How do birds search for breeding areas at the landscape level? Interpatch movements of male ortolan buntings

Svein Dale, Øyvind Steifetten, Tomasz S. Osiejuk, Katarzyna Losak and Jakub P. Cygan

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Animal movements at large spatial scales are of great importance in population ecology, yet little is known due to practical problems following individuals across landscapes. We studied the whole Norwegian population of a small songbird (ortolan bunting, *Emberiza hortulana*) occupying habitat patches dispersed over nearly 500 km^2. Movements of colour-ringed males were monitored during ten years, and extensive long-distance dispersal was recorded. More than half of all cases of breeding dispersal took place within one breeding season, and males moved up to 43 km between singing territories, using 1–22 d. Natal dispersal was usually to a habitat patch close to the natal patch, or within the natal patch if it was large. Breeding dispersal movements were often long-distance, beyond neighbouring patches, and up to 11–19 patches were overflown. Movements of at least 6–9 km across areas of unsuitable habitat occurred regularly. The number of patches visited was low (1–4) even though search costs in terms of time spent moving from one site to another were relatively low (often only a few days even for distances >10 km). Most males seemed to use a threshold tactic when choosing a patch, but returns to previously visited patches were recorded, including some cases of commuting. In conclusion, male ortolan buntings have a surprising ability to move quickly at the landscape level, and this resulted in a high connectivity of patches. We discuss our results in relation to optimal searching strategies, in particular the use of within-breeding season versus post-breeding season search, conspecific attraction and adaptive late arrival of young birds.

S. Dale (svein.dale@umb.no) and Ø. Steifetten, Dept. of Ecology and Natural Resource Management, Norwegian Univ. of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway. — T. S. Osiejuk and K. Losak, Dept. of Behavioural Ecology, Institute of Environmental Biology, Adam Mickiewicz Univ., Umultowska 89, PL-61-614, Poznan, Poland. — J. P. Cygan, Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, PL-00-679 Warszawa, Poland.

Animal movements at large spatial scales are of great importance in population ecology, because they affect patterns of distribution, abundance, extinction and colonization dynamics, population structure, and gene flow (MacArthur and Wilson 1967, MacArthur 1972, Hanski 1999, Clobert et al. 2001, Bullock et al. 2002, Bowne and Bowers 2004). Despite the need to understand how and why long-distance movements across landscapes occur, little is known due to the practical difficulties involved in tracking movements of individuals over large distances (Lima and Zollner 1996, Zollner and Lima 1999, Reed et al. 1999, Stamps 2001, Wiens 2001). For example, many population studies of birds have been conducted on study sites of only a few square kilometers even though many birds regularly perform inter-continental migrations. Natal and breeding dispersal distances of birds have usually been reported to be in the order of hundreds of meters up

to a few kilometers (Greenwood and Harvey 1982, Paradis et al. 1998), yet far longer movements are known to occur (Marzluff and Balda 1989, Moore and Dolbeer 1989, Paradis et al. 1998, Veit 2000). Long-distance movements may often be perfomed by a minority of individuals, but the population consequences of such rare events may be profound (Brown and Kodric-Brown 1977). Thus, it is essential to improve our understanding of when and how individuals search for new breeding areas, how the spatial and temporal search range is influenced by costs of dispersal and landscape structure, and how individuals decide when to stop searching and settle in a new site.

For birds, the traditional view has been that long-distance movements to new sites occur during natal dispersal, whereas breeding dispersal movements among adult individuals are fairly restricted (Greenwood and Harvey 1982, Paradis et al. 1998). Thus, it is often thought that young birds search for future breeding sites during the post-fledging period (i.e during late summer and autumn; Brewer and Harrison 1975, Adams and Brewer 1981, Morton et al. 1991, Reed et al. 1999). On the other hand, there are indications that at least some species (e.g. cavity-nesters) postpone prospecting for breeding sites until their first breeding season (Eadie and Gauthier 1985, Zicus and Hennes 1989, Reed and Oring 1992), and occasional long-distance movements within the breeding season have been observed (Newton 2000, Lang et al. 2002). Searching taking place either outside or within the breeding season may experience different costs and benefits. Studies have shown that individuals are often attracted to conspecifics (Stamps 1988, Reed and Dobson 1993, Ward and Schlossberg 2004), and even to heterospecifics (Mönkkönen et al. 1999), because this may increase the probability of locating high-quality breeding sites that are patchily distributed. In many bird species the possibility of using conspecifics to locate suitable breeding habitat is greatly increased within the breeding season when males sing. On these grounds, within-breeding-season movements can be expected to be more common than shown so far. An optimal searching strategy for birds using conspecifics to locate new breeding areas, may be to return to the natal area (short natal dispersal), but disperse in search of new sites within the breeding season if unsuccessful in attracting a mate in the natal area (long breeding dispersal; Dale et al. 2005).

Birds with their power of flight and navigational skills may at first sight be expected to have a well-developed ability to move through landscapes and locate distant areas of breeding habitat. Surprisingly, experimental translocations of birds indicate that enforced travel distances of only a few kilometers through unfamiliar terrain may present serious obstacles. Forest birds used longer time to return to their territory when they had to cross open habitats, whereas forest reduced travelling speed of open-country species (Bélisle et al. 2001, Gobeil and Villard 2002, Harris and Reed 2002, Castellon and Sieving 2005). Even at a smaller scale, forest gaps within territories present barriers to movements of forest birds (Desrochers and Hannon 1997, Develey and Stouffer 2001, Harris and Reed 2002). Thus, even though movement distances may in principle represent negligible costs in terms of time and energy to birds, travelling through unfamiliar areas apparently can impose costs, perhaps because of increased predation risk, encounters with aggressive conspecifics along the route, time needed to locate a safe route, or some other unknown cause (Yoder et al. 2004, Zollner and Lima 2005, Stamps et al. 2005).

Crossing inhospitable areas would be most likely if distances are short and preferred habitat can be seen before leaving a favourable patch. The ability to move through landscapes will therefore depend on the perceptual range of each species (Zollner and Lima 1997, Zollner 2000, Olden et al. 2004), which is expected to increase with body size (Mech and Zollner 2002), and should also depend on locomotory patterns. Among birds, species that depend on forest cover during movements (Bélisle et al. 2001, Gobeil and Villard 2002, Castellon and Sieving 2005) may have a more limited perceptual range than species willing to move through open areas or fly above treetops, but virtually nothing is known about how long-distance movements actually take place.

Finally, it is important to understand how searching for new breeding areas is terminated. Do individuals settle in the first patch of suitable habitat with an empty territory exceeding a specific quality threshold, or do they sample several sites and choose the best one among those? This is analogous to mate sampling among female animals (Janetos 1980, Real 1990), where evidence is accumulating that the number of mates sampled is restricted and can follow both threshold and pool-comparison rules (Dale et al. 1990, Dale and Slagsvold 1996, Gibson and Langen 1996). A restricted search for mates may be due both to direct costs of searching and competition between searchers for available options (Milinski and Bakker 1992, Dale et al. 1992). In contrast, the lack of data on sampling behaviour during breeding site search at the landscape level is striking.

The Norwegian population of ortolan buntings *Emberiza hortulana* is particularly well suited for studies of dispersal and movements at a large spatial scale. The ortolan bunting is a small-sized (20–25 g), migratory passerine bird wintering in Africa and breeding in open habitats in western Eurasia. The known population in Norway currently contains ca 150 singing males, with nearly all individuals distributed in ca 50 well-defined habitat patches in an area of nearly 500 km^2. Previous studies have indicated that

extraordinary long-distance movements, up to 45 km between breeding habitat patches, occur regularly (Dale et al. 2005). In this paper we analyse all observed movements including natal dispersal and changes in breeding sites (breeding dispersal) from a ten-year period. We analyse the temporal and spatial pattern of movements, and test the following hypotheses: 1) searching should be costly, and longer movements should therefore take longer time, 2) a limited perceptual range should limit the number of movements across long stretches of inhospitable areas, and 3) search costs should favour the use of a threshold strategy over a pool-comparison strategy (Janetos 1980, Real 1990). We also discuss the implications of the results for current understanding of patterns and processes of animal movements across landscapes.

Methods

Study area

Most Norwegian ortolan buntings occur in central Hedmark County (60.29–60.53°N, 11.40–12.18°E, maximum extent of this area was 40 km both north-south and east-west). Minor relict populations (<10 males) occur 50–80 km to the south and south-west in Akershus County. The Norwegian population is separated from the closest neighbouring population (in Sweden) by ca 250 km. A total of ca 50 habitat patches have been used by ortolan buntings during the study period 1996-2005 (Fig. 1), and the number of males in each patch has varied between 1 and 50.

All habitat patches are located in agricultural areas due to the use of cereal fields during foraging by ortolan buntings (Dale 2000, Dale and Olsen 2002). Many patches are surrounded by farmland on most sides, or they are situated at the edge between farmland and continuous boreal forest. Although the ortolan bunting can breed within wholly cultivated land in other countries (Cramp and Perrins 1994), in Norway they are totally dependent on specific habitat patches with open, sparse vegetation, especially heather *Calluna vulgaris* and scattered Scots pines *Pinus sylvestris* for nesting. Such habitats include raised peat bogs, recent forest clear-cuts on poor sand, land being cleared for cultivation, and one forest burn (Dale and Hagen 1997, Dale 2001a). Habitat patches are well-defined against surrounding matrix, and are easy to identify both on the ground and from the air. In the agricultural part of the landscape, potential habitat patches constitute <5% of the landscape. Distances between habitat patches were measured as the shortest stretch of unsuitable breeding habitat between edges of patches (unsuitable habitat was defined as areas not containing nesting habitat as described above, regardless of whether it was farmland

or forest, but in most cases there was >50% farmland between patches).

Field procedures

Adult birds, mostly males, were captured in mist nets with the aid of playback of song, and were given a combination of one metal ring and three colour rings to permit individual identification. All habitat patches known to have been used by ortolan buntings were visited at regular intervals (usually 2 d) throughout the breeding season to record the identity of individuals present. Other potentially suitable, although hitherto unused, habitat patches (n >30) were also visited frequently. During 1996–1998, males were captured and ringed in one large sub-population, where local ornithologists also had ringed some birds during 1991–1993. During 1999–2005, surveys and ringing took place in all known breeding areas in Norway. A total of 419 males had colour-rings as adults. In the period 1999–2005, at least 55–85% of all males had colour-rings each year (median 78%). In combination with the low number of individuals and habitat patches, this greatly increased the chances of documenting dispersal events. Analyses were restricted to males because females often behave cryptically and dispersal events can therefore be missed, in particular those movements that might occur before females become mated. Age was known with certainty only for birds ringed in the nest (nestlings were scored as 1K according to the Euring system). All birds ringed for the first time as adults were scored as first year or older (2K+ in the Euring system). The term "young" males refers to those being 2K or 2K+, whereas "older" males were at least 3K or 3K+ (in the American system: SY and ASY, respectively).

Definitions of dispersal

Natal dispersal of a male was defined as the movement between the place of birth (ringed as nestling) and the first singing territory, whereas breeding dispersal was defined as movements involving a change of singing territory [Dale et al. 2005; following Greenwood and Harvey (1982) and Paradis et al. (1998); see Dale et al. (2005) for a thorough discussion of definitions of dispersal]. Territories of ortolan buntings are roughly 100 m in diameter (Cramp and Perrins 1994, Dale and Olsen 2002), which is typical for small passerine birds. Territory changes were therefore defined as movements >200 m. All observations concern typical defended territories (i.e. singing territories).

For dispersal movements between habitat patches, we measured the longest stretch moved across unsuitable habitat (defined as areas where no ortolan buntings had been recorded), and the number of suitable habitat

Fig. 1. Map of main study area showing all habitat patches (dark areas) that were used by ortolan buntings at least once during 1999–2005. The figure also shows movements (arrows) made by three selected males identified in Table 2. Location of the study area (black circle) in Norway is indicated in top right corner.

5 km

N
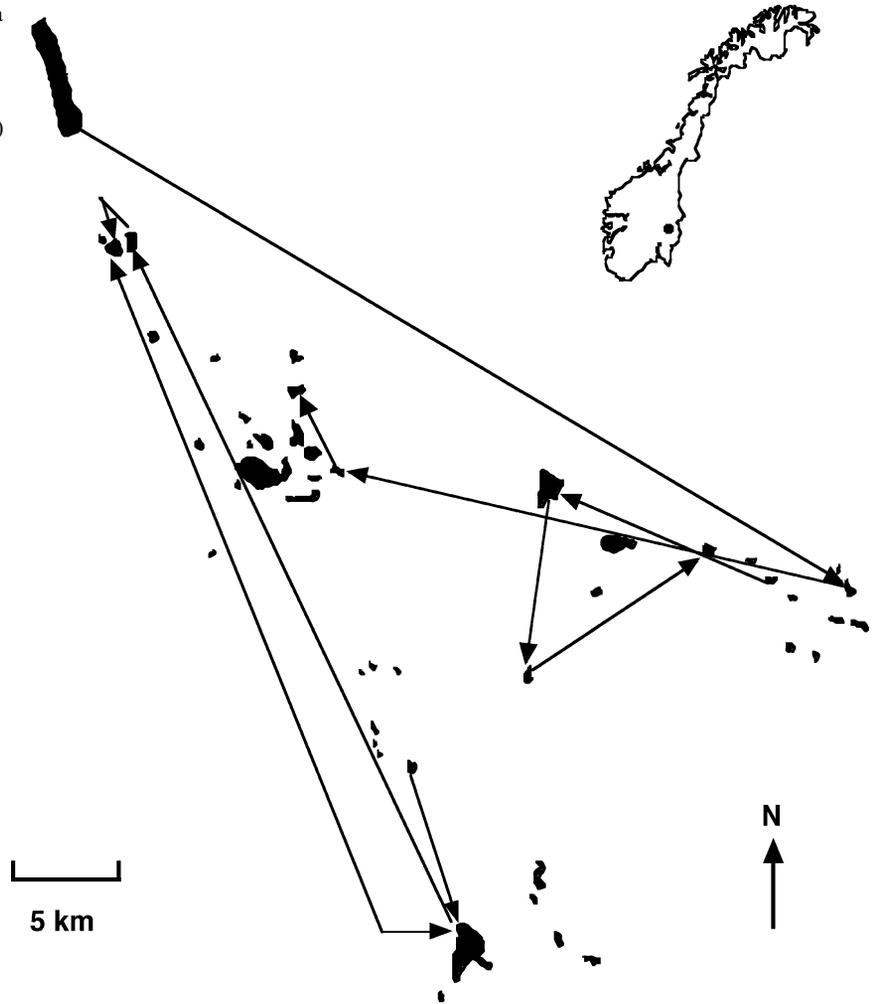
patches overflown (patches that had been used by ortolan buntings). These measurements were made using two different methods. In the first method (termed stepping-stone), we assumed that each leg of a movement made by a dispersing individual was to the closest suitable habitat patch which at the same time reduced the distance to the final habitat patch. In the second method (termed straight-line), we assumed that movements took place as straight-line movements, and we included all habitat patches within one km to each side of the line of movement. The first method may overestimate the number of habitat patches overflown, but underestimate the longest movements across unsuitable habitat. For the second method, biases may be in the opposite directions. Thus, we believe that the true search paths of dispersing ortolan buntings may lie somewhere between the two estimates. The first method may perhaps represent real movements best because it takes into account the spatial configuration of habitat patches which is likely to affect movement patterns (Lima and Zollner 1996, Wiens 2001).

Arrival times

Arrival times after spring migration varied significantly between years (Kruskal-Wallis test of 876 observations from nine years: $H = 80.9$, $p < 0.0001$), and, consequently, values used in analyses were taken as the deviation from the median value for each year. Data from 1996 were excluded because arrival time was not recorded in detail. In analyses of arrival time in relation to age, data on new birds from 1999 were excluded because many birds were captured for the first time (enlargement of study area; see above) and age was scored as 2K+ for all of these.

Statistical analyses

Non-parametric tests were used in most cases due to skewed distributions of many variables. All statistical tests were two-tailed. In the datasets for several types of analyses we have some cases of two or more observations of the same males. In order to avoid pseudoreplication,

we generally analysed the data using each male only once, and we report statistical results using the median of multiple observations of each male. However, to avoid discarding valuable information present in the full datasets, we also report the results of analyses of full datasets, and figures display full datasets.

Results

Timing of movements

Of all recorded breeding dispersal events (n = 324), more than half occurred within one breeding season (n = 175 observations of 111 different individuals; between breeding seasons: n = 142 observations of 117 different individuals; seven observations of seven different individuals were of unknown timing). Males were present in their first territory 1–38 d (median 5 d, n = 168; using median values for each individual: range 1–38, median 5, n = 111), and used 1–22 d (median 5 d, n = 168; median values for each individual: range 1–22, median 5.3, n = 110) to move to their second territory which was 0.2–43.1 km away (median 2.5 km, mean 7.0 km, n = 175; median values for each individual: median 2.9 km, mean 7.3 km, n = 111). Two males had attracted a mate in the first territory, and they moved after probable loss of female and nest failure, respectively. The other males did not attract a female in the first territory.

Males that moved within one breeding season had arrived on average 1.5 d later to the study area than males that did not move (U-test: $z = -3.68$, $n_{moved} = 122$, $n_{remained} = 754$, $p = 0.0002$; using median values for each individual: 1.6 d later, $z = -1.85$, $n_{moved} = 108$, $n_{remained} = 357$, $p = 0.065$), mainly because young males were overrepresented among males moving (106 movements by males in their first year as adults vs 68 older males), and young birds arrived later than older birds (U-test: $z = -11.44$, $n_{young} = 354$, $n_{old} = 522$, $p < 0.0001$; median values for each individual: $z = -8.33$, $n_{young} = 354$, $n_{old} = 243$, $p < 0.0001$). Thus, movers did not arrive later than non-movers within age-classes (U-tests: young males, $p = 0.12$; older males, $p = 0.76$; each male included only once in test for young males; using median values for each of older males: $p = 0.62$). Overall, searching for a new breeding site took place after many males had arrived, and arrival to the second territory was usually well into the breeding season (median 26 May; for most breeding pairs this is during egg-laying or the first part of the incubation period; median arrival date to first territory of all males was 11 May).

Between breeding seasons, males moved 0.2–52.8 km (median 1.0 km, mean 5.8 km, n = 142; using median values for each individual: median 1.1 km, mean 6.1 km, n = 117). These movements may have taken place either at the end of the first breeding season (year x) without being detected, or early in the next breeding season (year x + 1). The latter was apparently supported by the full dataset because arrival in year x + 1 of males that had moved was later than for males that returned to the same territory they had in year x (difference 1.6 d; U-test: $z = -2.81$, $n_{moved} = 135$, $n_{returned} = 382$, $p = 0.005$). However, when using median values for each individual, this trend disappeared (difference 0.9 d; U-test: $z = -1.25$, $n_{moved} = 112$, $n_{returned} = 190$, $p = 0.21$). Furthermore, in the full dataset the difference in arrival time did not hold when taking age into account (U-tests: second year as adults, $p = 0.25$; third year as adults or older, $p = 0.30$). In addition, there was no relationship between the distance moved and the arrival time in year x + 1 ($r_s = 0.00$, $n = 135$, $p = 0.99$). Thus, it seems that the time needed to locate the new site was spent in year x and not in year x + 1.

The distances moved for the seven cases of breeding dispersal for which timing was unknown was 17.8–44.5 km (median 22.1 km, mean 27.8 km).

Spatial pattern of movements

Natal dispersal of ortolan buntings was shorter than breeding dispersal [Wilcoxon matched-pairs signed ranks test comparing natal dispersal distance (median 3.3 km, mean 6.4 km) with combined breeding dispersal distances (median 5.2 km, mean 12.5 km) for each male, including all males for which both dispersal types had been recorded: $z = -2.08$, $n = 41$, $p = 0.038$; expanded dataset compared to Dale et al. (2005)]. Natal dispersal was often within the natal habitat patch if it was large (10/20 within patch for the three largest patches), or to another patch if it was smaller (2/35 within patch for other patches; $\chi^2 = 12.15$, DF = 1, $p = 0.0005$). For interpatch movements, the number of habitat patches overflown during breeding dispersal was not significantly different from during natal dispersal (Table 1, Fig. 2). Unsurprisingly, the distance moved increased with the distance to the closest neighbouring patch (natal dispersal: $r_s = 0.60$, $n = 46$, $p < 0.001$; Fig. 3a; breeding dispersal: $r_s = 0.35$, $n = 175$, $p < 0.0001$; Fig. 3b; using median values for each individual: $r_s = 0.36$, $n = 110$, $p = 0.0002$). However, the difference between the actual distance moved and the distance to the closest patch differed between dispersal types; movements during breeding dispersal were further beyond the closest neighbouring patch than during natal dispersal (U-test: $z = -1.04$, $n_{natal} = 46$, $n_{breeding} = 175$, $p = 0.30$; using median values for each individual ($n_{breeding} = 110$): $z = -2.18$, $p = 0.030$). The effect was stronger when the test was restricted to a comparison between natal dispersal and breeding dispersal of young males (U-test: $z = -1.78$, $n_{natal} = 46$, $n_{breeding} = 122$, $p = 0.076$; using median values for each individual ($n_{breeding} = 92$): $z = -2.51$, $p = 0.012$).

Table 1. Comparisons of number of habitat patches overflown during natal and breeding dispersal of male ortolan buntings. The number of habitat patches overflown was estimated with two different methods (stepping-stone and straight-line, see Methods for explanations).

Dispersal type	Number of habitat patches overflown			
	N	Median	Mean	P[1]
Stepping-stone method				
Natal dispersal	46	2.0	3.5	
Breeding dispersal				
All observations	175	3.0	4.5	0.40
Median values for each male	110	4.0	4.9	0.062
Straight-line method				
Natal dispersal	46	2.0	2.3	
Breeding dispersal				
All observations	175	1.0	2.2	0.43
Median values for each male	110	2.0	2.4	0.87

[1]p-values for U-tests of the difference between natal and breeding dispersal for each method used.

This indicates that young ortolan buntings often start their first year as adults by returning to their natal area or the immediate surroundings to establish a territory. If unsuccessful in attracting a mate, males often change territory, and in many cases they search for a new territory far beyond the local neighbourhood (Fig. 2). Among young birds of known age (2K), only 6% (4/63) attracted a female in their first territory, and 82% of
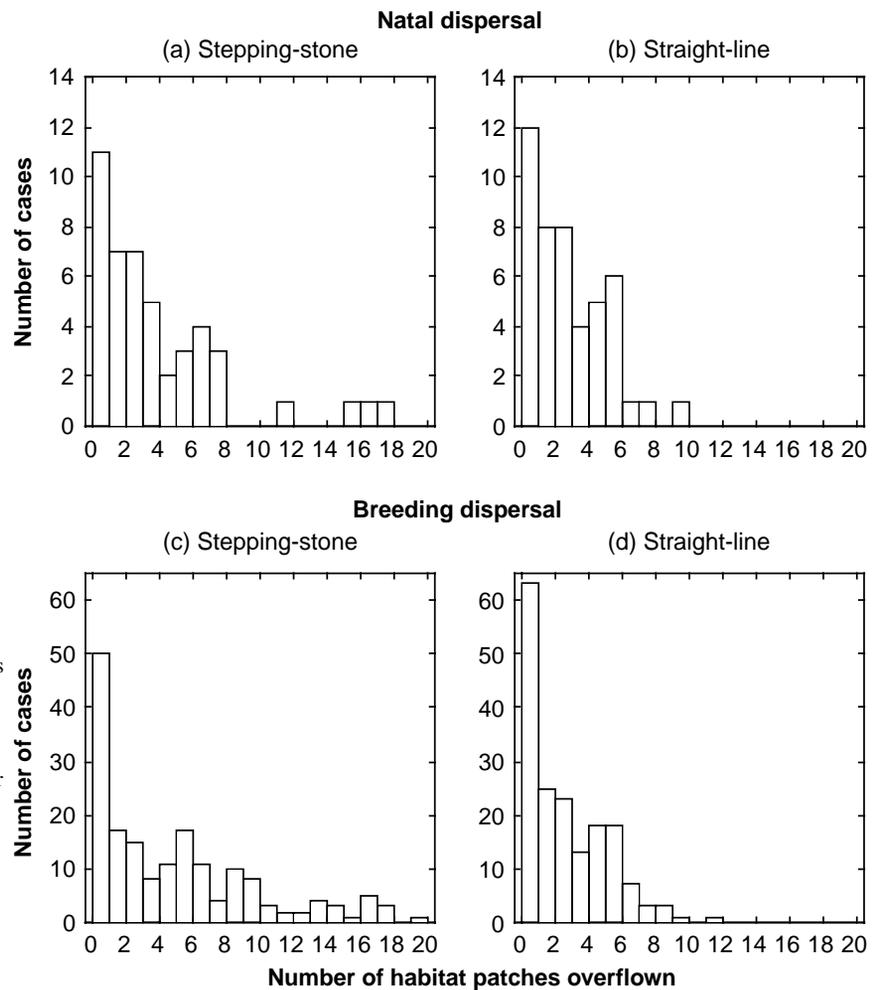

Fig. 2. Frequency distributions of the number of habitat patches overflown by male ortolan buntings during (a, b) natal dispersal, and (c, d) breeding dispersal. The number of habitat patches overflown was estimated with two different methods; (a, c) stepping-stone and (b, d) straight-line (see Methods for explanations). Only males that changed habitat patch are included, movements within a patch are excluded.

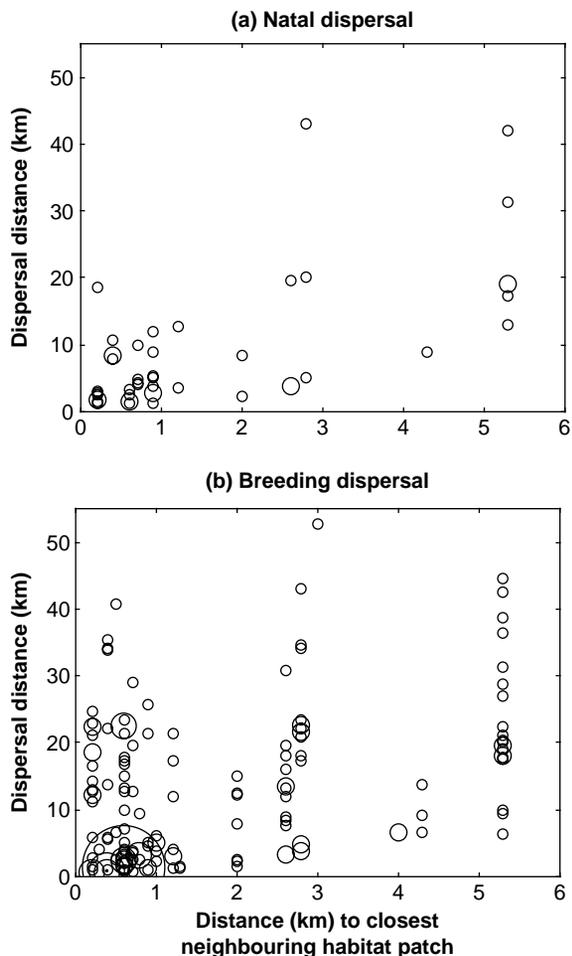**(a) Natal dispersal**

(b) Breeding dispersal

Fig. 3. Dispersal distances of male ortolan buntings in relation to the distance to the closest neighbouring habitat patch for (a) natal dispersal, and (b) breeding dispersal. Only males that changed habitat patch are included, movements within a patch are excluded. Larger symbols indicate overlapping data points (the largest symbols represent n = 2 and n = 10 in a and b, respectively).
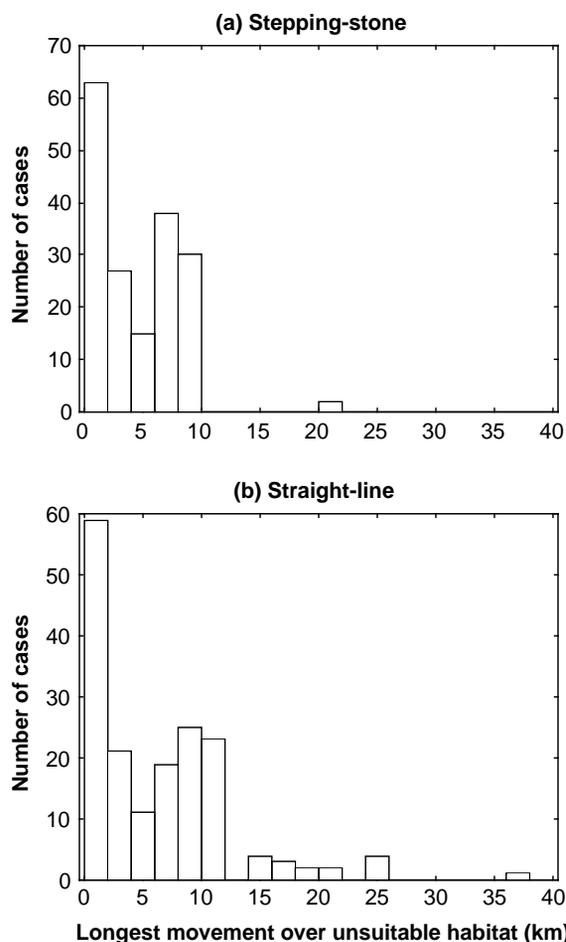

(a) Stepping-stone

(b) Straight-line

Fig. 4. Frequency distribution of longest distance moved across unsuitable habitat between suitable habitat patches for each observed breeding dispersal by male ortolan buntings. The number of habitat patches overflown was estimated with two different methods; (a) stepping-stone and (b) straight-line (see Methods for explanations).

those which did not attract a female (23/28, including only males that were seen the next year) dispersed to another site.

Dispersal events regularly included movements between habitat patches separated by >5 km of unsuitable habitat (Fig. 4). Many individuals moved between patches far apart (Fig. 1).

Number of patches visited

Male ortolan buntings stopped searching for new habitat patches after having visited 1–4 patches (mean 1.35; Table 2). The number of patches visited as adults increased with number of years observed ($r_s = 0.23$, n = 414, p < 0.0001). Among males observed at least two years, however, there was no relationship between

number of patches visited and years observed ($r_s = -0.01$, n = 248, p = 0.88), but mean number of patches visited was still only 1.48. Most individuals seemed to use a threshold strategy (86 individuals settled in the last patch visited and had visited at least two patches; Table 2). However, 24 cases of returns to previously visited habitat patches were recorded (Table 2) which could indicate a pool-comparison strategy. Seven of the latter cases involved commuting, i.e. moving between two patches at least three times (Table 2). Commuting took place within one breeding season in three cases, and over the course of 2–3 yr for the remaining four males. Commuters were generally older males (one male commuted in his seventh year as adult, and only two first-year adults did so and both completed their commuting in a later year). Commuting distances were 0.8–34.1 km (median 3.1 km).

Table 2. Breeding area search strategies of male ortolan buntings. Letters denote different habitat patches used by each individual (a =natal patch; A,B,C,D =different patches used as adult birds; A =a for birds known from birth).

	Number of individuals	Number of years observed as adult								
		1	2	3	4	5	6	7	8	9
Natal patch known (=a)										
aA	11	9			1				1	
aB	25	18	3	3			1			
aAB	5		1	3				1		
aBC	11	2	3	4	2					
aBA	2	1			1					
aBCD	4	2	2							
aABCD[1]	1	1								
aBCA	1	1								
aBCAD	1	1								
aBAC	1		1							
aABCBCBCBC	1									1
Natal patch not known[2]										
A	268	118	73	27	23	12	10	3	1	1
AB	53	12	19	11	3	3	5			
ABC	9	1	3	3	1		1			
ABCD	3		2		1[1]					
ABCDBDB[1]	1				1					
ABA	8	1	2	4		1				
ABAB	3		1	1	1					
ABACD	1			1						
ABAC	1	1								
ABCA	2		1	1						
ABCBC	1			1						
ABCBCB	1			1						

[1]Spatial pattern of movements shown in Fig. 1.
[2]Note that these males were aged as 2K+ when ringed, and the true age of some of those may have been >2K. Because males perform movements especially when young (Dale et al. 2005), this means that the reported search strategies may underestimate the real extent of the search. This applies especially to some males in the group with search strategy "A" (n=268).

Cost of searching

There was a signficant increase in dispersal distance with increasing time spent dispersing (r_s =0.23, n =168, p = 0.0027; Fig. 5; using median values for each individual: r_s =0.27, n =110, p =0.0055). However, this was mainly due to the short time used in short-distance movements. Considering only long-distance movements (here arbitrarily set at ≥5 km), there was no significant relation between time used and distance moved (r_s =0.03, n =59, p =0.84; using median values for each individual: r_s = 0.25, n =44, p =0.10).

Were overflown patches visited?

The low number of habitat patches visited was based on observations of singing territories. Up to 19 habitat patches were overflown (stepping-stone method) during movements between two singing territories, or between the natal patch and the first singing territory (Fig. 2). Is it likely that many or all overflown habitat patches were visited, but rejected without establishment of a singing territory? The number of habitat patches overflown increased with the time spent dispersing (stepping-stone method: r_s =0.26, n =110, p =0.0061; Fig. 6a; using median values for each individual: r_s =0.39, n =64, p = 0.002; straight-line method: r_s =0.17, n =110, p =0.070;

Fig. 6b; using median values for each individual: r_s = 0.23, n =64, p =0.073), suggesting that dispersing individuals have spent time in the overflown patches. However, this relationship was to some degree due to the fact that individuals moving to a neighbouring patch
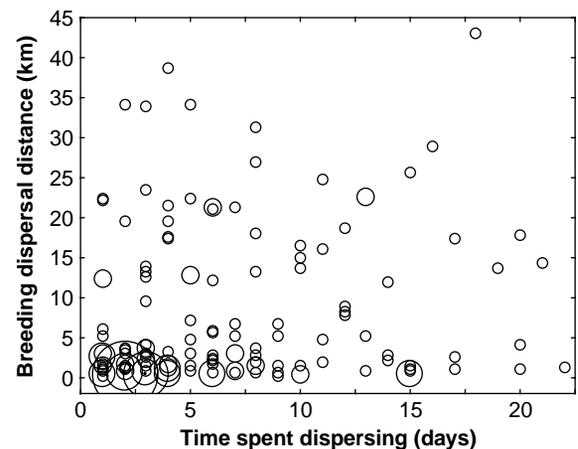

Fig. 5. Breeding dispersal distance of male ortolan buntings in relation to the time spent dispersing. Time used was defined as the time between the last observation at the first site and the first observation at the second site, and thus represents an upper limit to the actual time used for dispersing. Larger symbols indicate overlapping data points (the largest symbol represents n =8).
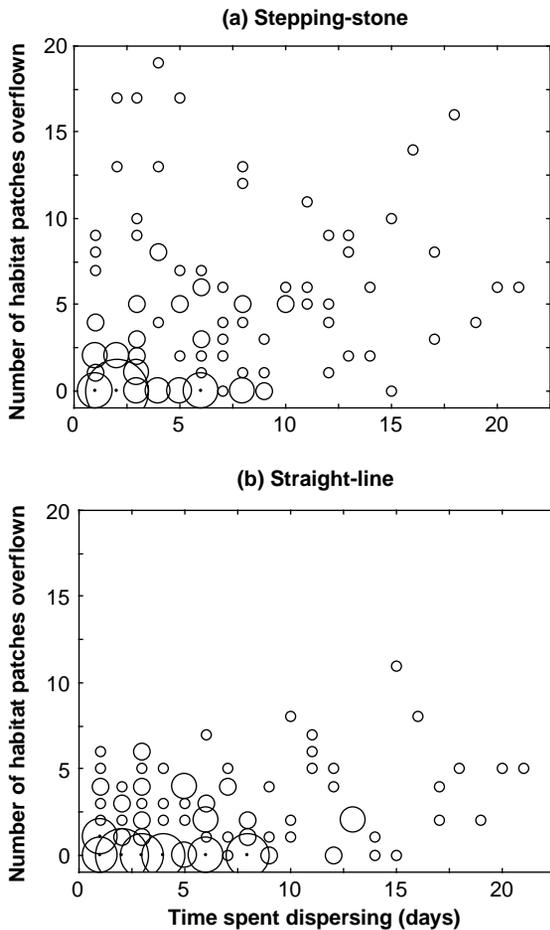
(a) Stepping-stone

(b) Straight-line

Fig. 6. Number of habitat patches overflown by male ortolan buntings in relation to time spent dispersing during breeding dispersal. The number of habitat patches overflown was estimated with two different methods; (a) stepping-stone and (b) straight-line (see Methods for explanations). Only males that changed habitat patch are included, movements within a patch are excluded. Larger symbols indicate overlapping data points (the largest symbols represent n =8 and n =6 in a and b, respectively).

used only a short time. Thus, among males that moved to patches farther away (>2 patches overflown according to stepping-stone method), there was no significant relationship between time spent dispersing and number of patches overflown ($r_s = -0.05$, n =57, p =0.73; using median values for each individual: $r_s = 0.23$, n =39, p = 0.16). Among these males, some moved so quickly from one patch to another that it is unlikely that they had time to sample several patches on the way (upper left data points in Fig. 6a). However, a similar analysis using the straight-line method for males that moved farther away (>2 patches overflown) suggested that there might still be an effect of the number of intervening patches ($r_s = 0.38$, n =39, p =0.020; using median values for each individual: $r_s = 0.31$, n =27, p =0.11), but note that this

method included a much lower number of patches overflown than the stepping-stone method.

Discussion

When to search for breeding areas

Young birds have often been thought to select future breeding sites during exploratory movements during the post-fledging period, i.e. during summer and autumn (see references cited in Introduction). These ideas have been based partly on species that are resident or short-distance migrants which spend a considerable time in the breeding areas after breeding. In contrast, the ortolan bunting is a long-distance migrant which spends only about one month in the breeding areas after fledglings have become independent. During this period preparations for migration to Africa have to be made (moulting, fat deposition), and these activities may interfere with exploration of large areas. Furthermore, during this period ortolan buntings are extremely inconspicuous compared to during the breeding season when males sing even into the nestling period, and individuals of both sexes perch openly and fly frequently between nesting and foraging areas (Dale 2000, Dale and Olsen 2002). Thus, if young ortolan bunting males searching for new breeding areas should take advantage of conspecifics to locate breeding areas and perhaps assess the quality of these (Stamps 1988, 2001, Reed and Dobson 1993, Doligez et al. 1999, 2004, Ward and Schlossberg 2004), prospecting within the breeding season would be far more efficient than after the breeding season.

In line with this reasoning, more than half the observed breeding dispersal movements in this study occurred within the breeding season, with males changing territories and moving up to 43 km within a few days or weeks. The other observations involved birds appearing in a new site the following year. Their arrival time in the new place was not significantly later than that of males which had been site faithful, suggesting that they had located the new site in the previous year. Whether they found the new site within the main breeding period (up to the nestling period) or during the post-breeding period (from fledging onwards) cannot be determined, but the fact that several of these males disappeared from their first site quite early in the breeding season suggests that the former is likely in several cases. Combined with the observation that natal dispersal in the ortolan bunting was relatively short, often within the natal patch or to a neighbouring patch (Dale et al. 2005), the following scenario for how ortolan buntings establish territories is suggested: Young males return to the surroundings of their natal site and establish their first territory. If they are unsuccessful in attracting a mate, many of them perform long-distance movements within the same breeding season using

conspecifics to find a new site. Later in life, ortolan bunting males may be faithful to their territories year after year (Dale et al. 2005). The ortolan bunting pattern of short natal dispersal and long breeding dispersal at young age (Dale et al. 2005), contrasts with the classical view of long natal dispersal and short breeding dispersal (Greenwood and Harvey 1982), and this has implications for when breeding habitat search should take place across species. Note that natal dispersal distances of ortolan buntings are similar to those recorded for other passerine birds (Paradis et al. 1998), and the term short natal dispersal is therefore relative to the distances moved during breeding dispersal by many individuals.

We suggest that the use of within-breeding-season prospecting for new breeding areas may be particularly common in long-distance migratory species because they have short time to locate new areas during the post-fledging period compared to resident species. Time constraints may also favour within-breeding-season search for short-lived species because a larger proportion of lifetime reproductive success is lost if one full breeding season is wasted in an inferior habitat patch compared to long-lived species. Colonial species may also favour within-breeding-season prospecting, whereas species that are solitary during the breeding season, but social outside the breeding season, may gain more information outside the breeding season, e.g. if winter flock ranges cover several breeding territories. We also suggest that factors such as patchy habitat distribution and low population densities may promote the use of within-breeding-season prospecting compared to prospecting outside the breeding season. However, there are little data available to test these ideas, and more research is clearly needed to understand how temporal search strategies vary as a function of life history and ecological factors.

Adaptive late arrival

In many species of migratory birds, it is commonly observed that young individuals arrive later to the breeding areas than old ones. This delay in arrival has usually been explained as resulting from constraints on young birds, especially because they are in lower body condition than older birds (Møller 1994, Kokko 1999). However, this may not be the case in species where searching for breeding areas occurs within the breeding season with song of established territory holders being used as a cue to locate suitable areas. In such cases, the search will be more effective if young birds arrive after many or most old birds have returned. Thus, late arrival may be an adaptive strategy for young males which need to locate new breeding sites. In the ortolan bunting, the timing of the movements was such that the searching phase occurred at a time when most males were present

and singing actively. The possible advantages of late arrival must be weighed against the costs in terms of e.g. lower competitive ability of late-arriving individuals in contests over territories. Thus, adaptive late arrival may be more common in species and populations in which population density is below carrying capacity.

How do birds move through the landscape?

There are a number of factors which can affect how a bird should move through the landscape in search of a suitable breeding area. First, the form of the movement trajectory will depend on whether the bird has decided to move in one specific direction to search, to move at least a specific distance before starting to search, or whether the bird searches opportunistically from the point of origin. Thus, straight-line movements or more sinuous trails can occur (Johnson et al. 1992, Zollner and Lima 1999). In either case, it seems logical that birds may have a hierarchical search procedure; first locate an area with suitable habitat, and next select a specific territory in that area. Searching for the right kind of habitat seems to be most efficient if done from the air, both because habitat patches are more easy to see from a distance the higher up the observer is, and because flight is unobstructed above treetops. Do birds fly above e.g. forest when searching, or do they stay in cover? Some types of evidence indicate that movements of many birds (especially in forest) take place within the cover of the vegetation, and that they hesitate to move into open areas (Haas 1995, Machtans et al. 1996, Desrochers and Hannon 1997, Grubb and Doherty 1999, Belisle et al. 2001, Gobeil and Villard 2002, Bosschieter and Goedhart 2005) despite the loss of movement efficiency. Predation risk in unfamiliar habitats has been proposed as an explanation for such observations (Lima and Dill 1990, Rodríguez et al. 2001, Yoder et al. 2004), yet the clear view of surroundings when in the open air could help in predator vigilance, at least for some species.

We have made one observation of an ortolan bunting moving past areas with unsuitable habitat (>5 km from occupied habitat patches), and this bird flew ca 10 m above treetops. Furthermore, during feeding trips to farmland situated up to several kilometers from territories, ortolan buntings usually fly 20–50 m above open ground, and above treetops (Dale and Olsen 2002). On the other hand, as an open-country species, the ortolan bunting may differ fundamentally from forest species in anti-predator strategies and preferred movement patterns. This idea was also supported by the fact that stretches of at least 6–9 km of unsuitable habitat were crossed regularly and in a short time by dispersing males, whereas forest gaps of only a few hundred meters may present barriers to forest birds (Lens and Dhondt 1994, Desrochers and Hannon 1997; but see Fraser and

Stutchbury 2004). Based on aerial surveys of the study area, our impression is that patches 6–9 km away cannot easily be seen before a height of several hundred meters has been reached, and there is yet no evidence that ortolan buntings fly this high during the breeding season. This suggests that movements did not depend on the detection of a new suitable habitat patch at the time of leaving a patch, and that unsuitable habitat stretching beyond the perceptual range does not necessarily represent a barrier to ortolan bunting movements.

Extent of search and when to stop searching

Male ortolan buntings stopped searching for new habitat patches after having visited 1–4 patches. This was based on observations of singing territories, and it cannot be excluded that additional patches were visited without attempts to establish territories (see below). Sampling of a low number of alternatives has also been observed in mate search of female birds, where 1–6 males are commonly inspected before the final mate choice (Dale and Slagsvold 1996, Gibson and Langen 1996). Searching for breeding areas at the landscape level may be more costly in terms of time and energy than searching for a mate among males in one local population (Janetos 1980, Real 1990, Milinski and Bakker 1992). Costs of searching are also expected to favour a threshold strategy over a pool-comparison strategy (Janetos 1980, Real 1990). Although cases of returns to previously visited habitat patches were recorded, ortolan buntings seemed to use mostly a threshold tactic which may suggest some kind of search cost (see below).

The search trajectories of many individuals must have passed several habitat patches other than the one selected. Is it likely that many or all overflown habitat patches were sampled, but rejected without establishment of a singing territory? There was evidence that the time needed to complete long-distance movements did not depend strongly on the number of intervening habitat patches. In one extreme case, a male passed nine patches in less than one day (according to the stepping-stone method of estimating number of patches overflown). One might expect that sampling of one patch would require at least a few hours to provide a reasonable idea of the quality of the patch and the availability of territories. Thus, it seems likely that at least some patches may be overflown without being assessed, and one possibility is that once the patch of origin has been rejected, neighbouring patches may also be regarded as unacceptable so that sampling in reality starts only after a longer movement has been undertaken. Furthermore, we have never observed any male visiting a patch as a "sneaker" or "floater" despite approximately 20 000 h of field work, so we consider it unlikely that males have a strategy of assessing patches inconspicuously and rejecting patches without having established singing territories. A final resolution of this issue would require e.g. radio telemetry of dispersing individuals.

Costs of searching

Movements in the range recorded in this study (up to 53 km) did not seem to impose high search costs in terms of time used for ortolan buntings. Movements of up to 53 km should not impose excessively high costs in terms of energy either, because the flying time, assuming a direct flight line, would be little more than one hour for the ortolan bunting. The risk of mortality during long-distance movements for ortolan buntings cannot be assessed at present, but it seems unlikely that the risk is high considering that the ortolan bunting migrates thousands of kilometers to wintering areas in tropical Africa every year, and survival of adult males is in general high (Dale 2001a).

We suggest that the most likely cost that could explain the seemingly low number of habitat patches visited, is the risk of not finding a new breeding area with vacant territories if search is continued. If the search is extended without success, vacant territories may have been occupied by competing males if the searching individual decides to return (cf. Dale et al. 1992). In natural populations close to carrying capacity, the chance of finding an empty territory of reasonable quality may be low, so that birds are selected to settle at first opportunity. The Norwegian population of ortolan buntings is declining, and there is probably a surplus of suitable habitat (Dale 2001a), and dispersing males may therefore have the opportunity to settle at most sites inspected. In this view, rapid settlement has been selected because it is adaptive in normal populations, even though more sites could easily have been inspected in the study population. Hence, a higher proportion of saturated patches in natural populations could force some males to extend their search compared to what was observed in this study.

Conclusions

This study has shown that male ortolan buntings move surprisingly long distances during a short time, and that at least some individuals are able to visit several habitat patches before settling in one. This ability may have been selected due to the generally patchy distribution of the ortolan bunting (Cramp and Perrins 1994), and frequency and range of such movements in our population may have increased due to the small population size and lack of females (Dale 2001a,b). One may therefore argue that the ortolan bunting represents an unusual situation, and that the observed behaviour is not representative for birds in general. Previous studies have, however, often

been too restricted in spatial extent, and we consider it likely that large-scale studies may challenge established patterns even in well-studied species (Koenig et al. 1996). Thus, we suggest that future studies of patterns and processes of dispersal should attempt to achieve a landscape coverage of the movements of individual birds, in order to provide less biased descriptions and interpretations of dispersal behaviour. Our conclusions were based on data on the behaviour of male ortolan buntings. We had too few colour-ringed females to assess how they behave, but if males move extensively due to a lack of females, one might expect that females should move much less because they have easy access to unpaired males in most patches. However, this remains to be tested.

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