in residual syllable rate (T_6 = 0.4, p = 0.70), but they produced song of significantly higher residual performance (T_6 = 4.2, p = 0.006; the effect remains significant after Bonferroni correction).

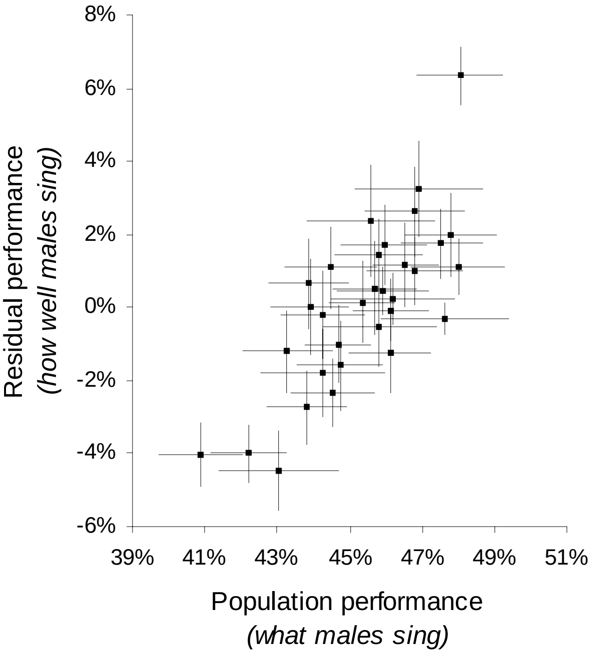


Figure 10.2. Residual performance (mean ± SE) versus population performance (mean ± SE) for 32 males. Residual performance reflects how much individual males deviate from the population mean in the percentage peak performance of a given syllable type (averaged over all types), and thus indicates how well males sing relative to others. Population performance reflects which syllable types males include in their repertoire, and thus indicates what males sing. Individuals with high scores selected those syllable types that have an inherently higher performance (population-wide means). The graph shows that males singing high performance syllable types also sing those types with a higher performance relative to other males. Note that total performance of individual males can be calculated as population performance plus residual performance.

As I found a female preference for males producing song with a higher residual performance (a measure of how well males perform relative to others), I wondered whether the use of different syllable types (i.e. what males sing) also reflected male quality. This question arises because different syllable types vary greatly in performance at the population level (average ‘population performance’ ranging from 21.4% to 62.0%; see Appendix). By averaging the ‘population performance’ of all syllable types included in a male’s repertoire, I can quantify the degree to which a given male uses syllable types of inherently high or low performance. The residual performance of 32 males was strongly positively correlated with this measure of syllable use (Figure 10.2; reduced major axis regression, $r^2 = 0.594$, $n = 32$, $p < 0.0001$). This means that males singing high performance syllable types, also sing those types with a higher performance relative to other males.

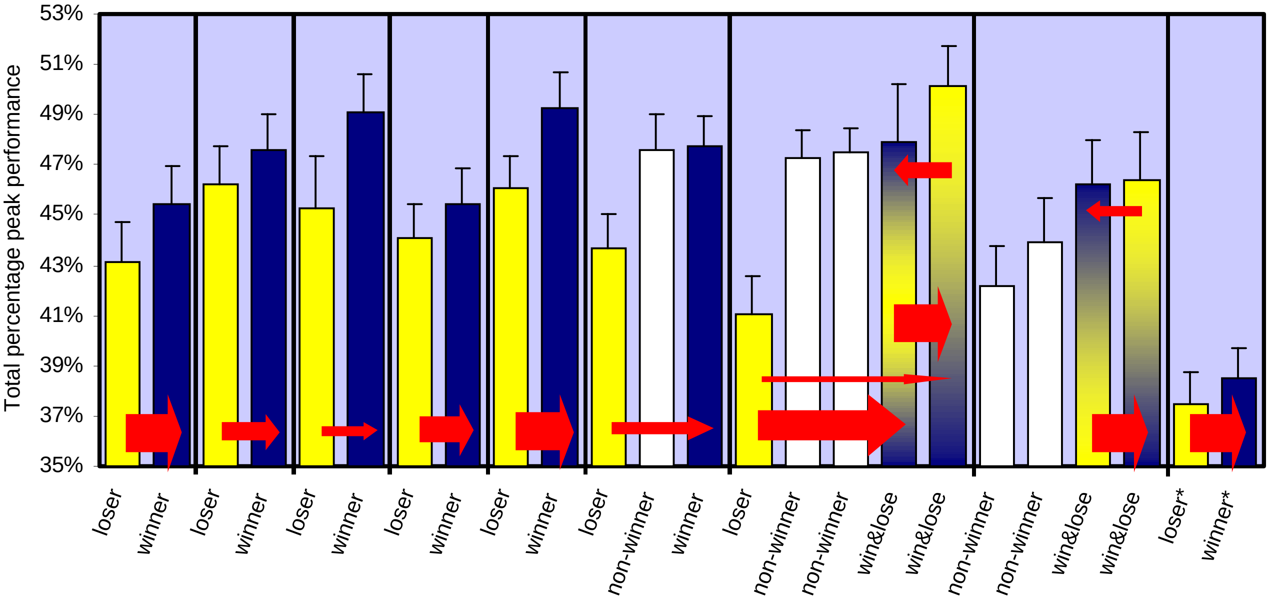


Figure 10.3. Within-brood comparisons of the singing performance of losers and winners of paternity. I compared males that lost paternity in their own nest (‘loser’) with the extra-pair males that fathered offspring in these nests (‘winner’). Males that did not gain any paternity in those nests despite singing closer to the nest than the ‘winner’ are referred to as ‘non-winner’. In two cases males exchanged paternity reciprocally (both called ‘win&lose’). In all cases ‘winners’ produced song of a higher percentage peak performance compared to both ‘losers’ and ‘non-winners’. The width of arrows reflects the percentage of nestlings lost (range: 17% to 100%). The last case (*) does not represent extra-pair paternity, but a case where two males were mated socially to the same female (polyandry) and both males were feeding at the nest. In all other cases, extra-pair fathers never helped at the nest.

I then ranked males according to their total performance (= residual performance + population performance; Figure 10.2). If females prefer higher ranked males as fathers of their offspring, I predict that (1) extra-pair fathers should rank higher than the male they cuckolded, (2) extra-pair fathers should rank higher than all other available males (i.e. males breeding nearer to the female), (3) if two males reciprocally exchange paternity, then the male fathering most offspring should be higher ranked, and (4) in the one polyandrous case, the male fathering most offspring should be higher ranked. All 16 comparisons that could be made were in the predicted direction (multinomial test, $n = 9$, $p = 0.00002$, Figure 10.3). When I use each of the two variables ‘residual performance’ and ‘population performance’ separately to rank males, in both cases 15 out of 16 comparisons were in the predicted direction ($p = 0.0008$). Thus, what males sing (syllable types) and how well they sing (residual performance) can explain paternity patterns equally well. I found that nine out of ten males that did not lose paternity in their own nest (including five males shown in Figure 10.3) had a total performance above the overall population mean (binomial test, $p = 0.011$).

The parameter ‘total performance’ was not correlated with any other male trait (Table 10.1). There was only a non-significant tendency for older males to sing with a higher performance than first-year males. Singing performance was also unrelated to parameters reflecting territory quality (food abundance) and social pairing success (mating status, pairing date; Table 10.1). To date there is very limited support for the idea that female preferences evolved through underlying genetic rather than direct benefits (Searcy & Yasukawa 1996). To my knowledge this is the first study reporting a female preference for a song trait that is fully unrelated to direct benefits.

Table 10.1. Relationships between singing performance and other male and territory characteristics.

Trait	n	Statistics	p
Repertoire size	32	r = - 0.24	0.18
Song rate	15	r = - 0.28	0.32
Mating status*	39	t = - 0.16	0.87
Male age⁺	46	t = - 1.59	0.12
Arrival date	37	r = - 0.26	0.13
Pairing date	36	r = - 0.06	0.72
Paternal care	30	r = 0.27	0.15
Wing length	44	r = 0.07	0.65
Tail length	43	r = - 0.07	0.66
Tarsus length	46	r = - 0.19	0.20
Body mass	45	r = - 0.07	0.65
Food abundance	46	r = - 0.10	0.49

* monogamous (n = 31) vs. polygynous (n = 8)
⁺ first-year (n = 17) vs. older (n = 29)

To investigate whether females obtained indirect benefits from extra-pair copulations with ‘better’ singing males (good-genes hypothesis), I would have liked to compare the survival of within- and extra-pair offspring. However, given that the great majority of surviving young settles far from the natal area, these data are hard to obtain. Instead, I analyse the probability of adult male winter survival in relation to singing performance. Adult males show strong site tenacity and often defend territories during late summer, before departure to the winter-quarters. They thus seem to pre-occupy territories in anticipation of the next breeding season. From 18 males defending territories in late summer 1997 or 1998, eight (44%) returned to exactly the same territory in the following breeding season. Total singing performance was positively correlated with the probability of winter survival (logistic regression, $Chi^2 = 5.2$, $p = 0.022$) and no other parameter explained the observed patterns of survival. This strongly suggests that females obtain viability genes for their offspring by copulating with good singers (Hasselquist et al. 1996, Kempenaers et al. 1992, 1997).

Given the high rate of extra-pair paternity in this species and the importance of singing performance, one could expect males to follow different mating strategies depending on their singing ability (Kempenaers et al. 2001). I observed nine long-lasting fights (minimum 2 hours) between males over the possession of a territory where a female had just settled. In all nine cases, the winners of these fights sang with a lower total performance compared to the losers (paired t-test, $T_8 = -3.8$, $p = 0.005$). Eight ‘losers’ settled in a neighbouring territory and five of them remained unmated. However, I had paternity data for three nests of ‘winners’ and found that the nearby ‘loser’ had fathered 20%, 100% and 100% of the offspring, respectively. Thus, males with good singing ability might invest less in territorial fights, because they can reproduce via extra-pair paternity.

This field study may stimulate new directions of research on acoustic communication as it is the first to indicate that females may listen to (1) *what* males sing (syllable types differing in ‘performance’), and (2) *how* males sing (performance relative to other males). It therefore supports the idea of ‘sexy syllables’ (Vallet et al. 1998) and suggests that physiological limitations may reinforce the honesty of signals (Lambrechts 1996, Suthers & Goller 1997, Lambrechts & Dhondt 1986). Males may sing close to a limit set by respiratory or phonetic motor constraints, which could render signals uncheatable (Lambrechts 1996, Suthers & Goller 1997, Vallet et al. 1998). The presented findings suggest that the speed at which the air sacs can be refilled by taking ‘minibreaths’ (Suthers & Goller 1997) between syllables may be limited and that it may be difficult to maintain a high amplitude over the course of the most rapid frequency modulations (Figure 10.1). Since the vast majority of passerines sing series of notes interrupted by short pauses, the presented measure of singing performance can be studied in almost any other songbird species.

APPENDIX: METHODOLOGICAL DETAILS

Morphology and food availability

Males were captured in mist nets, colour-banded, blood-sampled and the following morphological measurements were taken: wing length, wing formula, tail length, tarsus length and body mass. Male age was determined as first year or older partly based on ringing data, partly on a discriminant analysis using morphological characteristics (tail length, wing length and wing shape). The latter analysis correctly classified 91% of 65 males of known age (Figure 7.1). Food availability on territories and male contribution to feeding the offspring (corrected for hatching date) was measured as described in Chapter 5.

Paternity analysis

In 1998 and 1999 I studied paternity using the microsatellite markers Phtr1, Phtr2, Phtr3 (Fridolfsson et al. 1997), Pocc5 (Bensch et al. 1997), FhU2 (Primmer et al. 1996), HrU7 (Primmer et al. 1995) and Gf05 (Petren 1998). DNA was extracted from blood samples using the QIAamp Blood Kit. PCR's were done with fluorescence-labelled primers (otherwise following Bensch et al. 1997), and products were scored on an ABI 377 sequencer. The seven markers allowed to assign offspring to potential fathers with an average error probability (Kempenaers et al. 1999) of $p = 0.016$ (range: 0.00002-0.117, n = 195, 17 cases with $p > 0.05$). For the data used in Figure 10.3 this average probability was $p = 0.008$ (range: 0.00002-0.095, n = 49, one case with $p > 0.04$, the latter was assigned to the same father as its nest sib). Phtr3 and Pocc5 are located on the Z-chromosome (Phtr3: 76% of 174 males, but 0% of 135 females were heterozygote; Pocc5: 54% of males and 0% of females heterozygote; birds were sexed genetically following Griffith et al. 1998). For HrU7 the observed rate of heterozygosity (60.2%, n = 93 adults) was significantly lower than expected under Hardy-Weinberg equilibrium (72.6%; binomial exact test: $p = 0.0033$). Moreover, 12 of 195 nestlings (from 6 nests) were lacking the paternal allele of the (seemingly homozygote) social father (n = 3 males involved). The remaining 6 microsatellite loci confirmed that these nestlings were sired by the social fathers (mean error probability: $p = 0.008$; range: 0.0004-0.027). I therefore conclude that approximately 12% of the individuals must have carried a null-allele for HrU7. No other locus showed such patterns. For 99 nestlings (53 sons, 46 daughters) from 24 nests, DNA-samples of the social mother (19 different females) were available, allowing 601 mother-child comparisons (99x5 loci plus 53x2 loci). There were no mismatches in this sample, suggesting that mutations were very rare. After allowing for the presence of null-alleles at HrU7, 88 of 195 nestlings showed at least one mismatch (9x1, 22x2, 29x3, 21x4, 6x5, 1x6 mismatches) with the social father. These were considered extra-pair young. I identified the genetic fathers of 74% and 100% of the extra-pair young from 1998 and 1999, respectively. In 1998 I failed to collect blood samples from 26% of breeding males (n = 58).

Song recording and analysis

Singing males were recorded using a Nagra SN recorder and a Sennheiser MKH815T directional microphone in 1997, a Sony TCM-459V recorder and a Shure Prologue 16AM microphone in 1998, a Sony TC-D5 PROII recorder and a Sennheiser K6M67 microphone in 1999. I could not detect any influence of recording equipment on the parameters measured here. Moreover, all comparisons presented here are made within years (with the same equipment), and results were consistent among the years. Recordings were analysed with Avisoft SASLab Pro 3.4 using the following settings: sampling frequency 22,050 Hz, 16 bit, time resolution 5.8 ms, bandwidth 111 Hz. To remove background noise, all recordings were filtered using the FIR high-pass filter in Avisoft (corner frequency: 1.5 kHz) prior to analysis. I categorised syllable-types by visual inspection of printed spectrograms (see Figures 9.1 and 10.1). The dusky warbler has two distinct song types, a stereotype territorial song and a variable advertising song. My analysis is restricted to the latter because this song is used most during the period when females are fertile (Chapter 9). This song type is structured in discrete strophes of 1-2 seconds, separated by pauses of ca. 5 seconds. A strophe consists of identically repeated syllables (mean ± SD = 5.9 ± 2.0 syllables, n = 2920), but often includes a switch of syllable type (mean 0.5 switches, range 0-4, n = 2920). I recorded 60 strophes of each of 46 males during the egg-laying period. For a subset of 32 males where I had paternity data I classified all syllables into 205 types. I define repertoire size as the number of different syllable types sung by each male (mean: 27, range: 10-40). For each syllable type, I calculated syllable rate within strophes as the number of syllables sung per second and the percentage peak performance as the proportion of time where the sound amplitude exceeded 20% of the maximum value for that strophe (Figure 10.1). To measure the length of the time intervals, I used the automatic gate function (signal/silence duration) tool of the Avisoft software (settings: threshold 20%, delay 1 ms, time constant 1 ms). The threshold of 20% was chosen arbitrarily to avoid interference by background noise. For each male multiple measures of the same syllable type were averaged (using all 60 strophes). For each syllable type a population mean of ‘syllable rate’ and ‘percentage peak performance’ was calculated by averaging among male means (range: 2.5-9.8 syllables/s and 21.4-62.0%; n = 205). To compare males, I used residual ‘syllable rate’ and residual ‘percentage peak performance’ calculated for each syllable type as the deviation from the population mean and then averaged over all syllable types (range: -0.45 to +0.38 syllables/s and -4.5% to +6.3%; n = 32 males). Variation in recording date, vegetation density and distance from the microphone did not obviously bias my estimates. Note that the parameter ‘population performance’ is independent of such potentially confounding factors. In 1998 song rate was measured by counting once per day (between 4:30-10:00 am) the number of songs sung by each of 15 males within a 10 min interval (for details see Chapter 9).

11. Discussion

11.1. The female perspective

Individual reproductive tactics and strategies

Before looking at individual reproductive strategies, it is necessary to summarise which factors influence the reproductive success of females. As reliable estimates of reproductive success would require a huge data set which is not available (even not for much better studied species; see Searcy & Yasukawa 1995), the outlined patterns have to remain somewhat hypothetical. Life-time reproductive success can be split into three components: seasonal reproductive success, female over-winter survival, and offspring viability (see Figure 11.1).

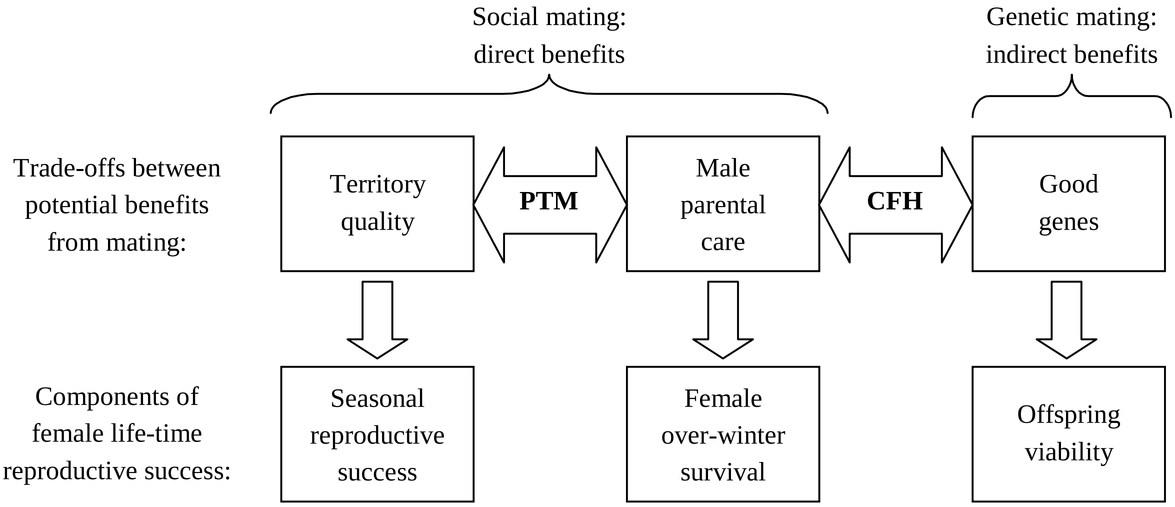


Figure 11.1. Main factors influencing female life-time reproductive success and trade-offs between these factors. For late arriving females there is typically a trade-off between male parental care and territory quality, as described by the polygyny-threshold model (PTM). The constrained-female hypothesis (CFH) describes the trade-off between unconstrained genetic mating (extra-pair fertilisation) and the need for assistance in brood care by the social partner.

The figure illustrates, in a simplified manner, how these components of reproductive success are influenced by the different types of benefits that females have to trade against each other when making their mating decisions (see Introduction). Seasonal reproductive success was predominantly affected by territory quality. Females breeding on polygynous territories fledged 50% more young per season as compared with monogamous females (Table 4.3). To some extent this was due to lower predator densities on polygynous territories (as was found in other polygynous warblers, Temrin & Jakobsson 1988, Bell 1997, Hansson et al. 2000), but mostly this resulted from a higher re-nesting frequency after predation. Re-laying may have been induced by high territory quality (e.g. food availability) but more likely was attributable to intrinsic female characteristics. Females that replaced clutches after nest predation almost never received any male assistance in brood care, as males were ‘busy’ with their postnuptial moult (Figure 6.2). Re-nesting females, however, suffered from greatly increased winter mortality, probably because they were unable to finish their postnuptial moult. Thus the data suggest that the influence of male parental care on female over-winter survival (Figure 11.1) is indirect rather than causal. In fact, it appears as if females that were not prepared to forgo male help, did not replace lost clutches and consequently they had better chances to survive the winter. It is plausible that territory quality also had some positive effect on female over-winter survival, and that male parental care also positively influenced seasonal reproductive success.

However, this is not indicated in Figure 11.1, because the actually observed correlation was in the opposite direction. In fact, females that bred on high-quality territories had low over-winter survival (because they tried to maximise their within-season success), while females that received male help had lower seasonal success (as most of them were not ready to replace lost clutches).

The third component of female reproductive success, namely offspring viability, is almost impossible to measure directly for the dusky warbler (see Chapter 3: 'site tenacity'). A meta-analysis including 22 studies (Møller & Alatalo 1999) found that offspring viability was positively correlated with the degree of sexual ornamentation of the genetic father, which supports the 'good genes' hypothesis (see also Jennions & Petrie 2000). Female dusky warblers preferred males with better singing performance as copulation partners, and singing performance was positively correlated with adult male over-winter survival (Chapter 10). Thus it is very tempting to conclude that females preferred good singers to increase the viability of their progeny. Again, other factors besides 'good genes' may have contributed to offspring viability, but there were no or only little indications that male assistance or food availability correlated with nestling body condition (a possible correlate of viability; see e.g. Lindén et al. 1992).

Even though it is partly speculative which factors contribute how much to each component of female fitness, there is no doubt that all three factors (territory quality, paternal care and good genes) are beneficial to females, and that the majority of females is unlikely to find a partner who will maximise all of these potential benefits. In other words, there are trade-offs. The female that is the first to arrive at breeding grounds will most likely succeed in finding an attractive, unmated partner on a high-quality territory, but the later a female arrives, the stronger the trade-offs get. This situation is described by the classical 'polygyny-threshold model' (PTM; Verner 1964, Orians 1969). A late arriving female has to decide which of the two potential direct benefits of mate choice she wants to take. Because males in high-quality territories most likely will be already mated, she can either mate monogamously (i.e. a helping male) on low-quality habitat, or polygynously (i.e. a non-helping male) on a high-quality territory. If a female decides to take the latter option, she has already solved the second trade-off which is described by the 'constrained-female hypothesis' (CFH; Gowaty 1996). A female, who's social partner will not provide brood care anyway, is 'unconstrained' in her choice of copulation partners. She may have extra-pair copulations with the male of highest genetic quality, without running the risk of losing her partner's assistance. Thus the pivotal question is how much help a female needs for raising her brood. Other behaviours may be interpreted as resulting from this decision (Table 11.1).

Table 11.1. Alternative female mating behaviours

Dependence on male help:	**'emancipated'**	**'help-dependent'**
Social pairing strategy:	- take the best territory	- find an unmated male, other things being as good as possible
Site tenacity:	- few reasons to change territory between years	- necessity to move if the former male is already paired
Polygyny:	- mate as a secondary female if the territory owner is already paired	- avoid partners that are already paired
Clutch replacement:	- replace clutch after predation	- do not replace, because the male will not help with late broods
Extra-pair paternity:	- unconstrained genetic mating	- constrained by the risk to lose male assistance

A female that is able to raise her brood without male assistance may primarily search for the optimal place for nesting when she arrives at the breeding grounds. If the owner of her favourite territory is already mated, she is not bound to search for an unmated partner as she can also pair as a secondary female. For genetic mating, such a female is free to mate with the most attractive male in the area (eight out of nine secondary females had extra-pair fertilisations; the one that did not have extra-pair young was paired to the second best singer out of 46 males analysed). In contrast, a female that is dependent on male assistance is forced to search for the best unmated male that is available at the time when she arrives. This means that she will most probably end up in a territory of lower quality than the 'emancipated' female. The need to search for an unmated male will result in lower breeding site tenacity as compared to independent females. Lost clutches cannot be replaced, as males do not provide care for nests late in the season (Figure 6.2). Finally, such a female will be more constrained in her choice of the most attractive copulation partner, as extra-pair copulations may induce the social partner to withdraw paternal care.

Two female characteristics were correlated with the degree of emancipation from dependence on the male. Late arriving first-year females preferred to mate monogamously, while simultaneously arriving older females more frequently mated as secondary females (Chapter 4). It may be argued that females with prior breeding experience may more easily raise a brood unassisted, thus the cost of polygyny may be lower to older females. In addition, the potential benefits that arise from having a free choice between territories may be larger for experienced females that have information about breeding success in previous years (Boulinier & Danchin 1997). Thus mating as a secondary female may be a conditional strategy, where the ability to care for the brood and the knowledge about territory qualities decide about which tactic is the best to apply.

The second female characteristic correlated with emancipation was the depth of the female's bill, a morphological trait that is expected to be highly heritable (Chapter 5). Deep-billed females settled in territories with more food, received less male assistance, mated as a secondary female more often, replaced lost clutches more often, had a higher chance to have extra-pair young, and showed significantly higher breeding-site tenacity between years as compared to shallow-billed females (results, partly shown in Chapters 4, 5 and 6, are summarised in Table 11.2). This is interpreted as reflecting a morphological adaptation to capture arthropods under conditions of uni-parental (vs. bi-parental) brood care. The same pattern is observed in a between-species comparison (Leisler & Catchpole 1992). Species with uni-parental care have deep bills, catch large prey items and breed in habitats with high food abundance, while species with bi-parental care have shallow bills, catch small prey and occupy rather unproductive habitats (see Chapter 5).

The presumed heritability of bill morphology (see Chapter 5) implies that there is genetic variation underlying these alternative reproductive behaviours. This means that both, the deep-billed genotype that most often applies the 'emancipated' tactic and the shallow-billed genotype that typically applies the 'help-dependent' tactic, must have equal reproductive success. More probably, as judging from the Gaussian distribution of bill-depth phenotypes (Figure 5.1), the underlying genetic variation is almost continuous. Thus strategies may vary continuously, with most individuals being of an intermediate type. Although these intermediate types may be not optimally adapted for either of these tactics, they may profit from having a greater flexibility, i.e. tactics may be applied in dependence on age (see above).

I agree with Dominey (1984) that probably the vast majority of alternative mating tactics is due neither to a simple genetic polymorphism of alternative strategies, nor to a single conditional strategy with genetic 'equipotence' of all individuals. This dichotomy between purely genetic and purely conditional determination, as outlined in Gross's review on alternative mating strategies (Gross 1996), is an artificial simplification. There are only a few examples where genetic control over alternative mating strategies is predominating (e.g. Shuster & Wade 1991, Ryan et al. 1992, Lank et al. 1995). In the vast majority of cases, the influences of environment and ontogeny are so dominant (Caro & Bateson 1986), that genetic uniformity has been invoked (Gross 1996). However, the present findings (like those of Cade 1981, Cade & Wyatt 1984) empirically support the statement of Dominey (1984) that largely condition-dependent expression of alternative mating tactics must not be equated with genetic uniformity. There may be almost continuous genetic variation of strategies with respect to 'switch points' between alternative tactics. Two females, of same condition, but differing in heritable components of bill morphology, may switch from monogamy to polygyny at different points in the polygyny-threshold model.

Another interesting aspect of this behavioural variation is how the correlation between female bill morphology and mating behaviour is brought about. Principally, there are two possibilities. (1) Deep-billed females may learn to prefer rich habitats, while shallow-billed females may do this only to a minor extent as they might be less well adapted to the kind of prey that is available there. Other behavioural differences may then follow from the different situations that the females encounter in their habitats. This explanation is unlikely as bill depth shows independent correlations with several behavioural components listed in Table 11.1, even when habitat differences are statistically controlled for (Table 11.2). It may be possible that females could learn to select habitats in relation to their own bill morphology. However, it is unlikely that they will learn to adjust site tenacity and copulation behaviour to their morphological phenotype. (2) Morphology and behaviour may be genetically correlated. Pleiotropic effects of a single gene on both the morphological and the behavioural trait could cause such co-inheritance (Falconer 1989). A well studied example is the occurrence of pleiotropic effects of testosterone, which affects both behaviour and some morphological characters as well (Wingfield et al. 1990). For instance, in male humans there is a correlation between the width of jaws and behavioural dominance, a correlation that possibly is mediated by testosterone (Müller & Mazur 1997).

Table 11.2. Correlations between female bill depth and aspects of female mating behaviour. The table summarises results from chapters 4, 5 and 6, and shows that most correlations do not disappear when variation in food availability is statistically controlled for, a result which is important in the context of this Discussion chapter.

	Correlation with bill depth		Correlation with bill depth after controlling for food density	
Paternal care (correlation)	r = -0.35	p = 0.003	r = -0.31	p = 0.010
Food density (correlation)	r = 0.31	p = 0.012	-	-
Site tenacity (logistic regression)	Chi^2 = 6.6	p = 0.010	Chi^2 = 7.7	p = 0.005
Mating status (logistic regression)	Chi^2 = 3.6	p = 0.058	Chi^2 = 1.6	p = 0.207
Clutch replacement (logistic regression)	Chi^2 = 3.3	p = 0.070	Chi^2 = 2.2	p = 0.137
Extra-pair paternity (logistic regression)	Chi^2 = 2.8	p = 0.095	Chi^2 = 2.9	p = 0.091

To summarise, the most important factor influencing female reproductive success is the date of arrival at the breeding grounds. Early arriving females are likely to succeed in obtaining an attractive male, which owns a high-quality territory and is also ready to assist in brood care. The later a female arrives, the stronger the trade-offs between these kinds of benefits get. As reproductive success declines with the date of arrival (see literature cited in Chapter 8), it is very likely that arrival date honestly reflects the phenotypic quality of females (Kokko 1999). The female in best body condition will be able to pay the costs of advancing her arrival, and will subsequently have the highest reproductive success. Females that arrive later at breeding grounds can choose between two mating tactics. The 'emancipated' tactic maximises the gains from high territory quality and from unconstrained genetic mating on the cost of having no male assistance in brood care. Females applying the 'help-dependent' tactic aim for male assistance while accepting lower-quality territories and genetic mates. Females appear to adopt these mating tactics in dependence on their age (a conditional strategy) and on their bill morphology (probably reflecting continuous genetic variation in strategies).

Implications for mating-system theories

Individual variation in female mating behaviour has received only limited attention so far (see Gross 1996, Gowaty 1996). This is surprising, because the evolution of avian mating systems has been studied extensively in the light of the PTM (Searcy & Yasukawa 1989, Slagsvold & Lifjeld 1994, Ligon 1999). Dozens of studies have compared the reproductive success of secondary females with that of simultaneously breeding monogamous females (reviewed by Slagsvold & Lifjeld 1994), while no investigation to date has focussed on characteristics of the individual female adopting either of the two mating tactics. This may partly be because the PTM is not applicable to all study systems, e.g. when there is a skewed sex-ratio (Searcy & Yasukawa 1989). Partly, however, researchers may have avoided to carefully look for individual variation in female mating behaviours, as such variation seems to make tests of the PTM even more complicated than was already suggested (see Davies 1989). However, a detailed analysis of individual behaviours may open a new way to examine the general idea behind the classical PTM. The most commonly used approaches to test the PTM have proven to be rather unsatisfying (Davies 1989, Ligon 1999). If we alternatively were able to show that the costs and / or benefits of polygyny vary with female age and with female bill morphology, and that females make their choices accordingly, this would be strong support for a modified version of the PTM that allows the polygyny threshold to vary with female phenotypes.

Research on social polygyny has been most active during the 80ies and the early 90ies, while the phenomenon of extra-pair paternity is currently receiving much attention. The development of the CFH by Gowaty (1996) is one of the major advancements in the latter field (Birkhead & Møller 1996, Ligon 1999, Amrhein 1999), as the hypothesis emphasises the role of individual variation in females, which has largely been ignored so far. Although the CFH was originally developed to explain patterns of extra-pair paternity, it can readily be extended to other aspects of female behaviours that are related to female dependence on male assistance (see Chapter 5). This extension can be the first step of introducing individual variation as a novel factor into models of social mating systems (e.g. the PTM).

The above outlined relationships between female help-dependence and female mating behaviours show, how the original CFH can be extended to explain both, the genetic and the social mating system. At the same time, it gets clear that there is a need to introduce the existence of individual variation in female qualities into the classical PTM. Existing theories have to be extended and to be combined with each other, by using an individual-based approach to female mating behaviours.

11.2. The male perspective

Individual reproductive tactics and strategies

In the previous section (11.1) I have shown that there are three main targets of female choice: territory quality, male parental care and male genetic quality. Thus three kinds of male qualities will enhance male mating success: (1) the ability to successfully compete for territories, (2) parental qualities and (3) attractiveness as a copulation partner (Figure 11.2).

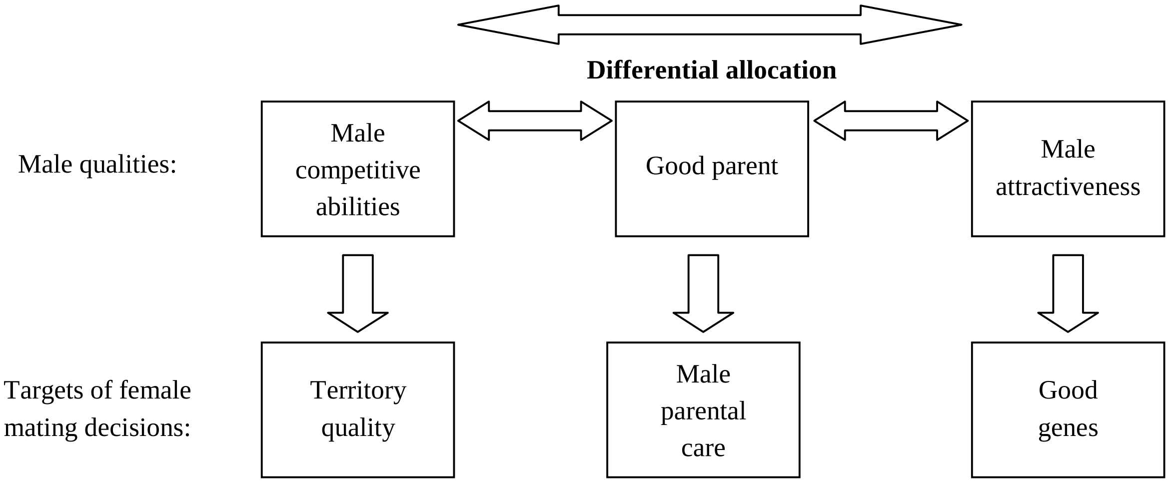


Figure 11.2. Male qualities that contribute to male mating success. Individual variation in these qualities may promote alternative reproductive behaviours through differential allocation of efforts.

Depending on individual qualities males may differentially invest in male-male competition, in parental effort or in sexual display (e.g. Studd & Robertson 1988, Magrath & Elgar 1997). To look whether this leads to the existence of alternative reproductive strategies, I first will consider which male characteristics correlate with these male qualities and whether these characteristics are heritable or conditional. Success in male-male competition over the possession of high-quality territories was positively correlated with male age and body mass (as reflecting body condition; see Chapter 7). Young males did invest noticeably less than old males in competition for territories, as reflected by their late arrival at breeding grounds (Chapter 8). Only one trait was correlated with male parental effort, namely tail length. Individuals with short tails (controlled for age) provided significantly more brood care than long-tailed males (Chapter 7). Finally, male attractiveness depended on singing performance. Males that sang notes at a constantly high sound amplitude with only short pauses between the notes were consistently preferred as copulation partners (Chapter 10). None of the above male characteristics is likely to be highly heritable. Thus it might be expected that individual variation in reproductive behaviours will be largely condition dependent (Austad 1984, Caro & Bateson 1986, Gross 1996).

Only one type of differential allocation was apparent. Males that were the better singers invested less in competition for territories than low-quality singers (Chapter 10). Direct conflicts over the possession of a territory were always won by the worse singing male, but the loser of the conflict stayed nearby and managed to sire most of the young due to his greater attractiveness. Thus increased investment in competition for territories by low-quality singers appears to be an example of ‘making the best of a bad job’. It may also be expected that unattractive males would invest more in parental effort (see Burley 1986, Sheldon 2000, Sanz 2001), but this may be neutralised by lower certainty of paternity (see Kempenaers & Sheldon 1997). In other words, a male may be ready to compensate for its low genetic attractiveness by showing a greater readiness to care for the brood, but as he runs a great risk of being cuckolded by a more attractive male, his parental effort may be reduced. This can potentially explain the fact that there was neither a correlation between male parental effort and actual paternity (Kempenaers & Sheldon 1997), nor a correlation between male singing performance and paternal care.

The correlation between male tail length and paternal care might actually be an indication for differential investment, although, with the data available, this remains highly speculative. The analogy to the case of the barn swallow, *Hirundo rustica*, suggests that male tail length (the most sexually dimorphic trait) may reflect androgen levels (Saino & Møller 1994, Saino et al. 1995). A great number of studies has shown that testosterone is involved in the trade-off between investment in parental care (low testosterone) and investment in territoriality and sexual display (high testosterone; Raouf et al. 1997, De Ridder et al. 2000, Ketterson & Nolan 1999). Females showed a significant preference to pair socially with short-tailed males (as presumably indicating parental qualities). As short-tailedness, in the dusky warbler, cannot be an honest indicator for parental qualities through condition-dependent expression (the ‘good parent’ process; Hoelzer 1989), this finding can only be explained by differential investment, if we search for an evolutionary stable solution. The mating advantage of the short-tailed male must be balanced by lower success in male-male competition and / or extra-pair paternity. The latter could not be demonstrated with significance, but this may have been due to low statistical power. Wilson (2000) found that, in the closely related willow warbler *Phylloscopus trochilus*, winners of extra-pair paternity had significantly longer tails than the males they cuckolded.

In summary, there is some evidence for differential allocation, i.e. how much energy males invest in the different ways of increasing their mating success. With the possible exception of the speculations concerning testosterone, individual behavioural variation appeared to be due to status dependence rather than to genetic variation. This is inferred from the fact that male traits that correlate with success in competition (age, body mass) show no or very low heritabilities (e.g. for body mass: $h^2 = 0.41 \pm 0.21$ SE, using 135 nestlings with genetically identified parents; $h^2 = -0.47 \pm 0.39$ SE, using a sub-sample of 44 extra-pair young to reduce the effect of shared environments). Moreover, males lacking these favoured traits have greatly reduced fitness, thus they can only try to ‘make the best of a bad job’.

In contrast, there was one other finding indicating the existence of alternative strategies. This finding concerns the way of how males that differ in structural body size engaged in competition for territories. Smaller males with presumably lower resource-holding power invested more in gaining prior ownership of territories than did large males (Chapter 8). They invested more in territoriality during postnuptial moult, which probably gave them an advantage in reoccupying these territories in the following breeding season (due to value asymmetries; Krebs 1982). It appears also plausible that these smaller males could simply afford to spend more energy for territorial defence as compared to large males that presumably had higher energy expenditure for the moulting process. There is a high heritability for structural body size ($h^2 = 0.79 \pm 0.10$ SE, for tarsus length of 140 nestlings with genetically identified parents; $h^2 = 0.86 \pm 0.16$ SE, using a sub-sample of 49 extra-pair young), and small and large males had approximately equal success in competition (no correlation between body size and harem size). This indicates that there is genetic variation underlying male competitive strategies and that alternative strategies have probably equal fitness. As in the case of female mating strategies related to bill morphology (Chapter 11.1), strategies are not discrete as suggested by the Gaussian distribution of male body sizes. Thus in both cases there appears to be continuous additive genetic variation underlying the behavioural strategies. Again, there are several alternative ways how the correlation between male body size and competitive strategy may be caused. (1) Males of small structural size may learn that they have to invest more energy in territorial defence to be able to successfully compete with larger individuals. (2) Small males may have additional energy ‘left’ that they can allocate for territoriality, as they have lower energetic costs for maintenance which might be most apparent during the moulting period. (3) There may be a genetic correlation between male body size and territorial behaviour. This can be achieved by one genetic factor having pleiotropic effects on both, morphology and behaviour (see e.g. Shuster & Wade 1991). The available data do not allow to reject any of these possibilities in favour of others.

General contributions to behavioural ecology

The unusual singing behaviour of male dusky warblers was one of the main reasons to initiate this study (see Introduction). In contrast to the large majority of other passerine birds, male dusky warblers do not guard their females during the fertile period, but spend most of the daytime singing (see Birkhead & Møller 1992, Gil et al. 1999, Chapter 9). Moreover, at the end of the breeding season, when males are moulting, they still do not stop singing and defending their territories, unlike virtually all other species do. The analysis of the function of these behaviours yielded some highly interesting results that deserve special mention at this place, as they make general contributions to the theories of resource competition, honest signalling and sexual selection.

Competition for early arrival at breeding grounds

In both male and female dusky warblers individuals profit from arriving early at breeding grounds as they are free to choose between territories. So why do late arriving individuals not advance their migration, if they could thereby increase their reproductive success? Models describing competition for early arrival have suggested that arrival order will honestly reflect an individual's phenotypic quality as the *costs* of advanced arrival would be larger to individuals in worse condition (Kokko 1999). This scenario is very likely to be true for female dusky warblers (see above). With regard to male dusky warblers, this model neglects the fact that there are also differences in the magnitude of *benefits* that an individual can obtain from arriving early. In Chapter 8, I have shown that individuals that defended high-quality territories during the previous autumn, arrive earlier than individuals that owned a low-quality territory, as the first group has more to win (and to lose) than the latter. Thus the case of the dusky warbler shows that both, the costs and the benefits related to arrival time have to be taken into account. It also shows that the intensity of competition for a given resource will influence arrival patterns. This may apply to comparisons within males, but also to the comparison between sexes. The fact that male reproductive success is much more variable than that of females (Figure 7.5 and Table 4.3) may be the reason for why males arrive well in advance of females (see Francis & Cooke 1990).

Testing the fertility announcement hypothesis

While in some species males stop singing once they have paired with a female, males of other species continue to sing intensively after pairing. Møller (1991) suggested with the 'fertility announcement hypothesis' (FAH), that singing after social pairing functioned to increase a male's success in obtaining copulations. Møller hypothesised that females would prefer to copulate with males that sing at a high rate, as only the best males could afford the energy to sing with only little interruption. Previous tests of the FAH have rejected the hypothesis mostly because their study species did not sing at a high rate during the period when females were fertile (reviewed by Gil et al. 1999). In most of these cases, males preferred to guard their female directly instead of spending energy in singing, in order to ensure that they would fertilise the eggs of their female. The dusky warbler, in contrast, appears to be the ideal organism to test the applicability of the FAH, as males do actually prefer singing over mate guarding during the fertile period of their females. In the Chapters 9 and 10, I have shown that, on the one hand, males sing to increase their success in obtaining copulations (supporting the FAH), but on the other hand, females do not prefer to copulate with males that sing at a high rate (contradicting the FAH). Thus males do signal their quality through their song, but other criteria than the energy required to maintain a high song rate must reinforce the honesty of signalling.

How can song honestly signal male genetic qualities?

Bird song has received much attention during the past decades, but until now, most researchers have measured the singing ability of males in a rather superficial way (either how much a bird sings, or how many different song types it sings). While several studies have shown a female preference for males with a high song rate or a large repertoire, these traits are typically confounded by variation in food availability, territory quality and/or male age (Searcy & Yasukawa 1996). Song rate is likely to reflect food availability in a territory, because males living in such territories can spend more time singing, as less time is needed for foraging (Davies & Lundberg 1984, Reid 1987, Gottlander 1987). Repertoire size can also be an indicator for territory quality (Searcy & Yasukawa 1996) as males appear to use their repertoires to specifically address individual neighbours by different syllable or song types (McGregor & Krebs 1989, Nordby et al. 1999, Beecher et al. 2000). Thus males in good territories may have large repertoires as they often have to defend their territories against a large number of competing neighbours. As such, there is still considerable doubt that song can be an honest indicator of a male's genetic quality, at least when measured by means of song rate or repertoire size (Searcy & Yasukawa 1996). Recent physiological work offers a new solution: birds may reach physiological limitations during sound production (Suthers & Goller 1997). Thus very subtle differences in sounds should have the potential to honestly reflect male quality.

In Chapter 10 I have shown that such fine-scaled variation in sound output correlates with both male success in obtaining extra-pair copulations and with male longevity. Males varied considerably in their performance during sound production, namely in their ability to sing with short pauses between notes and to maintain a high sound amplitude within notes in spite of rapid frequency modulation. This finding is intriguing as it highlights an interesting analogy between human vocalisation characteristics and bird song. In humans there exist great individual differences in sound production abilities and these differences are key to our estimation of sound quality. My findings suggest that such differences exist in birds as well, offering a new way to think about how female birds may judge the 'beauty' of a male's song.

Should females prefer dominant males as genetic partners?

In their recent paper Quarnström & Forsgren (1998) review studies showing that it is not always advantageous for females to mate with dominant males. Their reasoning is mostly concerned with direct benefits resulting from social pairing, namely whether males owning the best territories are also likely to be good parents, which often is not the case because of differential allocation (see above). Mostly due to the lack of data, little attention was paid to indirect benefits, namely whether dominant males are expected to be of superior genetic quality. This question has important implications for the relationship between the social and the genetic mating system (Møller & Ninni 1998, Hasselquist & Sherman in press). Because there is tremendous variation in both, social and genetic mating success of males (Figure 7.5), the dusky warbler offers an excellent opportunity to study this question. Although it is typically expected that male dominance will also reflect male genetic quality, female dusky warblers selected their copulation partners independently of male social status (Figure 7.6) and based their choice on male singing abilities instead. As low-quality singers invested more in competition over territories, females even preferred the losers of territorial fights as copulation partners (Chapter 10). The fact that male singing performance was correlated with male longevity, while male mating status (as reflecting dominance) was not, suggests that natural selection has shaped female mating preferences. This finding is in accordance with handicap-models of sexual selection (Zahavi 1975, Iwasa & Pomiankowski 1991) as opposed to models of Fisherian runaway (Lande 1981) or sensory exploitation processes (Ryan et al. 1990). Generally it is clear that all three types of mechanisms may occur, but evidence is accumulating that natural selection will favour female preferences for honest indicators of male genetic quality (Jennions et al. 2001).

12. Summary

This study investigates mechanisms and consequences of sexual selection in a polygynous population of dusky warblers *Phylloscopus fuscatus*, breeding near Magadan in the Russian Far East. In particular, the study focuses on individual variation in the reproductive behaviours of both females and males. The mating system of this population is characterised by facultative polygyny (17% of the males mated with more than one female), and by an outstandingly high rate of extra-pair paternity (45% of the offspring was not sired by the social partner of the female). The occurrence of polygyny is best explained by the 'polygyny-threshold model' (PTM). A female that arrives early at breeding grounds is free to select the best nesting territory, offering high food abundance and safety from predators. However, late-arriving females will find that the owners of high-quality territories are already mated. The PTM describes the trade-off faced by these females. They can either become secondary females on good territories, in which case it is unlikely that they will receive any assistance with brood care; or they can mate monogamously in low quality habitat, a situation in which they normally will receive male help. The data presented here indicate that benefits from high territory quality outweigh the costs of getting no male assistance, a finding which is consistent with the PTM. A novel finding of this study is that female mating decisions follow a conditional strategy. First-year females that have no prior breeding experience prefer monogamy over territory quality, while older females more often mate polygynously. I argue that the costs of receiving no male help may be higher for inexperienced females, while the benefits of having a free choice between territories may be higher for individuals that know which territories had the highest breeding success in previous years.

In this study I find support for the existence of another trade-off in female mating decisions, which is described by the 'constrained-female hypothesis' (CFH). Females that are paired to males of low attractiveness (presumably reflecting low genetic quality; see below) may seek extra-pair copulations with males of higher genetic quality, but this may lead to reduced parental effort by the social partner. Secondary females, however, that have no male assistance to lose are unconstrained, i.e. their choice of genetic father has no consequences for the level of care given to their brood. The combination of the two trade-offs described above, gives rise to two different female mating tactics. The 'emancipated' female which is not dependent on male help, is free to choose the best territory and the best copulation partners. The 'help-dependent' female, in contrast, is bound to find a partner who is willing to assist her with brood care, thus she will have to accept territories and genetic fathers of lesser quality. The need to search for an unmated male will result in lower breeding site tenacity than that of independent females. In addition, help-dependent females are less capable of replacing predated clutches, as males do not provide any care for late broods. The most unexpected finding on female mating behaviours is that this dichotomy between emancipated and help-dependent females is accompanied by morphological specialisation, which indicates that there is genetic variation underlying these female mating strategies. Females with a deep bill settled in territories with more food, received less male help, mated as a secondary female more often, replaced lost clutches more often, had more extra-pair young and showed a higher breeding site tenacity between years compared to shallow-billed females. This is interpreted as reflecting a morphological adaptation to capture arthropods under conditions of uni-parental (vs. bi-parental) brood care. The same pattern of morphological specialisation in relation to the system of brood care was also found in a between-species comparison in the closely related genus of *Acrocephalus* warblers.

Not only does the present study provide support for the CFH and the PTM, it also shows that female mating behaviours vary individually, a fact that has so far not been accounted for in models and theories on the evolution of social polygyny.

Male mating behaviours are characterised by competition for ownership of the best territories and by advertisement of male quality to females, as these are the factors which largely determine male reproductive success. To enhance their success in competition for territories, males often occupied high-quality territories after they had finished breeding, before their departure to winter-quarters. Prior ownership is known to increase the chances of regaining this territory in the

following year. Interestingly, late-territories were more often held by males of small body size, perhaps to compensate for their inferiority in physical conflicts. The timing of spring arrival at breeding grounds was also related to male size and to the chances of a male to successfully defend a high-quality territory. Previous models investigating the competition of males for early arrival have neglected such individual variation. The presented data indicate that the strategies followed by small and large males had equal fitness. The high heritability of body size also suggests that there is genetic variation underlying these strategies.

Male success in obtaining copulations depended on the quality of their song, a fact that explains why males spend most of the daytime singing during the period when females are fertile. Individuals that were able to maintain a relatively high sound amplitude during rapid frequency modulations were consistently preferred by females as copulation partners. Studies of physiological limitations on sound production suggest that such subtle differences in male singing performance can provide an honest reflection of male quality. The present study is the first to indicate that females may judge the quality of a male’s song by his performance in sound production. Quality of song was also related to winter survival, which suggests that females can enhance the viability of their offspring by seeking extra-pair fertilisations from good singers (good-genes hypothesis). Low-quality singers sometimes tried to enhance their access to females by forcibly taking over the territories of other males. Data indicated that this was an example of unattractive males ‘making the best of a bad job’.

In general, the present study demonstrates that a complete understanding of avian mating systems is not possible without a detailed analysis of alternative behavioural strategies and of how individuals adjust their reproductive tactics according to their individual needs and abilities.

Zusammenfassung

Die vorliegende Arbeit beschäftigt sich mit den Mechanismen und Auswirkungen sexueller Selektion, untersucht an einer polygynen Population des Dunkellaubsängers *Phylloscopus fuscatus*, in der Nähe von Magadan im russischen Fernen Osten. Das Hauptanliegen ist die Untersuchung individueller Unterschiede in reproduktiven Strategien, sowohl bei Weibchen als auch bei Männchen. Das Paarungssystem der untersuchten Population ist durch das Vorkommen sozialer Polygynie gekennzeichnet (17% aller Männchen waren mit mehr als einem Weibchen verpaart), sowie durch eine ungewöhnlich hohe Rate außerpaarlicher Vaterschaften (45% des Nachwuchses stammte nicht vom sozialen Partner des Weibchens ab). Das Auftreten sozialer Polygynie lässt sich am besten durch das „Polygynie-Schwellen-Modell" (PSM) erklären. Weibchen, die im Frühjahr als erste das Brutgebiet erreichen, genießen den Vorteil einer freien Auswahl an Brutplätzen, so dass sie sich für nahrungsreiche und prädatorenfreie Territorien entscheiden können. Spät ankommende Weibchen müssen feststellen, dass sämtliche Besitzer guter Territorien bereits verpaart sind. Diese Weibchen stehen vor einem Dilemma, das durch das PSM beschrieben wird: Sie haben die Wahl, entweder Sekundärweibchen eines bereits verpaarten Männchens (das ihnen keine Hilfe bei der Aufzucht der Brut zukommen lässt, jedoch ein hochwertiges Revier besitzt) zu werden oder sich monogam mit dem Besitzer eines minderwertigen Reviers zu verpaaren, welcher allerdings bei der Jungenaufzucht helfen wird. Wie die Daten nahe legen, werden die Kosten fehlender Hilfe durch die Unterschiede in der Revierqualität ausgeglichen, was das PSM bestätigt. Ein neuartiger Befund dieser Untersuchung ist, dass diese Entscheidung zur Partnerwahl einer konditionellen Strategie unterliegt: Unerfahrene, einjährige Weibchen scheinen die Monogamie der Wahlfreiheit eines Reviers vorzuziehen, während ältere Weibchen öfter in polygynen Beziehungen zu finden sind. Man könnte vermuten, dass die Kosten fehlender Hilfe für unerfahrene Weibchen besonders groß sind, während die Vorteile einer freien Auswahl an Territorien nur von solchen Weibchen optimal genützt werden können, die den zu erwartenden Bruterfolg für die einzelnen Territorien aus den Erfahrungen der letzten Jahre abschätzen können.

Die Untersuchung findet auch Unterstützung für die „Hypothese der eingeschränkten Weibchenwahl". Weibchen, die mit wenig attraktiven Männchen liiert sind (d.h. mit Männchen geringer genetischer Qualität; siehe unten), würden andere Männchen als Kopulationspartner bevorzugen, doch könnten sie dadurch die Hilfsbereitschaft ihres Partners aufs Spiel setzen. Sekundärweibchen polygyner Männchen haben in dieser Hinsicht nichts zu verlieren, sie sind also frei in der Wahl des genetisch besten Kopulationspartners. Die Kombination aus Vor- und Nachteilen von Monogamie und Polygynie begünstigt die Entstehung von zwei alternativen weiblichen Paarungstaktiken: „Emanzipierte" Weibchen haben eine freie Auswahl an Brutterritorien und Kopulationspartnern. „Abhängige" Weibchen müssen einen Paarungspartner finden, der bereit ist, bei der Jungenaufzucht zu helfen, weshalb sie sich oft mit weniger guten Revieren und Geschlechtspartnern zufrieden geben müssen. Die Notwendigkeit ein unverpaartes Männchen finden zu müssen, führt zu häufigerem Wechsel des Brutreviers zwischen den Jahren, als dies bei „emanzipierten" Weibchen der Fall ist. Darüber hinaus sind „abhängige" Weibchen dahingehend eingeschränkt, dass sie bei Verlust der Brut kein Ersatzgelege beginnen können, da Männchen bei der Aufzucht solcher späten Bruten grundsätzlich keine Unterstützung leisten. Der überraschendste Befund hierzu ist, dass die Aufspaltung in „emanzipierte" und „abhängige" Weibchen mit einer morphologischen Spezialisierung des Schnabels einhergeht. Dies bedingt, dass auch erbliche Komponenten zu diesem Verhaltensunterschied beitragen. Weibchen mit kräftigeren Schnäbeln brüteten in nahrungsreicheren Revieren, erhielten weniger männliche Unterstützung, wurden häufiger Sekundärweibchen, zeitigten öfter Ersatzgelege, hatten mehr außerpaarliche Junge und zeigten eine höhere Brutortstreue im Vergleich zu flachschnäbligen Weibchen. Diese morphologische Spezialisierung wird als Anpassung an unterschiedliche Strategien der Nahrungssuche bei einelterlicher gegenüber beidelterlicher Brutfürsorge gedeutet. Ähnliche morphologische Anpassungen an das System der Brutfürsorge wurde im zwischenartlichen Vergleich bei der nah verwandten Gruppe der Rohrsänger gefunden.

Insgesamt bietet die vorliegende Studie nicht nur Unterstützung für das PSM und die Hypothese der eingeschränkten Weibchenwahl, sondern sie zeigt auch, dass verschiedene Weibchen unterschiedlichen Paarungsstrategien folgen können, was bestehenden Theorien zur Evolution polygyner Paarungssysteme

eine neue Komponente verleiht.

Männliches Paarungsverhalten ist gekennzeichnet von Konkurrenz um den Besitz der besten Brutreviere und vom Anpreisen eigener Qualitäten gegenüber den Weibchen, da diese Faktoren den Reproduktionserfolg der Männchen bestimmen. Unmittelbar vor ihrem Wegzug ins Winterquartier präokkupieren Männchen hochwertige Reviere, da ihnen eine solche Vorbesetzung Vorteile bei der Wiedererlangung dieses Territoriums im darauf folgenden Frühjahr einbringt. Interessanterweise war dieses Verhalten bei kleineren Männchen ausgeprägter als bei großen, vermutlich um die mögliche physische Unterlegenheit bei aggressiven Auseinandersetzungen auszugleichen. Der Ankunftszeitpunkt der Männchen im Frühjahr zeigte ebenfalls Abhängigkeiten von der Körpergröße und von den Erfolgsaussichten eines Männchens bei der Auseinandersetzung um hochwertige Reviere. Theoretische Modelle, die sich mit dem Problem befasst haben, welches Männchen als erstes im Brutgebiet eintrifft, haben solch individuelle Variation bislang nicht berücksichtigt. Die vorliegenden Daten lassen vermuten, dass beide Strategien, die von großen und die von kleinen Männchen, gleiche Fitness mit sich bringen. Die hohe Erblichkeit von Unterschieden in der Körpergröße bedingt, dass auch erbliche Komponenten Einfluss auf diese Strategien haben.

Welchen Erfolg Männchen beim Erlangen von Kopulationen hatten, hing in erster Linie von der Qualität ihres Gesangs ab. Ein Befund, der erklärt, warum Männchen, in der Zeit, wenn Weibchen fruchtbar sind, den Großteil des Tages mit Singen verbringen. Weibchen bevorzugten solche Männchen als Kopulationspartner, die in der Lage waren, Töne mit steilen Frequenzmodulationen mit konstant hoher Lautstärke zu singen. Untersuchungen zu physiologischen Limitierungen der Tonerzeugung legen nahe, dass feine Unterschiede in der Qualität der Darbietung durchaus ein ehrliches Signal für die Qualität des Männchens sein können. Die vorliegende Studie ist die erste, die nahe legt, dass Weibchen die Qualität männlichen Gesangs an feinen Unterschieden in der Tonproduktion festmachen könnten. Diese Beobachtung erinnert daran, dass auch wir die Fähigkeiten eines menschlichen Sängers an (im weiteren Sinne) ähnlichen Kriterien messen. Interessanterweise hatten, beim Dunkellaubsänger, gute Sänger bessere Chancen, den Winter zu überleben. Dies weist darauf hin, dass Weibchen die Lebensfähigkeit ihres Nachwuchses dadurch erhöhen, dass sie außerpaarliche Kopulationen mit guten Sängern suchen („Gute-Gene-Hypothese“). Unbegabte und damit wenig attraktive Sänger versuchten in einigen Fällen ihren Paarungserfolg zu erhöhen, indem sie anderen Männchen ihr Revier mitsamt Weibchen abnahmen. Die Daten zeigen jedoch, dass der Erfolg dieser Taktik wegen der Untreue dieser Weibchen deutlich begrenzt war.

Im allgemeinen zeigt die vorliegende Arbeit, dass für ein umfassendes Verständnis eines Paarungssystems eine detaillierte Analyse alternativer Verhaltensstrategien und individueller reproduktiver Taktiken notwendig ist.

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14. Acknowledgements

First and foremost I would like to thank Vladimir Arkhipov for his great efforts and for the time he invested to organise and accompany the ’98 and ’99 expeditions to Malkachan. The present study would not have been possible without his support.

I am indebted to my supervisor, Bernd Leisler, for investing large amounts of time and energy. He was always there when I needed advice and he provided very constructive support. I wish to thank him for spending uncountable hours in very inspiring discussions.

I am grateful to Peter Berthold for providing logistic and financial support.

Hans-Heiner Bergmann deserves special mention, not just because he suggested me to join his ’97 expedition to work with him on the dusky warbler, but for encouraging me to carry on with this project at a time when everything seemed to fail. He always supported me where ever he could, but in the first place I will never forget the very exciting time we had doing field work together.

I wish to thank Karl Eduard Linsenmair for supporting encouragement and for his readiness to be my official supervisor at Würzburg University.

Bart Kempenaers spent considerable amount of time helping me with data analysis, improving my manuscripts and providing invaluable advice in every respect.

A number of people contributed greatly to this study by carrying out field work. In the first place these are Hans-Heiner Bergmann in ‘97, Cornelia van Hulten, Dries Kuijper and Maarten van Steenis in ’98, and Lars Schmidt-Eisenlohr and Ingo Weiß in ‘99. Additional help came from Wiltraud Engländer, Alexander Kondratjev, Maria Jerabek and some more people in ’97, Vladimir Arkhipov and Olga Mochalova in ’98, and from Vladimir Arkhipov and Iwan Fedutin in ’99. A heartfelt thanks to all of them.

An even greater number of people provided logistic support during the expeditions: Olga Mochalova, Indira Hardani, Vladimir Arkhipov, Iwan Fedutin, Olga Butorina, Alexander Andreev, Arkady Reimers, Kira Regel, Tolya Subakin, Vasya from Brochovo, Igor, Tolya, Sergei and Ira from the meteorological station, Igor and Lydia Merijulov, and Vladimir and Kolya from the fisherman’s camp. Thankyou to all those who supported us.

Separate and especial thanks go to Oleg Bourski and Sanya Panaiotidi for their support, guidance, discussions and hospitality. I really owe them a lot.

I also thank Tonya Alexandrova and Boris Sheftel, as well as Nikita Chernetsov for support and hospitality.

Karl-Heinz Siebenrock helped greatly with preparing my expeditions and other members of the Vogelwarte provided support throughout the years.

I thank Thorsten Balsby for help with the song analyses, for being a good company and for a lot more other things.

Topac Ertan, Jens Seckinger, Tony Wilson, Henner Brinkmann and Ursula Topel helped in the lab at Konstanz University, where Axel Meyer kindly allowed me to work. Benedikt Gießing and Petra Heidrich tested some primers for me and Staffan Bensch, Sonja Ihle and Topac Ertan provided some primers.

Markus Neuhäuser helped greatly to increase my knowledge about statistics and he did the most sophisticated calculations (see Table 5.1 and Figure 8.4).

The following people provided helpful comments on my manuscripts: Jan Beck, Staffan Bensch, Hans-Heiner Bergmann, Tim Birkhead, Donald Blomquist, Clive Catchpole, Diego Gil, Benedikt Gießing, Franz Goller, Patricia Gowaty, Dennis Hasselquist, Bart Kempenaers, Jan Lifjeld, Peter McGregor, Axel Meyer, Mark Naguib, Francisco Pulido, Raimund Specht, Mark Wilson, several anonymous referees, and of course my supervisors Bernd Leisler and Karl Eduard Linsenmair.

Mark Wilson, Bart Kempenaers and Rupert Marshall, but also Tony Wilson and Andy Terry helped greatly to improve my English. Maria Jerabek, Dorothee Haese, Günther Bauer and Carin Forstmeier helped with corrections.

Lars Schmidt-Eisenlohr kindly provided some of his excellent photographs.

I am indebted to the Studienstiftung des deutschen Volkes for financing me throughout this study. The Stifterverband für die Deutsche Wissenschaft also provided financial support for the ’98 expedition (Flora Immerschitt-Stiftung: T 181/08.005/98).

The Ornithological Department of the Zoological Museum of Moscow University, the Zoological Museum of the Russian Academy of Sciences in St. Petersburg, and the Natural History Museum in Tring allowed access to their skin collections.

Last, but not least, I thank Maria Jerabek for her patience and support.

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Erklärung

Hiermit versichere ich ehrenwörtlich, dass ich die vorliegende Dissertation in allen Teilen selbständig angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.
Die vorliegende Dissertation hat weder in dieser noch in ähnlicher Form je in einem anderen Prüfungsverfahren vorgelegen, und ich habe nie zuvor derartige akademische Grade erworben oder versucht zu erwerben.

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