

Habitat Selection: Demography and Individual Decisions

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Abstract

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Habitat selection is the behavioural process determining the distribution of individuals among habitats varying in quality, thus affecting individual fitness and population growth. Models of population dynamics often assume that individuals have perfect knowledge about habitat qualities and settle accordingly in the best habitats available. Many studies of dispersal have focused on the movements of individuals away from a site, but knowledge on settlement decisions is still scarce.

I investigated settlement and departure decisions in a long-distant migrant, the northern wheatear (*Oenanthe oenanthe*), breeding in a heterogeneous agricultural landscape. First, I investigated the settlement of wheatears choosing a new territory at the time of territory establishment in spring. I show that territory selection is non-ideal as wheatears did not prefer territories with characteristics most closely predicting individual fitness. Second, I studied the territory selection of experienced breeders which may use many potential cues as they have been breeding in the same area before. The results show that information gathering of experienced breeders is constrained, and that they cannot always settle at a preferred site probably because of the earlier establishment by other individuals. Third, I show that such a priority constraint in territory site selection may be a proximate cause for female-biased dispersal in wheatears and possibly in many other bird species. Fourth, as a first step to link habitat selection behaviour and population dynamics, I investigated habitat-specific population growth.

Overall, I show that constraints acting on individual habitat selection result in a greater proportion of individuals breeding in poorer habitats than would be expected from ideal selection, which has consequences for population persistence.

Keywords: dispersal, ecological trap, farmland birds, habitat quality, *Oenanthe oenanthe*, population dynamics, post-breeding movements, preference, settlement, site fidelity

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Contents

Introduction, 7

The Study System, 9

Habitat selection: ideal, non-ideal or an ecological trap?, 12

Habitat selection of experienced breeders, 15

Sex-biased dispersal, 19

Habitat-specific population growth, 21

Concluding remarks and future prospects, 24

Acknowledgements, 25

References, 25

Tack, 29

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I.** Arlt, D. & Pärt, T. 2007. Nonideal breeding habitat selection: a mismatch between preference and fitness. *Ecology*, in press.
- II.** Arlt, D. & Pärt, T. The timing of habitat selection: a study of post-breeding movements and breeding territory shifts. (Manuscript).
- III.** Arlt, D. & Pärt, T. Sex-biased dispersal: males constrain female site selection. (Manuscript).
- IV.** Arlt, D., Forslund, P., Jeppsson, T. & Pärt, T. Habitat-specific population growth of a farmland bird. (Manuscript).

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Fig. 1. Wheatear in a landscape consisting of a mosaic of pastures, crop fields and forest, Finland. (© Tomi Muukkonen)

Introduction

The dynamics of many populations are inevitably linked to the behaviour of individuals. Behavioural decisions and strategies affect individual fitness and thus the demography of populations. An important aspect for population persistence in heterogeneous environments is how individuals are distributed among habitats varying in quality, as habitat quality affects rates of reproduction and survival (cf. Morrison et al. 1992). Individual distributions are determined by dispersal, i.e. the movement between an area of origin and a new site (Clobert et al. 2001). Dispersal is thus concerned with individuals' decisions to leave a site, the movement between sites, and settlement decisions. Nevertheless, dispersal studies have tended to focus on movements away from a natal or breeding site, whereas the aggregation of individuals into a new habitat (or settlement) has been the focus of studies on habitat selection (Stamps 2001). Even though dispersal and habitat selection have been frequently treated separately, they are inherently related to the same behavioural processes of individuals searching for and finding a new habitat, which involve collecting and assessing the information in order to do so, as well as the ability to settle at a chosen site (Stamps 2001). Both habitat selection and dispersal are partly an evolutionary consequence of habitats differing in their effects on individual fitness.

Although habitat selection behaviour is central for population processes, the majority of studies claiming to have investigated habitat selection have only looked at the distribution of individuals among habitats (Jones 2001). If habitat selection is ideal, i.e. when individuals have perfect knowledge on habitat quality and are free

to settle in the best habitats (Fretwell & Lucas 1970), individuals may in fact be found in the best habitats. There are, however, several reasons why density may not always reflect habitat quality. For example, social interactions between individuals lead to dominance hierarchies or systems with territorial exclusions where some individuals exclude others from the best habitats. In such systems subordinate individuals will be forced into poorer habitats where they may occur at higher densities (Parker & Sutherland 1986; Bernstein et al. 1991; Pulliam & Danielson 1991). Individuals, however, may make errors when assessing habitat quality, either caused by systematically biased judgement of habitat qualities or by sampling errors resulting in limited knowledge (Kokko & Sutherland 2001), such errors leading to non-ideal settlement. Non-ideal habitat selection can have profound consequences for individual fitness and population persistence (e.g. Pulliam & Danielson 1991; Delibes et al. 2001; Donovan & Thompson 2001; Kristan 2003). Non-ideal selection has received some theoretical attention (e.g. Abrahams 1986; Pulliam & Danielson 1991; and for mate choice: e.g. Johnstone & Earn 1999; Neff 2000; Luttbeg 2002), but empirical evidence is mostly limited to the extreme case of ecological traps (Schlaepfer et al. 2002; Battin 2004; Robertson & Hutto 2006).

Habitat selection is best studied by following individual movements between habitats. Habitat preferences can then be related to habitat characteristics and habitat characteristics can be tested for their link to individual fitness. In this way one can also investigate which potential cues (i.e. habitat characteristics potentially related to fitness) are used to assess habitat quality and guide individual decisions as these will determine the behavioural strategies used for collecting information.

In this thesis I focus on breeding habitat selection, investigating both departure and settlement decisions. I used data from a long-term population study of migratory northern wheatears (*Oenanthe oenanthe*) breeding in a heterogeneous agricultural landscape. In *Paper I* I tested whether habitat selection of male wheatears deviated from ideal habitat selection. I examined habitat selection by means of settlement patterns of individuals choosing a new territory at the time of territory establishment in spring and by analysing the links between preference and territory quality. I also tried to identify the potential causes of non-adaptive selection of breeding sites. Poor choices may be adjusted when choosing new habitats by learning and collecting more information about habitat qualities. Studies on prospecting, i.e. information gathering, suggest that individuals use information gathered in a previous year to select a (new) breeding habitat. These studies, however, have mainly concerned non-breeding individuals (Reed & Oring 1992; Doligez et al. 2004; Dittmann et al. 2005), but few studies have investigated prospecting strategies of experienced breeders (but see Ward 2005). In *Paper II* I therefore investigated the potential for post-breeding prospecting, and explored site shift decisions of experienced breeders to investigate whether they adjust their territory choice strategically to improve fitness prospects. *Paper III* focuses on a direct link between habitat selection and an observed dispersal pattern. Specifically, I examined whether a constraint on site selection may explain the widely found pattern of sex-biased dispersal patterns. Finally, to link individual habitat selection behaviour and population dynamics a first step is to investigate habitat-specific population growth. This was the objective of *Paper IV*.

The study system

I used data from a long-term study of a population of northern wheatears (*Oenanthe oenanthe*, hereafter wheatears) breeding in a heterogeneous agricultural landscape. By using observations of individually marked birds it was possible to collect data on local juvenile and adult survival, and on movements within and between years, the latter being the base for inferring individual decisions within the habitat selection process.

Study species. - Wheatears are small, long-distance migrants wintering south of the Saharan desert. They are insectivorous ground foraging birds with a main distribution in open habitats consisting of short field layers, i.e. bare ground or low height of grasses and forbs forming the layer of vegetation (Cramp 1988; Panov 2005; Fig. 2). Wheatears forage by mainly visually scanning for food items, and they frequently hop on the ground or scan from outlooks such as stones or fence posts. Field layer height has been shown to be negatively related to prey availability (Tye 1992) and positively to risk of nest predation (Pärt 2001a, b). Wheatears nest in different types of cavities, usually at the ground (Cramp 1988; Conder 1989; Panov 2005). In the study area nest sites are abundant and nests are placed either at the ground under stones (mainly in stone piles and stone walls) or under roof tiles of barns (20%).



Fig. 2. Male northern wheatear in typical habitat, The Great Orme, Wales. (© Adrian Foster)

Study area. - The study area of about 60 km² is located southeast of Uppsala in southern Central Sweden (59°50' N, 17°50' E). It consists of different parts based on the intensity of data collection and the use of data for estimating population parameters (see below; Fig. 3). The study area is located in an agricultural landscape consisting of a mosaic of grazed and ungrazed grasslands (11%), crop fields (68%), woodlands and forest (21%) (Arlt & Pärt 2007; Fig. 3). The agricultural landscape extends to the north and south of the study area, but the area

is delimited by forested areas in the east and west. Territory sites of wheatears were located in grasslands (59%), crop fields (28%) and on farmyards (13%) (Fig. 4).

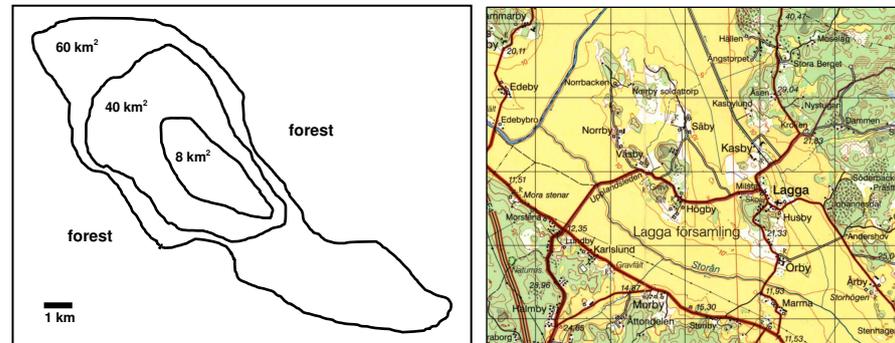


Fig. 3. The different parts of the study area southeast of Uppsala (left) and map extract (right) showing the landscape composition where green refers to forest, yellow to crop fields and white to pastures, farms and settlements (1 square = 1 km²).



Fig. 4. Typical wheatear breeding habitat in a pasture (left) and on a crop field (right). (photo: D. Arlt)

Long-term data. - Since 1993 all previously occupied territory sites and all sites potentially suitable for wheatears in the 60 km² area (229 territory sites, average number of pairs: 120-180 pairs) were monitored. All potential breeding sites were visited at least every third to fifth day from mid April to the end of June and data were recorded on territory occupancy and arrival date (Pärt 2001a, b; Arlt & Pärt 2007). All breeding attempts were recorded and marked individuals identified. All males and a large proportion of females were aged as either one year old or older based on plumage characteristics (Svensson 1992; Jenni & Winkler 1994; Pärt 2001a). Nests were searched for during nest building, but most nests were found after hatching when parents started to feed young. Hatching date was estimated from the age of nestlings. Breeding success was recorded as either successful or failed, where breeding was defined to be successful when we observed fledglings or heard intense warning calls of the parents after fledging (≥ 15 days after hatching). Nest failures, 15-40% of all attempts per year (average 29%), were mostly due to predation (Pärt 2001a). Nest failures during the incubation period were recognized by obvious behavioural changes of males and females (Pärt &

Arlt, personal observation). Nestlings were ringed when 5-8 days old. For successful attempts the number of fledged young was assumed to equal the number of nestlings at the time of ringing minus the number of dead chicks found in the nest after fledging. Within a more intensively studied 40 km² area (149 territory sites, average number of pairs: 80-120) nestlings from 69% of all nest sites (31% were inaccessible, e.g. because of heavy stones in rock piles) and many adults were marked with an aluminium ring and a unique combination of colour rings (Pärt 2001a, b; Arlt & Pärt 2007; Fig. 4). This resulted in nestlings from on average 90% of all successful breeding attempts and 57% of adults being marked at the end of each breeding season. Outside the 40 km² area sites were visited less frequently and often only breeding success was recorded.



Fig. 5. Individually marked male and female wheatear. (photo: D. Arlt)

Data on the number of local recruits (individuals marked as nestlings and returning to breed in the 60 km² study area) was based on young originating from the most central part of our study area (8 km², 83 territory sites, average number of pairs: 45-75) to avoid biases due to natal dispersal out of a restricted area (for details see Arlt & Pärt 2007). Because adults dispersed much shorter distances (between centres of territory sites occupied in two subsequent years; median=292 m, 10/90% quantile=139/1452, N=263) than juveniles (median=1250 m, 10/90% quantile=427/3658, N=289; t-test (log-transformed distances): t=-16.30, DF=550, P<0.0001; based on birds originating from the 8 km² area) estimation of adult survival was based on adults that originally bred in the central 40 km² area. Survival was estimated by the return of ringed adults to the 60 km² study area in subsequent years as the resighting probability was 98% (2% of adults were recorded in non-consecutive years, i.e. they escaped detection in one year).

Territory characteristics. - Territories were delimited by the outermost positions of the majority (>90%) of all recorded positions of the resident pair (or unpaired male). Territory sites, i.e. the locations of individual territories, were relatively stable across years irrespective of territory holder, probably because wheatears frequently use landscape features such as prominent stones, stonewalls or fences as territory boundaries (see Pärt 2001a, b; Arlt & Pärt 2007). At each territory site field layer height was estimated by eye as proportions of short (<5 cm), medium (5 cm - 15 cm) or high (>15 cm) field layer within territories at four occasions during the breeding season (Pärt 2001a for validation of the method). Territories were classified as having either a permanently short field layer (short field layer on

all four occasions on at least 0.25 ha, i.e. the minimum territory size, within 50 m of the nest site; grazed grasslands and farm yards) or a growing/tall field layer (ungrazed or late grazed grasslands, fallow fields, and crop fields). For each territory site long-term occupancy, reflecting its attractiveness as a breeding site (Arlt & Pärt 2007) was calculated as the number of years a territory site had been occupied during the years 1993-2004. Since territory sites were located in clusters of 2-5 sites or solitary (30% of all sites), territory cluster size was the number of neighbouring territory sites, i.e. adjacent territory sites sharing boundaries. For each territory site the number of established pairs and the number of successful pairs were counted on the neighbouring territory sites (data were missing when the breeding success of at least one of the pairs was unknown).

Habitat selection: ideal, non-ideal or an ecological trap?

Habitat selection theory assumes that individuals can assess the quality of habitats and settle according to the gradient of habitat qualities. To maximize the probability of choosing the best habitat available individuals are expected to use habitat characteristics (cues) that predict individual fitness because habitat quality affects rates of reproduction and survival (Morrison et al. 1992; Hall et al. 1997; e.g. Korpimäki 1988; Newton 1991; Holmes et al. 1996; Petit & Petit 1996; Pärt 2001b). According to ideal habitat selection (see Ideal Free Distribution, IFD, Fretwell & Lucas 1970; Ideal Despotic Distribution, IDD, Fretwell 1969; Pulliam & Danielson 1991) individuals are assumed to have perfect knowledge on the quality of different habitats and prefer the best over the poorer ones. Poor choices, however, may be common due to e.g. imperfect spatial knowledge, limited availability of cues, or poor relationships between cues and habitat quality (Orians & Wittenberger 1991; Pulliam & Danielson 1991; Lima & Zollner 1996; Kokko & Sutherland 2001; Schlaepfer et al. 2002). In *Paper I* I asked whether wheatears preferred habitats of highest quality at the time of territory establishment in spring. Because habitats rarely occur in uniform patches average estimates of habitat preferences at the patch level may obscure the links between individual preferences and their fitness consequences. Since wheatear breeding habitat in the study area was characterised by a small scale mosaic of different habitats, I therefore investigated habitat selection by means of territory selection at the scale of individual territories.

Different habitat selection scenarios are best tested by a two-step protocol investigating (1) which habitat or territory characteristics (i.e. cues potentially used by individuals to assess habitat or territory quality) predict individual fitness, and (2) the type of relationship between individual preferences and these potential cues (Fig. 6). Ideal selection can be inferred when individuals prefer the sites with characteristics predicting fitness (best sites). The opposite situation when individuals prefer sites with characteristics predicting low fitness (poor sites) is referred to as ecological trap (Schlaepfer et al. 2002; Battin 2004; Robertson & Hutto 2006). In between these two extreme situations there exist situations with no clear relationship between preference and characteristics predicting fitness (Kristan

2003) which I refer to as non-ideal habitat selection (“non-preference trap”, cf. Robertson & Hutto 2006) (Fig. 6).

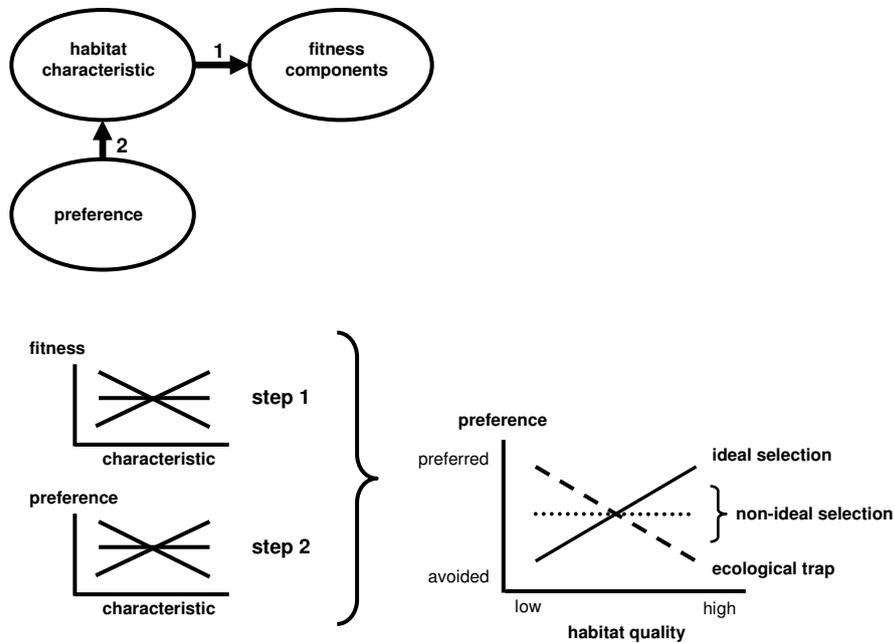


Fig. 6. The two-step individual model to infer the type habitat selection (ideal, non-ideal, ecological trap).

I investigated different territory characteristics potentially predicting individual fitness: territory field layer height class, territory cluster size, breeding success in year t-1, the number of breeding neighbours in year t and year t-1, and the number of successfully breeding neighbours in year t and year t-1. Cues based on the presence and success of conspecifics may be used as cues for future breeding habitat selection (Reed & Dobson 1993; Boulinier & Danchin 1997; Danchin et al. 2001; Doligez et al. 2003). Such information collected during the year prior to territory selection has to be correlated across years. In the study area breeding success ($P=0.026$), number of fledglings ($P=0.095$), and number of local recruits ($P<0.0001$) were positively correlated across years at the territory scale, although correlations were generally weak (*Paper I*). Territory field layer height at the time nestlings were fed was also positively correlated across years ($P<0.0001$). Thus, the wheatears could potentially use information on territories collected in year t-1 to predict their quality in year t.

The analyses of step one of the two-step protocol (Fig. 6) showed that only territory field layer height was significantly linked to three of four investigated fitness components (including also male survival), breeding success ($P<0.0001$), number of fledglings ($P<0.0001$), and number of local recruits ($P=0.0002$), where reproductive performance was higher for wheatears breeding at territories with

permanently short field layer. All other investigated territory characteristics were poor predictors of individual fitness (all $P > 0.4$). So therefore, did wheatears also used territory field layer height as a cue when selecting territories?

I estimated territory preferences of males (males establish territories before females) by the order of territory establishment in spring in years 2002 and 2003 (according to arrival date at territories which was defined as the first day a male was observed on a territory site), assuming that the first territories chosen were the most preferred ones. Because territory preference might be biased by prior occupancy I investigated preferences of males that established a new territory, i.e. excluding old males that displayed between-year site fidelity and males whose former territory occupation was unknown. In contrast to expectations from ideal selection, territory preference was not related to territory field layer height (Fig. 7). Instead, preference was positively related to territory cluster size, where males settled earlier at territory sites sharing borders with several adjacent sites than at those with few or no adjacent sites (Fig. 7). Males settled also earlier at territory sites that had more breeding neighbours ($P = 0.067$), or more successful neighbours in the year $t-1$ ($P = 0.069$). Territory preference was also associated with long-term territory occupancy ($P < 0.0001$), suggesting that territories being preferred in previous years also were the ones to be occupied first in the spring.

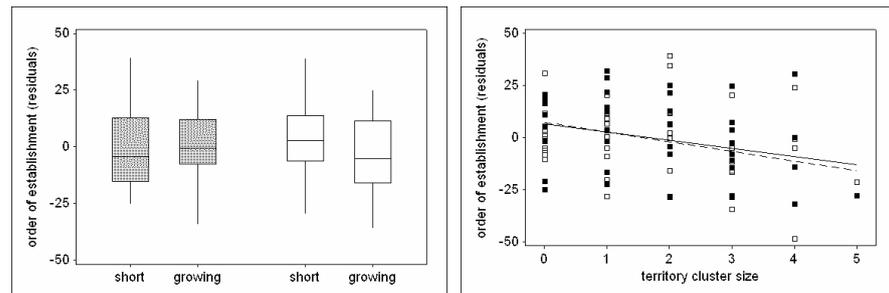


Fig. 7. Order of establishment was not related to territory field layer height (left; shaded boxes = 2002, open boxes = 2003; $P = 0.41$), but to territory cluster size (right; solid symbols and solid line = 2002, open symbols and dashed line = 2003; $P = 0.006$). Y-axis shows partial residuals from a mixed-model ANCOVA including territory identity as random factor and fixed factors year, male age, and territory field layer height class (top) or territory cluster size (bottom) and with order of establishment as dependent variable (low values correspond to early establishment).

Clearly, there was a mismatch between territory characteristics linked to preference and those linked to individual fitness. The mismatch between preference and fitness was evident for all fitness components investigated and thus, cannot be explained by fitness compensations (Battin 2004). Individual variation and deviations from ideal choices have been almost neglected in breeding habitat selection studies, except in cases of ecological traps (see above; Schlaepfer et al. 2002; Battin 2004). Ecological traps are assumed to arise when environmental change is fast (e.g. due to human alterations), thus changing the links between evolved preferences based on cues of quality and the true quality of the habitat (Kokko & Sutherland 2001; Schlaepfer et al. 2002; Battin 2004; Robertson & Hutto 2006). My results suggest a case of non-ideal habitat selection (see above),

possibly because field layer heights at the time of territory establishment was a poor predictor for field layer heights at the time when nestlings were fed. Although wheatears did not prefer sites with a permanently short field layer they strongly preferred sites where field layers were short at the time of territory establishment. However, about 50% of all sites with short field layers in April grew tall field layers later on (Fig. 8).

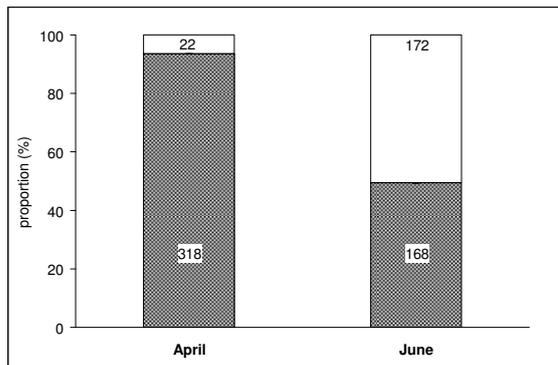


Fig. 8. Top: The proportion of territory sites with short (shaded) or tall (open) field layers at the time of territory establishment (April) and at the time when most pairs feed their young (June) in years 2002 and 2003. Numbers refer to number of territory sites. Bottom: A wheatear territory site with growing field layers in April (left) and in June (right). (photo: D. Arlt)

The preference of territory aggregations, apparently not linked to the investigated fitness components, could be linked to a facilitation of prospecting and finding a better future breeding site in the close neighbourhood, or the probability to establish a territory (see Getty 1981; Adams 2001; Ridley et al. 2004). These potential explanations for the preference of territory aggregations point to the probability of territory establishment as an important aspect of territory selection influencing settlement patterns, which previously has been generally neglected.

Habitat selection of experienced breeders

The non-ideal territory selection of individuals that chose a new territory may be because they have only poor information available. Experienced breeders, on the

other hand, may use a “smorgasbord” (cf. T.P.) of potential cues as they have been breeding in the same area before. Since several territory characteristics were correlated across years experienced breeders should be able to use information collected in the previous year. Experienced breeders may therefore be expected to reduce the information constraint. I therefore expected that experienced breeders use information on territory field layer height available to them at the time when young are fed for their future territory choice. Based on other studies I also expected that experienced breeders used their own previous breeding success (e.g. Harvey et al. 1979; Bollinger & Gavin 1989; Haas 1998; Hoover 2003) and information on the performance of conspecific neighbours (i.e. public information cf. Danchin et al. 2004; Bollinger & Gavin 1989; Hoover 2003; Ward 2005) for their future territory choice. Furthermore, movements during the post-breeding period have been reported for several species and suggested to be at least partly exploratory movements in terms of finding alternative breeding sites (i.e. prospecting; Baker 1993; Morton 1997; Reed et al. 1999). Similarly, prospecting has been shown to be more frequent late in the breeding season (Reed & Oring 1992; Boulinier et al. 1996; Ward 2005). Therefore I also expected experienced breeders to make part of their choice of a future breeding site directly following breeding, i.e. prospecting alternative sites during the post-breeding period before the migration to the winter quarters. Movements of colour-ringed wheatears during the post-breeding period had been recorded during eight years (1994-1998, 2002-2004) in the 8 km² central part of the study area. I investigated territory selection of experienced breeders by analysing territory site choice in relation to their breeding site. Specifically, I analysed the probability to shift sites at two different times when individuals may collect and use information, the post-breeding period and the time of territory establishment in the subsequent year.

Overall, most males (78%) and females (83%) stayed at their breeding territory site and its immediate surroundings (i.e. at neighbouring territory sites sharing boundaries) during the post-breeding period (Fig. 9). Compared to the probability of shifting territory between years (46% of all males and 32% of all females remained site faithful, i.e. returned to breed to the same territory site) these figures suggest that individuals are reluctant to move directly after breeding. Nevertheless, in line with my prediction both males and females were more likely to shift to a new post-breeding location (i.e. the area covered by the territory site with the majority of observations and its adjacent territory sites) when they had been breeding on territories with growing field layers (males: $P=0.005$, females: $P=0.0001$) and with no or few breeding neighbours (males: $P=0.0001$, females: $P=0.0015$). Females also moved away from less attractive territories (in terms of long-term occupancy; $P=0.005$). Thus, as expected, wheatears moved in response to field layer height, and also away from more isolated territory sites.

Most (91%) individuals moved to a post-breeding location characterised by short field layers. Of the wheatears that stayed at their breeding site 76% occupied territories with short field layers. There are two non-exclusive explanations for these observed movement patterns during the post-breeding period. The reluctance to move suggests that site-shifts may be costly for wheatears at this time of the life cycle, possibly because they undergo a complete moult (Ginn & Melville 1983). Individuals may generally benefit, in terms of future survival, by staying at a

familiar site, where they have detailed knowledge of foraging conditions and predator refuges. Thus, a shift may only be beneficial if foraging conditions at the breeding site are very poor, as may be the case at territory sites with tall and dense field layers and alternative patches with short field layers in the neighbourhood. Territory field layer height at the time of breeding, however, is also a strong predictor of site-specific reproductive performance (see above), and site shifts in response to tall field layers during the post-breeding period may therefore also be adaptive in terms of future breeding site selection. Thus, a shift from territories with tall to those with short field layers during the post-breeding period may be explained by the dual benefits of increased survival prospects and future territory choice opportunities.

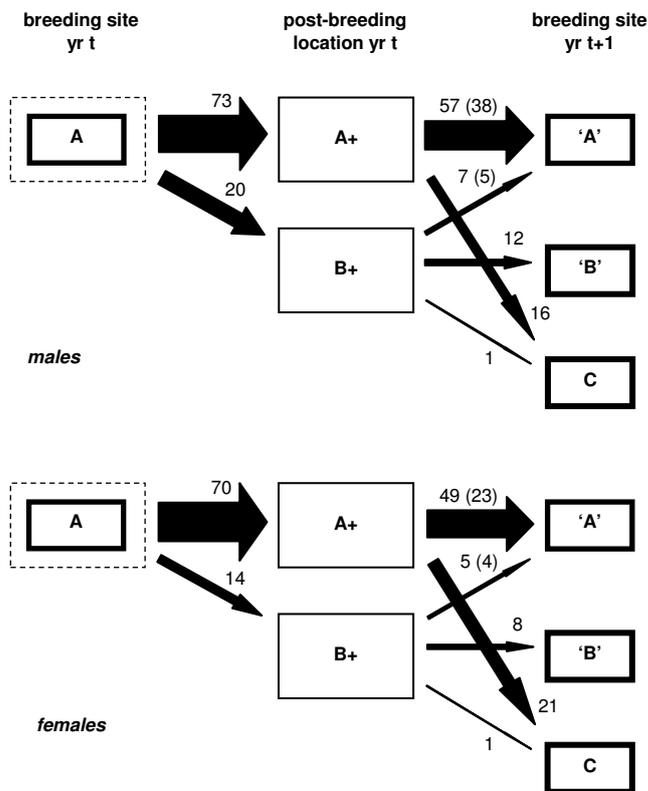


Fig. 9. Observed movements of males and females during two potential episodes of territory selection - the post-breeding period in year t and at territory establishment in year t+1. Arrow width indicates observed proportions of individuals, numbers refer to sample sizes. A: breeding territory site year t (dashed box indicates the area covered by the adjacent territory sites), A+: post-breeding location including adjacent territory sites centred around A, B+: as A+ but centred around B and no overlap with A+, 'A': breeding territory site year t+1 which is part of A+, 'B': breeding territory site year t+1 which is part of B+, C: breeding territory site year t+1 which is not part of A+ or B+. Numbers in parenthesis refer to individuals returning to breeding territory site A in year t+1 (i.e. territory site fidelity).

Between years more females (72%) than males (54%) shifted territory site, i.e. returned to breed at a different territory site than that occupied the previous year ($P=0.004$). Most of these territory shifts were over short distances, and 65% of males and 63% of females shifted within a distance of two territory sites. The probability to shift breeding territory sites between years was positively related to the probability to shift to a new post-breeding location at least among males ($P=0.028$; females: $P=0.75$). It therefore seemed that for some individuals the decision to shift to a new territory was partly determined already during the post-breeding season. The results, however, also suggest that the location of the breeding site in the subsequent year was largely determined at the time of establishment. On average about 26% of all males and 32% of all females did not return to breed at a territory site included in the post-breeding location. Among males, between-year territory site shifts were related to age, breeding success and territory attractiveness (in terms of long-term occupancy; Table 1). These factors did not influence their movement during the previous post-breeding period, although young males (which on average breed on poorer sites), failed males, and males breeding at less attractive sites would be expected to benefit most from prospecting during the post-breeding period. The decision to choose a new breeding site after e.g. a failed breeding attempt was therefore not realised immediately but at establishment in the next year. Unexpectedly, between-year site shifts were not related to territory field layer height in neither male nor females. At the same time, data suggested that males which arrived later on the breeding grounds were more likely to shift territory site, indicating that individuals cannot always return to preferred territory sites, possibly because a site might already be occupied by another male at the time of arrival.

Table 1. Factors associated with shifts to a new post-breeding location and between-year territory site shifts of males and females. Factors indicated in bold were significantly ($P<0.5$) related to site shifts. Factors in italics were only significant within the subset of individuals staying at their breeding site during the post-breeding period.

	post-breeding site shift	between-year site shift
<i>males</i>		
	age	age
	-	<i>arrival yr t+1</i>
	field layer height	field layer height
	occupancy	occupancy
	breeding success	breeding success
	no. neighbours	no. neighbours
	neighbour success	neighbour success
<i>females</i>		
	age	age
	-	arrival yr t+1
	field layer height	field layer height
	occupancy	occupancy
	breeding success	breeding success
	no. neighbours	no. neighbours
	neighbour success	neighbour success

Thus, the results from this study suggest that territory selection of experienced breeders is partly constrained by survival costs during the post-breeding period and by the establishment of earlier arriving individuals that sometimes can force individuals to shift site. These two factors are rarely considered in studies of habitat selection and dispersal, but are likely to be important for many species.

Sex-biased dispersal

In most bird species males choose the breeding site first in order to attract a female and females choose only sites defended by males. In such resource-defence mating system with asymmetrical roles of the sexes in territory defence, females will on average have fewer sites to choose from than males. As shown above (*Paper II*) site availability may affect patterns of dispersal and site fidelity. I therefore predicted that at the time of territory establishment females had on average fewer sites to choose from than males, and that females were less likely to find their previous year's territory site available. I expected that this sex-difference in site availability could cause the more frequent territory site shifts between years among females (see above, *Paper II*).

In general, sex-biased dispersal, i.e. the commonly more extensive dispersal among females in birds, or males in mammals, has received considerable attention in the literature. Greenwood (1980) related sex-biased dispersal to the general features of mating systems, i.e. resource defence in birds and mate defence in mammals, and which determines which sex settles first in relation to resources. Greenwood hypothesised that because in birds males compete for resources males also incur greater costs of establishing a new territory at an unfamiliar site, which could explain female-biased dispersal. Given Greenwoods hypothesis wheatear males should be less likely to shift sites than females when the previous year's territory site is available at the time of establishment for both sexes.

I estimated the number of available breeding sites within the study area and in the neighbourhood (i.e. an individual's previous year's territory site and the territory sites sharing boundaries) for each individual on its arrival date as the number of vacant territory sites (for males), or sites with an unpaired male (for females). Similarly, the previous year's territory site of an individual was defined to be available when it was vacant (for males), or defended by an unpaired male (for females).

Male wheatears had on average more sites available than females ($P < 0.0001$; Fig. 10). As predicted from this pattern, the probability to return to the territory site occupied in the previous year was on average higher for males than for females, i.e. returning males were more likely to find their previous year's territory site available (84.9%) than were females (52.7%; $P < 0.0001$). In this data set, males tended to shift breeding site between years less often (54.7%) than females (66.3%; $P = 0.079$; see also above, *Paper II*). The overall greater probability of between-year site shifts among females appeared to be mainly caused by the corresponding female-bias in the unavailability of the previous year's breeding site (*Fig. 11*), i.e. most site shifts among females were linked to the unavailability of the previous

year's breeding site whereas this was not true for males (sex difference: $P < 0.0001$). Among birds for which the previous year's territory site was available, however, there was no sex difference in between-year site shifts (males: 43.6%; females: 33.3%; $P = 0.266$). These results held also in a subset of birds that in the year before the investigated settlement were old and breeding successfully, i.e. removing young and failed breeders which had a higher propensity to shifts sites between years (see *Paper II*) and were more likely to shift sites voluntarily (Fig. 11).

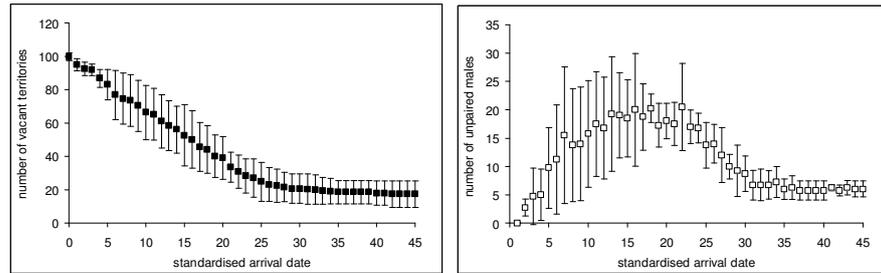


Fig. 10. Number of available sites for arriving male (solid symbols) and female (open symbols) wheatears in relation to arrival date (standardised for annual variation, day 1 = arrival of first male) in 2002-2005. Error bars refer to standard deviations.

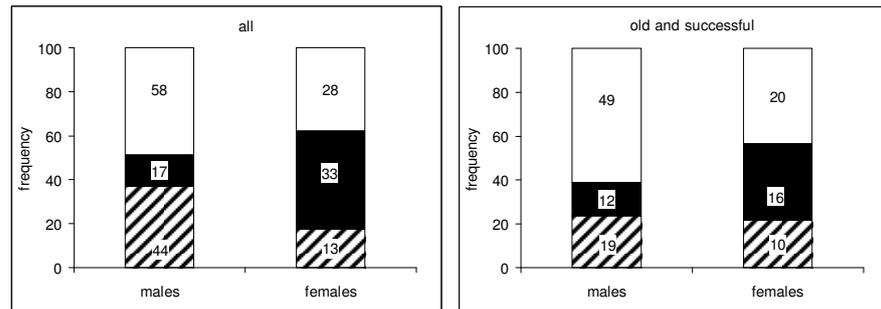


Fig. 11. Proportion of males and females that shifted sites between years when their previous year's site was available (hatched), unavailable (solid), or that remained site faithful (open), from all birds with known arrival dates and a subset of old successful wheatears (numbers refer to sample sizes).

These results supported my hypothesis that a female-biased constraint in site availability may be a proximate cause for sex-biased dispersal patterns. Simultaneously, my results did not support Greenwood's (1980) hypothesis of males being more constrained to move due to greater establishment costs, as males that had their previous year's site available were at least as likely to shift sites as were females. Present evidence from other bird species shows that the earlier arrival of one sex (usually males) and asymmetric roles in establishment seem to be a common phenomenon (Lack 1940; Morbey & Ydenberg 2001), and therefore one sex should be more constrained than the other in terms of selecting a specific breeding site, e.g. the "home" site. The possibility of a sex-difference in the

availability of breeding sites needs therefore to be taken into account when investigating the causes of sex-biased dispersal.

Habitat-specific population growth

One important step to link individual habitat selection behaviour and population dynamics is to investigate the contribution of different habitats to population growth. Habitats of different quality can be difficult to separate as there is usually a fine scale gradient in quality. Agricultural landscapes offer an opportunity to study habitat-specific population growth as they consist of distinct and relatively homogeneous habitat types. In *Paper IV* I move from classifying wheatear territories as characterised by either permanently short or growing (tall) field layers to examining the population growth rate of birds breeding in distinct land use types. Data on habitat-specific growth rates are needed if we want to identify the habitat types crucial to population persistence in agricultural landscapes. Farmland birds, and among them the wheatear, have been declining in many European countries during the last decades (Tucker & Heath 1994; Donald et al. 2001; Birdlife International 2004). These declines have been attributed mainly to changes caused by agricultural intensification (Chamberlain et al. 2000; Donald et al. 2001; Newton 2004), or abandonment (Suarez-Seoane et al. 2002; Wretenberg et al. 2006). Although there are studies investigating whether these suggested causes affect demographic rates of individuals (e.g. De Bruijn 1994; Wilson et al. 1997; Brickle et al. 2000; Smith & Bruun 2002), no study has fully investigated the effects on population growth, i.e. when the combined effects of survival and reproduction are taken into account. Therefore, I estimated population growth rate of wheatears breeding in distinct land use types to investigate the potential causes of the observed declines of wheatears in farmlands.

Each territory site was categorised each year as belonging to one of the following distinct land use types: farmyard, pasture grazed by cattle, pasture grazed by horses, spring-sown crop fields, autumn-sown crop fields, and mowed and unmanaged (residual) grasslands. The first three habitat types were generally characterised by a permanently short field layer, whereas the latter three habitat types were characterised by a growing (tall) field layer. This resulted in a fine-grained mosaic of territory sites of the different habitat types. Based on previous results where wheatears breeding territories characterised by permanently short field layers had a higher reproductive success (breeding success, number of fledged young, number of local recruits; see above, *Paper I*) I predicted that population growth rate would be greater in the first three habitat types.

To estimate population growth rate I used a male-based (as there were more complete age-specific data on males) two-stage (based on the two age classes) matrix model (Caswell 2001; Morris & Doak 2002), where the matrix elements are composed from different vital rates (i.e. demographic parameters). Of the vital rates breeding success (i.e. probability of successful breeding, see Methods), the number of fledged young, and local adult survival rates could be estimated for each habitat type, whereas uniform estimates (i.e. across all habitat types; due to small sample sizes in some habitats) were used for local first-year survival rate and

probability of breeding for both age classes. I estimated population growth rates for two scenarios, one using uniform and the other using habitat-specific adult survival rates, each using six habitat-specific matrices. Long-term population growth rate in the different habitats assuming temporal environmental variance, i.e. stochastic log growth rate $\log \lambda_s$, was calculated using computer simulation (Caswell 2001; Morris & Doak 2002). Temporal environmental variance could be calculated for breeding success, the number of fledged young and adult survival rate (first-year survival rate was assumed to have a similar environmental variance as adult survival rate; Kendall 1998; Caswell 2001; Morris & Doak 2002).

As predicted, $\log \lambda_s$ was greater in farmyard, cattle and horse pasture habitats, where population growth was close to $\log \lambda_s=0$ (i.e. $\lambda=1$, typical for stable populations), whereas population growth rate was below that value in spring crop, autumn crop and mowed/residual grassland habitats (Fig. 12). Although habitats appeared to differ most with respect to reproduction (number of fledglings produced; absolute differences between habitat types according to a Life Table Response Experiment, LTRE; Caswell 2001; *Paper IV*), adult survival rate had the strongest impact on differences in λ between the habitat types (Fig. 13).

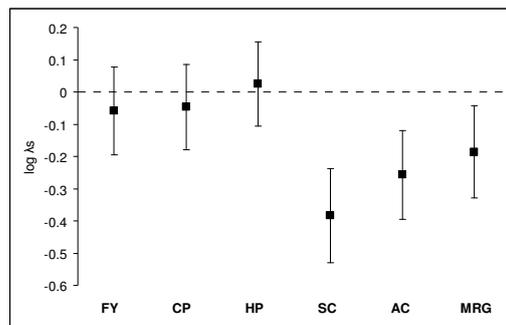


Fig. 12. Habitat-specific stochastic log growth rate $\log \lambda_s$ using habitat-specific male survival rates. Error bars refer to standard deviations (10,000 simulations of $\log \lambda_s$). FY: farmyard, CP: cattle pasture, HP: horse pasture, SC: spring crops, AC: autumn crops, MRG: mowed/residual grassland.

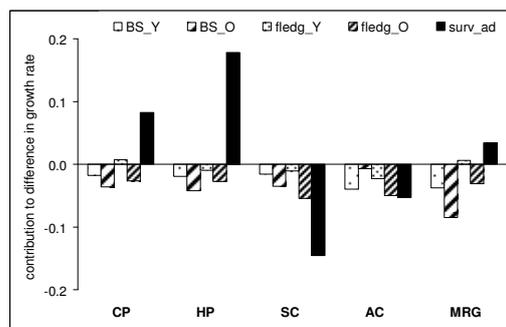


Fig. 13. Contributions of vital rates to differences in λ between each habitat type compared to the reference habitat FY (based on LTRE; Caswell 2001), using habitat-specific adult male survival rates. BS_Y, BS_O: breeding success of young (one year old) and old (older) males, fledg_Y, fledg_O: number of fledged young, surv_ad: male adult survival. See Fig. 12 for explanation of habitat types.

Overall, estimated population growth was most likely an underestimation because of long-distance dispersal out of a finite study area, even though I tried to minimize the influence of dispersal out of the study area on first-year and adult survival rates (see Methods). Despite underestimating adult survival rate, however, observed breeding dispersal distances did not differ between habitats, and therefore do not indicate a higher propensity to disperse from habitats with low estimates of

adult survival rates. Thus, based on the estimated habitat-specific growth rates, farmyard, and cattle and horse pasture habitats are likely to act as source habitats (i.e. habitats where reproduction exceeds mortality; Pulliam 1988). Growth rates were low especially for spring-sown and autumn-sown crop fields, suggesting that these habitats may potentially act as sink habitats (i.e. populations are maintained only by net immigration; Pulliam 1988). In Sweden, the area of semi-natural dry pastures has decreased steadily since the 1950's (30% decrease; Statistics Sweden 1996), and small-scale farming has become extensified or abandoned in several regions (Wretenberg et al. 2006). The loss and degradation of these high quality habitats for breeding wheatears may therefore have been a major factor for the observed decline in population numbers of the wheatear in Sweden (about 60% between 1976 and 2001; Wretenberg et al. 2006).

Territory preference and between-year site shifts in relation to the different habitat types

Having shown that different habitat (land use) types contributed differently to population growth it is interesting to ask how wheatear territory preference is related to these habitat types. As I have shown in *Paper I* wheatears displayed non-ideal habitat selection with respect to differences in territory field layer height. To repeat the preference analysis of *Paper I* with respect to the habitat types I used order of establishment (ranked arrival dates) of male wheatears from years 2001 to 2005 (to increase sample size per habitat type). As in *Paper I* territory preference was only related to territory cluster size but not to habitat type (mixed-model ANCOVA with territory identity as random factor, fixed factors year, age class, habitat type and territory cluster size, and order of establishment as dependent variable, $N=299$; cluster size effect: $F_{1,288}=12.62$, $P=0.0004$; habitat type: $F_{5,286}=0.82$, $P=0.54$). Hence, wheatear preference did not differ between the habitat types. Wheatears did not seem to avoid spring-sown and autumn-sown crop field at the time of territory establishment, even though these habitats contributed least to population growth. Thus, this result corroborates the conclusions from *Paper I* of non-ideal habitat selection with respect to habitat quality.

Data on between-year site shifts, however, indicate that experienced breeders move away from crop fields and mowed/residual grasslands to settle on a territory site within a different habitat type, mostly pastures and farmyards (Table 2). Thus, experienced breeders were able to adjust a previously poor choice, and avoided poor habitats in the subsequent year. Still, some individuals from higher quality habitats moved also into poorer quality habitat (Table 2), probably reflecting the constraints on settlement as shown in *Paper II* and *III*.

Table 2. Proportions (%) of individuals from different habitat types shifting territory site between years (site shift = yes) and returning to breed in a habitat type either characterised by population growth rates of $\lambda=1$ (FY, CP, HP) or $\lambda<1$ (SC, AC, MRG). FY: farmyard, CP: cattle pasture, HP: horse pasture, SC: spring crops, AC: autumn crops, MRG: mowed/residual grassland. For comparison also site faithful individuals (site shift = no) are shown. Data for individuals originally breeding at SC and AC territory sites were pooled due to small sample sizes. (Data from *Paper II*, see above, excluding individuals breeding 1995 and 1995 due to missing classifications of habitat types, including repeated observations for some individuals)

habitat type year t	site shift	FY, CP, HP year t+1	SC, AC, MRG year t+1	N
FY	yes	72	28	25
	no	100	-	7
CP	yes	82	18	122
	no	95	5	92
HP	yes	82	18	22
	no	96	4	24
SC, AC	yes	69	31	13
	no	-	100	5
MRG	yes	94	6	16
	no	17	83	12

Concluding remarks and future prospects

My thesis shows that individual based analyses of habitat preferences and dispersal behaviour are important if we want to make inferences about the habitat selection processes and their links to population growth. I show that individuals might not always select the best habitat available, because of several reasons. First, at the time of habitat selection habitat characteristics may not always be reliable cues to predict breeding performance which can lead to non-ideal habitat selection (*Paper I*). Such deviations from ideal habitat selection may be more common than generally assumed, especially in changing landscapes. Second, information gathering of experienced breeders by post-breeding prospecting may be limited by costs in terms of future survival (*Paper II*). It is thus important to consider costs and benefits of different habitat selection strategies for different types of individuals (see also Naves et al. 2006). Third, site-dominance of earlier arriving individuals may constrain the selection of the best or preferred sites (*Paper II* and *III*). The effects of the third constraint on sex-biased dispersal illustrate the close, but rarely investigated, links between habitat selection and dispersal. If we are to understand individual variation in dispersal we have to also understand individual habitat selection strategies and their constraints. Furthermore, I showed that farmland breeding habitats had different effects on demography and that these habitats differed in their contributions to population growth (*Paper IV*). In isolation such habitat-specific differences in demography have been used to infer habitat conservation strategies to increase population long-term persistence. However, if

individuals are not making an ideal selection of habitats, i.e. not always selecting the best habitat available, conservation strategies based on purely habitat-specific modelling will not result in the anticipated effect. My study strongly suggests that given the above constraints more individuals will be found in poor habitats than expected. Hence, population models assuming ideal habitat selection will always overestimate population long-term persistence (see also Pulliam & Danielsson 1991; Delibes et al. 2001; Kristan 2003).

How much, however, site selection and non-ideal selection will limit population growth and persistence will also depend on additional factors not addressed in this thesis. For example, landscape habitat composition will affect the proportions of individuals in the different habitats (see also Rodenhouse et al. 1997) and the spatial configuration of habitats will affect the movements of individuals between habitats (i.e. dispersal; Hanski 1999; Clobert et al. 2004; With 2004).

Landscapes do not only change in their amount and relative distribution of different habitat types, they may also change in the relative quality of these habitats. How quickly individuals can respond to such changes in relative habitat qualities (see e.g. Schlapfer et al. 2002, Kokko & Sutherland 2001) is at present not known. Therefore, for future habitat selection studies it will be important to investigate to what extent dispersal and habitat selection strategies are learned, condition-dependent (or state-dependent) and genetically determined (Roff & Fairbairn 2001; Clobert et al. 2004).

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TACK

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