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NONIDEAL BREEDING HABITAT SELECTION: A MISMATCH BETWEEN PREFERENCE AND FITNESS

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Abstract. The selection of breeding sites in heterogeneous habitats should ideally be based on cues closely reflecting habitat quality and thus predicting realized individual fitness. Using long-term population data and data on territory establishment of male Northern Wheatears (*Oenanthe oenanthe*), we examined whether territory characteristics linked to individual fitness (reproductive performance and survival) also were linked to territory preference. Breeding territories varied in their physical characteristics and their potential effects on reproductive performance, and this variation among territories was correlated from one year to the next. Of all measured territory characteristics (from the focal and the previous year) only territory field layer height predicted individual fitness, i.e., reproductive performance was higher in territories with permanently short rather than growing field layers. Territory preference, instead, was only linked to the size of territory aggregations, i.e., males settled earlier at territory sites sharing borders with several adjacent sites than at those with few or no adjacent sites. This mismatch between territory characteristics linked to fitness and those linked to territory preference was not explained by site fidelity or compensated for by the different fitness components measured. Because the results were not in agreement with an ecological trap scenario, where poor habitats are preferred over high-quality habitats, our results suggest a more general case of nonideal habitat selection. Whereas nonideal selection with respect to territory field layer height may be explained by its poor temporal predictability within the breeding season, the preference for territory aggregations is still open to alternative adaptive explanations. Our study suggests that nonideal habitat selection should be investigated by direct estimates of preferences (e.g., order of territory establishment) and their links to habitat characteristics and fitness components. Furthermore, we suggest that the probability of establishing a territory needs to be included as a factor influencing patterns of habitat selection.

Key words: conspecific attraction; ecological trap; farmland birds; habitat selection; occupancy; preference; public information; recruitment; territory quality and establishment.

Introduction

In heterogeneous environments habitats differ in quality, which likely causes individual reproduction and survival rates to be habitat specific (e.g., Korpimäki 1988, Newton 1991, Holmes et al. 1996, Petit and Petit 1996, Pärt 2001*a*). As a result natural selection should act on individual habitat selection strategies to maximize the probability of choosing the best habitat available. Models of habitat selection traditionally assume an ideal choice, i.e., individuals are able to accurately assess the relative qualities of alternative habitat patches in order to choose the best option available (Fretwell and Lucas 1970, but see Pulliam and Danielson 1991, Delibes et al. 2001, Jonzén et al. 2004).

Individuals are, however, unlikely to always select the best habitat available. Poor choices (nonideal habitat selection) may be due to imperfect spatial knowledge of available habitats (Lima and Zollner 1996), limited availability of cues used to assess habitat quality at the time of habitat selection (Orians and Wittenberger 1991), a poor relationship between the cues used to select habitats and habitat quality (Orians and Wittenberger 1991, Schlaepfer et al. 2002), or conflicting benefits such as mate choice (Kokko and Sutherland 2001) or site fidelity (Pulliam and Danielson 1991). Individual variation and deviations from ideal choices have been almost neglected in breeding habitat selection studies, except in cases of ecological traps, i.e., when poor-quality habitats are preferred over high-quality ones (Schlaepfer et al. 2002, Battin 2004). Ecological traps are assumed to arise when environmental change is rapid (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 and Sutherland 2001, Schlaepfer et al. 2002, Battin 2004, Robertson and Hutto 2006). Ecological traps have recently been recognized as an extreme case opposite to ideal habitat selection, leaving a continuum of many possible relationships between habitat preference and habitat quality (Kristan 2003). As ecological traps and nonideal habitat selection may have detrimental effects

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on population dynamics and long-term persistence (Pulliam and Danielson 1991, Delibes et al. 2001, Donovan and Thompson 2001, Kokko and Sutherland 2001, Kristan 2003) there has been an increasing interest in identifying and understanding the causes of such nonadaptive habitat selection.

Most previous studies of potential ecological traps lack direct estimates of habitat preference and instead use habitat-specific densities as a surrogate (Battin 2004, Robertson and Hutto 2006). For a variety of reasons, however, local breeding densities may not reflect preference (Van Horne 1983, Battin 2004). Another problem with previous studies is that data on several fitness components are lacking, and therefore an apparent maladaptive habitat selection with respect to one component (e.g., reproductive output) may be compensated for by another (e.g., survival) (Battin 2004). Reliable estimates on the relationship between habitat qualities and individual habitat preferences require data on preferences (e.g. arrival time, Robertson and Hutto 2006) in relation to potential cues of habitat quality, and links between these cues and fitness components. So far, few studies of ecological traps have fully investigated these links between habitat characteristics, fitness components, and preferences (Robertson and Hutto 2006).

Patterns of breeding habitat selection and ecological trap scenarios have mainly been studied by comparing averages of individual decisions and reproductive performances between habitat patches (e.g., in Robertson and Hutto 2006). Habitat patches are, however, rarely spatially distinct and uniform in quality (Kristan 2003). Therefore, average estimates at the patch level may obscure the links between preferences and their individual fitness consequences. Furthermore, breeding habitat selection is a result of individual behavioural decisions identifying, assessing, and establishing breeding sites (e.g., Fretwell and Lucas 1972, Pulliam and Danielson 1991). Thus, in order to investigate if the selection of breeding habitat is adaptive we need to study the links between individual preferences and their fitness consequences at the breeding site scale (e.g., territory).

Here, we studied breeding habitat selection by examining individual choices of breeding sites (territories) of male Northern Wheatears (*Oenanthe oenanthe*, hereafter wheatears) using data from a long-term population study in a heterogeneous agricultural landscape. In this population both adults and young display high return rates such that patterns of adult survival and local recruitment could be investigated. By investigating the links between territory characteristics, fitness components, and territory preference our aims were to test whether breeding territory selection of male wheatears deviated from the expectations of ideal selection, and if so, identify the potential causes of such nonadaptive selection of breeding sites. First, we investigated whether characteristics of territory sites predicted individual reproductive performance and subsequent survival. As breeding site selection may be determined by information collected in the previous breeding season, e.g., about conspecific presence and reproductive success (Stamps 1988, Boulinier and Danchin 1997, Danchin et al. 2004), we investigated territory characteristics both of the focal and the previous year. We separately analyzed the relationships of territory characteristics to four fitness components (breeding success, number of fledglings, number of local recruits, and male survival), as variation in these components may have different causes and thus compensatory effects. Second, we tested whether territory preference (order of territory establishment and long-term occupancy of territory sites) was related to the relative value of the above predictors of reproductive performance. Nonideal territory selection was identified when there was a mismatch between territory characteristics predicting fitness and those linked to preference.

METHODS

Study area and species

The study area (40 km^2) was situated in an agricultural landscape southeast of Uppsala in southern Central Sweden (59°50′ N, 17°50′ E). The landscape consisted of a mosaic of grazed and ungrazed grasslands (11%), crop fields (68%), and woodlands and forest (21%). Territory sites were spatially scattered and located in grasslands (58%), crop fields (28%), and on farmyards (13%), either solitary (on average 30%; mainly in fields and on farms) or in small clusters of 2–5 pairs (70%; mainly in grazed grasslands).

Wheatears are small, long-distance migrants wintering south of the Sahara. They are insectivorous ground-foraging birds with a main distribution in habitats consisting of short field layers (Cramp 1988). (A field layer consists of the grasses and forbs forming the layer of vegetation.) In our study area, nest sites are abundant and nests are placed either on the ground under stones (in stone piles and stone walls) or under roof tiles of buildings (on average; 20%, mainly barns). Previous studies show that wheatears prefer habitat patches with short field layers, which were positively related to prey availability (Tye 1992) and negatively related to risk of nest predation (Pärt 2001*a*, *b*). Breeding site selection may mainly be made upon arrival, but may also be determined by information collected in the previous breeding season, e.g., about conspecific presence and reproductive success (T. Pärt, D. Arlt, and A. Qvarnström, *unpublished manuscript*).

Long-term data

We collected data on long-term occupancy and reproductive performance on 146 territory sites (occupied by ~100 pairs each year) during 1993–2003. Each year, we monitored all previous territory sites (occupied ≥1 year) and all potential breeding sites every third to fifth day from mid-April to the end of June to collect data on occupancy, male age (yearling or older), hatching date, breeding success (successful vs. failed) and number of fledged young (for details see Pärt [2001*a*]). Breeding was defined to be successful when we observed fledglings or heard intense warning calls of the parents after fledging ($\geq$15 days after hatching). Nest failures, 15–40% of all attempts per year (average 29%), were mostly due to predation (Pärt 2001*a*). Nest failures during the incubation period were recognized by obvious behavioral changes of males and females (personal observation). We marked nestlings (5–8 days old) from 69% of all nest sites (31% were inaccessible, e.g., because of heavy stones in rock piles) and most adults with an aluminum ring and a unique combination of color rings. Data on the number of local recruits were restricted to territory sites ($n = 81$) at the central part of our study area (8 km^2) to avoid biases due to natal dispersal out of a restricted area. Since we identified all breeding pairs in an area covering 60 km^2 (130–190 pairs), all local recruits and adults dispersing within 6 km from our central territory sites were detected. There was no difference in recruitment or dispersal probability of juveniles (average recruitment = 16% of all fledged young from the central area) with respect to birth site location within this central area (central vs. peripheral territory sites, number of recruits: Wilcoxon $Z = 0.46$, $P = 0.646$, $n = 444$; natal dispersal distances [log transformed]: t test, $t = 0.24$, df = 188, $P = 0.810$, $n = 444$). Adult male survival was estimated by the return of ringed males to a 60-km^2 area in subsequent years, as only 2% of adults that survived in at least two years following their first breeding attempt escaped detection in one year.

Territories were recorded on detailed maps (scale 1:10 000). A territory was delimited by the outermost positions of the majority (>90%) of all recorded positions of the resident pair or unpaired male. Locations of territories (territory sites) were surprisingly stable across years irrespective of territory holder, because wheatears frequently use landscape features such as prominent stones, stone walls, and fences as territory boundaries. We defined that territories were identical between years (i.e., located at the same territory site) when territories overlapped by more than two-thirds and included nest sites from previous or subsequent years, or, in a few cases, when the distance between nest sites in consecutive years was <50 m (i.e., the average radius of a territory assumed a circular shape).

Territory predictors of reproductive performance

As estimators of territory site quality we used four fitness components: breeding success, number of fledged young, number of recruits, and adult male survival. The average quality of a territory site may also be estimated by the long-term probability of breeding success (proportion of successful breeding attempts out of the total number of breeding attempts at a territory site, 1993–2003, arcsine transformed). When a territory site was occupied by >1 breeding pair (12% of occupied sites per year) we included the breeding attempts of all pairs in our estimate of long-term probability of breeding success at that site. Results do not change when only the breeding success of the first established pair was included.

We tested whether certain territory characteristics (i.e., cues) could predict reproductive performance or male survival. We investigated the following territory site characteristics from the breeding year (year t: territory field layer height, territory cluster size); and five territory characteristics from the previous season (year $t - 1$) that could have been used as cues by prospecting wheatears (field layer height, presence of a breeding pair and its breeding success, number of breeding neighbors, and number of neighbors breeding successfully). Classification of field layer height was based on four (between late April/early May and late June) visual estimates of proportions of short (<5 cm high), medium (5–15 cm high), and high (>15 cm high) field layers. (For validation of the method see Pärt 2001*b*.) 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; mainly grazed grasslands and farm yards) or a growing field layer (nongrazed or late-grazed grasslands, fallow fields, and crop fields). At the time of territory establishment in April, on average 95% of all territory sites had a short field layer, but ~50% of these (fields, cultivated grasslands, nongrazed or late-grazed pastures) grew tall field layers later on. Clustering of territory sites may reflect local habitat quality if patches of higher habitat quality sustain more breeding pairs and thus lead to local concentrations of territory sites. For each territory site we determined territory cluster size as the number of neighboring territory sites, i.e., adjacent territory sites sharing boundaries.

Territory preference

Preferences can be inferred from observed settlement patterns (see also Robertson and Hutto 2006). We estimated territory preference by long-term occupancy or order of territory establishment (data from 2002–2003). For each territory site we calculated long-term occupancy (the number of years a territory site was occupied during 1993–2003) as an estimate of average preference for a territory site (Sergio and Newton 2003). As the primary measure of territory preference, however, we used order of territory establishment by males at the territory sites. Order of territory establishment was calculated by ranking (tied ranks) dates of site establishment recorded in 2002 and 2003. In both years we visited all sites once a day between 10 April (i.e., a few days before the first males arrive) and the end of May. A territory site was assumed to be established on the first day a male territory holder was observed at the site. Of the 146 territory sites, 89 were occupied in 2002 and 88 in 2003. When two males established a territory at the same site (9 sites in 2002, 10 in 2003), we used the first observation of the first arriving male as the date of site establishment. Males were identified by color rings (53%) or variable plumage characteristics. Because territory preference might be biased by prior occupancy, we primarily analyzed males choosing new territories, i.e., excluding males displaying site fidelity and males for which site fidelity status could not be determined. Males were site faithful when they returned to breed at either the same (68%) or the adjacent territory site (32%; males often defend a larger area including more than one territory site at arrival). Site fidelity status was unknown for unmarked old males on territory sites that had been occupied by an unmarked male in the preceding year. There were 15 and 21 site-faithful males and 17 and 12 males with unknown status in 2002 ($n = 89$) and 2003 ($n = 88$), respectively. Female territory preferences are complicated when a female's settlement is strongly dependent on the presence of an established unpaired male (correlation between male and female order of establishment: Spearman $r_S = 0.46$, $n = 141$, $P < 0.0001$) and therefore were not investigated here.

Statistics

We used generalized linear models (GLIM, PROC GENMOD, SAS 1999) to test the relationship between territory site characteristics and reproductive performance or male survival. We used binomial (with a logit link; for breeding success and survival) or Poisson (with a log link; for number of fledglings and recruits) models. Corrections for overdispersion were made when necessary. Results are based on log-likelihood ratio chi-square values. The repeated structure of the data (i.e., territory sites across years) was handled by generalized estimating equations (GEE; Diggle et al. 1994) using an autoregressive covariance structure of order one. The analyzed components of reproductive performance were partly dependent on each other because failed attempts were included in analyses of number fledged and recruits. We included failed attempts because small additive effects of each component may be masked by the use of independent components and therefore may not reveal fitness compensations. The relationship between order of territory establishment and territory characteristics was analyzed by a mixed model, with territory site identity as a random factor (PROC MIXED; SAS 1999). To separate the two episodes of territory selection, territory characteristics in year $t - 1$ were analyzed separately from those in year t. For territory characteristics in year $t - 1$ we investigated two alternative models, because data on breeding success was only available for occupied sites: Model 1 included field layer height and two occupancy variables (presence of a breeding pair at the territory site, number of breeding neighbors); Model 2 included field layer height and two success variables (territory breeding success and number of successful neighbors). In all models we included year and male age as independent variables. We tested for interactions between independent variables, which in no case were significant ($P > 0.05$). Sample sizes differ between different tests due to the use of subsets and missing values. Degrees of freedom associated with F values refer to numerator and denominator degrees of freedom: df = numerator, denominator. All data with error terms are presented as means ± SE.

TABLE 1. Between-year correlations for fitness components and field layer height at territory sites of Northern Wheatears.

Variable	n	χ^2	Correlation (r_S) or concordance†	P
Breeding success	666	4.94	66%	0.026
Number fledged	497		0.08	0.095
Number of recruits	527		0.41	<0.0001
Male survival	290	1.07	54%	0.301
Field layer height	685	296.03	83%	<0.0001

† Concordance (%) is reported for chi-sqare tests.

RESULTS

Territory sites varied considerably with respect to potential predictors of territory quality (Appendix). Territory sites also varied with respect to our fitness estimates of territory quality, i.e., the probability of annual breeding success, number of fledglings, number of recruits, probability of male survival, and long-term probability of breeding success (Appendix). Reproductive performance and field layer height in territories was to some extent temporally correlated (Table 1). Thus the wheatears potentially could use information on territories collected in year $t - 1$ to predict their quality in year t.

Predictors of reproductive performance and male survival

To investigate predictors of territory quality we analyzed the relationships between territory characteristics and all four fitness components. Territory characteristics from the year of breeding (year t) or from the previous year (year $t - 1$) were analyzed separately (see *Methods*).

Breeding success, number of fledged young, and number of recruits were significantly predicted only by territory field layer height in the year of breeding (Table 2). Reproductive performance was higher at territories with a permanently short field layer as compared with those with a growing field layer (univariate comparisons: breeding success, 83% vs. 63% successful attempts; number of fledged young, 4.04 ± 0.12 vs. 2.54 ± 0.13; number of recruits, 0.99 ± 0.06 vs. 0.66 ± 0.09). The results on number of fledged young and recruits were qualitatively the same when restricting the analysis only to successful breeding attempts (field layer height predicted variation of these fitness components, results not shown). Probability of male survival was not

TABLE 2. Repeated generalized linear models predicting breeding performance or male survival by territory characteristics in the year of breeding (year t).

Territory characteristics in year t	Estimate (mean ± SE)	df	χ^2	P
Breeding success ($n = 986$)				
Year	···	10	21.67	0.017
Male age	0.476 ± 0.173	1	6.50	0.011
Field layer height†	1.098 ± 0.189	1	25.53	<0.0001
Territory cluster size	−0.026 ± 0.066	1	0.17	0.685
Number fledged ($n = 787$)				
Year	···	10	25.12	0.005
Male age	0.189 ± 0.063	1	9.08	0.003
Field layer height†	0.442 ± 0.058	1	32.75	<0.0001
Territory cluster size	0.007 ± 0.017	1	0.15	0.696
Number of recruits ($n = 557$)				
Year	···	10	26.77	0.003
Male age	0.234 ± 0.139	1	2.86	0.091
Field layer height†	0.608 ± 0.153	1	14.00	0.0002
Territory cluster size	−0.004 ± 0.047	1	0.01	0.936
Male survival ($n = 448$)‡				
Male age	0.087 ± 0.207	1	0.17	0.680
Field layer height†	−0.091 ± 0.222	1	0.17	0.682
Territory cluster size	−0.069 ± 0.081	1	0.68	0.411

Notes: Estimates, χ^2, and P values refer to GEE estimates (model repeated for identity of territory sites, see *Methods: Statistics*). Territory cluster size is the total number of territory sites adjacent to the focal territory site (independent of occupancy status).

† Estimate refers to permanently short field layers.

‡ Year could not be included in the model because of convergence problems.

significantly related to any independent variable analyzed (Table 2).

Of the territory characteristics of year $t - 1$ only territory field layer height significantly predicted number of fledged young and number of recruits in both alternative models (see *Methods*; Model 1 including occupancy variables: Table 3). The two success variables did not predict reproductive performance (Model 2: $P > 0.17$). Restricting the analysis to only successful attempts in year t did not change the relationships to number of fledged young and recruits (results not shown). Male subsequent survival (between year t and $t + 1$) was not significantly associated with any territory characteristic of year $t - 1$ (Table 3; Model 2: all $P >$

TABLE 3. Repeated generalized linear models predicting reproductive performance or male survival by territory characteristics in the year previous to breeding (year $t - 1$).

Territory characteristics in year $t - 1$	Estimate (mean ± SE)	df	χ^2	P
Breeding success in year t ($n = 553$)				
Field layer height†	0.404 ± 0.274	1	1.87	0.172
Territory occupancy	−0.244 ± 0.491	1	0.26	0.610
Number of neighbor pairs	0.039 ± 0.076	1	0.27	0.606
Number fledged in year t ($n = 454$)				
Field layer height†	0.267 ± 0.106	1	6.11	0.013
Territory occupancy	−0.141 ± 0.170	1	0.68	0.411
Number of neighbor pairs	0.012 ± 0.023	1	0.29	0.592
Number of recruits in year t ($n = 354$)				
Field layer height†	0.424 ± 0.177	1	6.41	0.011
Territory occupancy	−0.163 ± 0.278	1	0.29	0.589
Number of neighbor pairs	0.007 ± 0.050	1	0.02	0.884
Male survival ($n = 294$)‡				
Field layer height†	0.440 ± 0.264	1	2.40	0.121
Territory occupancy	−0.660 ± 0.728	1	1.01	0.316
Number of neighbor pairs	−0.157 ± 0.074	1	4.22	0.040

Notes: Estimates, χ^2, and P values refer to GEE estimates (model repeated for identity of territory sites). Number of neighbor pairs is the total number of pairs occupying a territory on territory sites adjacent to the focal territory site. The effects of year and male age (year t) are not shown.

† Estimate refers to permanently short field layers.

‡ Year could not be included in the model because of convergence problems.

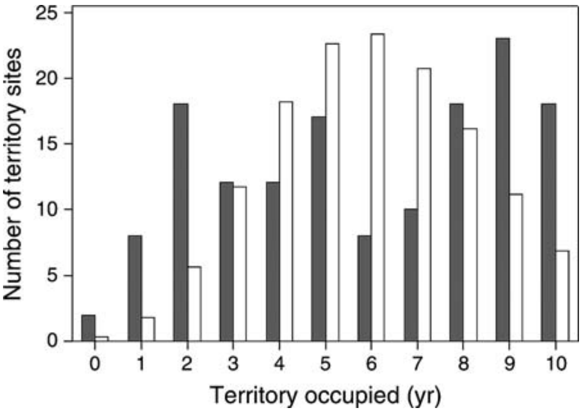

FIG. 1. Observed (shaded bars) and expected (open bars) number of territory sites for the number of years a territory was occupied during 1993–2002 (long-term occupancy). Expected values were calculated from a Poisson distribution.

0.38), except number of breeding neighbors. Males breeding at territories with more breeding neighbors in the previous year had a lower probability of survival than those breeding at sites with few or no neighbors.

Territory preference in relation to predictors of reproductive performance

Long-term occupancy varied among territories and this variation deviated from random expectations ($\chi^2 = 33.90$, df = 10, $P < 0.001$), with more sites occupied <3 years and >9 years than expected (Fig. 1). Long-term occupancy was positively associated with male age and size of territory clusters, but not with territory field layer height (repeated GLIM with year, male age, territory cluster size, field layer height as independent variables: effects of male age, $\chi^2 = 10.51$, df = 1, $P = 0.001$; territory cluster size, $\chi^2 = 11.71$, df = 1, $P = 0.0006$; field layer height, $\chi^2 = 2.15$, df = 1, $P = 0.143$). Order of territory establishment (in 2002–2003) was significantly associated with long-term occupancy (mixed-model ANCOVA with year, male age, long-term occupancy as independent variables: long-term occupancy effect, $F = 18.44$, df = 1, 46, $P < 0.0001$), suggesting that territories being preferred in previous years were also the ones to be taken first in the spring.

Order of establishment was primarily analyzed for males selecting new territory sites (excluding males displaying site fidelity and males of unknown status). Older males were the first to arrive and establish territories (Table 4). Concerning territory characteristics in the year of establishment (year t) the order of territory establishment was only related to territory cluster size, i.e., males settled earlier at territory sites sharing borders with several adjacent sites than at those with few or no adjacent sites (Table 4, Fig. 2A). Territory field layer height did not explain variation in order of establishment (Table 4, Fig. 2B). The same pattern was evident when all males (irrespective of site fidelity) were analyzed together, although the effect of territory cluster size was less strong (same model as in Table 4; territory cluster size effect: estimate = −3.060 ± 1.388, $F = 4.86$, df = 1, 46, $P = 0.033$).

The relationships between order of establishment and territory characteristics of the previous year ($t - 1$) were investigated by two alternative models (occupancy variables vs. success variables, see *Methods*). For males selecting a new territory, order of establishment tended to be positively related to the number of breeding neighbors (Table 4) or number of successful neighbors in the previous year (same model as in Table 4, but with success variables; number of successful neighbors effect: estimate = −5.161 ± 2.334, $F = 4.89$, df = 1, 6, $P = 0.069$, $n = 48$). This relationship was not evident when all males were included; instead order of establishment was significantly related only to the presence of a breeding pair year $t - 1$ (Model 1, occupancy variables: effects of territory occupancy, estimate = 10.504 ± 4.151, $F = 6.40$, df = 1, 42, $P = 0.015$; number of neighbor pairs, estimate = −1.515 ± 1.223, $F = 1.53$, df = 1, 42, $P = 0.222$, $n = 148$) (Model 2, success variables: territory breeding success,

TABLE 4. Preference of territory characteristics by males selecting new territories.†

Independent variables	Estimate ± SE	F	df	P
Territory characteristics in year t ($n = 95$)				
Year	···	0.15	1, 17	0.701
Male age	−12.055 ± 3.844	9.84	1, 17	0.006
Field layer height‡	3.418 ± 4.046	0.71	1, 17	0.410
Territory cluster size	−4.631 ± 1.480	9.79	1, 17	0.006
Territory characteristics in year $t - 1$ ($n = 93$)				
Year	···	0.07	1, 13	0.801
Male age	−12.211 ± 3.869	9.96	1, 13	0.008
Field layer height‡	0.536 ± 4.364	0.02	1, 13	0.904
Territory occupancy	−4.213 ± 4.303	0.96	1, 13	0.345
Number of neighbor pairs	−2.981 ± 1.492	3.99	1, 13	0.067

Notes: The data were analyzed by mixed-model ANCOVAs (with identity of territory sites as random factor) with order of establishment as dependent variable, and year, male age, and territory characteristics in year t or $t - 1$ as independent variables.

† Males that displayed site fidelity or were of unknown status were excluded, see *Methods*).

‡ Estimate refers to permanently short field layers.

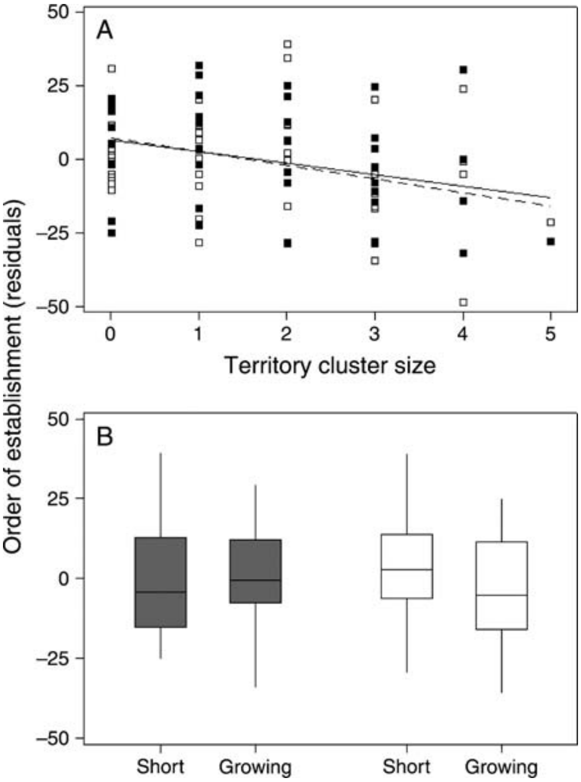

FIG. 2. The order of establishment (partial residuals [low values correspond to early establishment]; model with territory characteristics in year *t* as in Table 4) in relation to (A) territory cluster size (2002, solid symbols, solid line; 2003, open symbols, dashed line), and (B) field layer height (2002, shaded boxes; 2003, open boxes).

estimate $= -1.103 \pm 5.588$, $F = 0.04$, df = 1, 24, $P = 0.845$; number successful neighbors, estimate $= -2.752 \pm 1.766$, $F = 2.43$, df = 1, 24, $P = 0.132$, $n = 89$). As the size of territory clusters was correlated with the number of breeding neighbors (Spearman $r_S = 0.873$, $n = 941$, $P < 0.0001$) and the number of successful neighbors ($r_S = 0.843$, $n = 875$, $P < 0.0001$), both data on long-term occupancy and order of establishment suggest that male wheatears preferred territory aggregations.

Relationships between preference and reproductive performance

Long-term breeding success (number of successful attempts ÷ total number of attempts on a territory site) was not related to territory preference as estimated by long-term occupancy (GLIM, GEE estimate $= 0.017 \pm 0.050$, $\chi^2 = 0.11$, df = 1, $P = 0.736$, $n = 125$ territory sites). Similarly, annual probability of breeding success was not related to long-term occupancy (repeated GLIM with year, male age, long-term occupancy as independent variables; long-term occupancy effect, GEE estimate $= 0.037 \pm 0.033$, $\chi^2 = 1.27$, df = 1, $P = 0.261$, $n = 986$ breeding attempts). However, wheatears breeding on territories that had been occupied in many years tended to produce on average more fledglings (model as above; long-term occupancy effect, GEE estimate $= 0.024 \pm 0.013$, $\chi^2 = 3.62$, df = 1, $P = 0.057$, $n = 798$) and more recruits than those breeding on territories occupied only in a few years (long-term occupancy effect, GEE estimate $= 0.080 \pm 0.039$, $\chi^2 = 4.78$, df = 1, $P = 0.029$, $n = 561$).

Furthermore, breeding success and number of recruits were related to order of establishment (repeated GLIM with year, male age, order of establishment as independent variables: effects of order of establishment on breeding success, GEE estimate $= -0.026 \pm 0.012$, $\chi^2 = 3.88$, df = 1, $P = 0.049$, $n = 137$; number of fledged young, GEE estimate $= -0.004 \pm 0.003$, $\chi^2 = 1.47$, df = 1, $P = 0.226$, $n = 87$; number of recruits, GEE estimate $= -0.023 \pm 0.009$, $\chi^2 = 4.76$, df = 1, $P = 0.029$, $n = 77$). These relationships could, however, be caused by deteriorating breeding conditions over the course of the breeding season (Verhulst et al. 1995), as at least the number of recruits was negatively related to hatching date (repeated GLIM with year, male age, and hatching date [standardized for annual variation] as independent variables: hatching date effect on breeding success, GEE estimate $= -0.083 \pm 0.091$, $\chi^2 = 0.70$, df = 1, $P = 0.403$, $n = 112$; number of fledged young, GEE estimate $= -0.009 \pm 0.010$, $\chi^2 = 0.79$, df = 1, $P = 0.374$, $n = 76$; number of recruits, GEE estimate $= -0.122 \pm 0.032$, $\chi^2 = 7.23$, df = 1, $P = 0.007$, $n = 71$). Order of establishment and hatching date were correlated (Spearman $r_S = 0.59$, $P < 0.0001$, $n = 108$), but order of establishment had no additional independent effect on reproductive performance when the effect of breeding time was taken into account (analyses of residuals from GLIM models including year, male age, and hatching date as independent variables, mixed model: effects of order of establishment on residual variation for breeding success, estimate $= -0.003 \pm 0.004$, $F = 0.34$, df = 1, 102, $P = 0.561$, $n = 104$; number of fledged young, estimate $= -0.002 \pm 0.006$, $F = 0.18$, df = 1, 69, $P = 0.670$, $n = 71$; number of recruits, estimate $= -0.004 \pm 0.007$, $F = 0.35$, df = 1, 66, $P = 0.554$, $n = 68$).

Repeatability of territory preference

The relationship between order of establishment and long-term occupancy suggests that order of establishment should be repeatable across years. Among the 52 sites occupied in both years, site-specific order of establishment showed some repeatability (all territory sites, one-way ANOVA, $F = 2.57$, df = 1, 50, $P < 0.001$, repeatability $r = 0.44$; only territory sites occupied by different males in both years, $F = 2.24$, df = 1, 28, $P = 0.016$, $r = 0.38$).

DISCUSSION

Breeding territories of wheatears varied both in their physical characteristics and in their potential effects on individual fitness, and this variation among territories was temporally correlated across years, although weakly so for demographic parameters. Thus, the basic prerequisites were given for habitat selection in general, and for habitat selection based on cues collected a year ahead of breeding in specific (e.g., Boulinier and Danchin 1997, Doligez et al. 2003, Danchin et al. 2004). By linking realized preferences (i.e., observed territory establishment), territory characteristics, and several fitness components we were able to pinpoint some potential cues involved in the selection of breeding territories and test whether these were good predictors of territory quality. Our results show that wheatears preferred certain territory sites consistently over others according to long-term occupancy data (Fig. 1), the association between long-term occupancy and order of establishment (see also Brooke 1979), and the repeatability of order of territory establishment (see also Currie et al. 2000). Of all territory characteristics investigated male wheatears seemed to prefer only territories located in territory clusters (i.e., territory aggregations partly reflecting larger habitat patches and/or the presence of conspecifics). None of the territory characteristics related to clustering (territory cluster size, number and success of neighboring breeders), however, were related to any fitness component. Instead, the only territory characteristic linked to individual fitness was field layer height. Clearly, there was a mismatch between territory characteristics linked to preference and those linked to individual fitness. Site fidelity of individuals could potentially confound preference (e.g., when site-faithful males were included in the analyses, preference was related to territory occupancy year $t - 1$), but our results concerning preference for territory aggregations were more robust when we excluded individuals displaying site fidelity. The mismatch between preference and fitness was evident for all fitness components investigated, and thus our results cannot be explained by fitness compensations (sensu Battin 2004).

Measures of reproductive performance and survival are expected to reflect breeding territory or habitat quality because they integrate the effects of several components of quality (e.g., predation risk, food abundance, local climate) on individual fitness (e.g., Danchin et al. 2001, Doligez et al. 2003). There is a risk, however, that such estimates of habitat quality are inflated when habitat quality and individual quality are correlated. Currie et al. (2000) found that territory quality as opposed to individual quality appeared to explain much of the variation of breeding success in Northern Wheatears. Similarly, a previous experimental study in our study population showed strong environmental effects, but no individual (including age) effects, on reproductive performance in male wheatears (Pärt 2001*b*). Therefore, variation in individual quality could only have minor effects on our results concerning the links between territory characteristics and fitness components.

One could argue that we missed a preferred habitat characteristic linked to individual fitness, since data on long-term occupancy suggest that at least the production of recruits, on average, was higher in attractive than in less attractive territories. Furthermore, reproductive performance (breeding success and number of recruits) declined with order of establishment. A problem when investigating fitness consequences related to preferences, however, is that this relationship may be confounded by a general decline in breeding conditions over the course of the breeding season (Price et al. 1988, Verhulst et al. 1995) as estimates of preference are related to breeding time. (Here: long-term occupancy was correlated with order of territory establishment, and order of territory establishment was correlated with hatching date.) Empirical evidence suggests that breeding conditions generally decline over the course of the breeding season in songbirds (Verhulst et al. 1995, Svensson 1997, Verboven and Visser 1998). Although experimental data are needed to disentangle the effects of breeding time and order of establishment (as reflecting territory quality), at least our data do not reject the potential effect of deteriorating breeding conditions. Nonetheless, our results are robust regarding the mismatch between investigated habitat characteristics linked to fitness and those linked to preference.

To summarize, our study suggests a case of nonideal habitat selection, but not an ecological trap in its strict sense, since poor-quality habitats (i.e., territories with growing field layers) were not preferred over high-quality ones.

Why a mismatch between preference and reproductive performance?

There are several nonexclusive reasons why individuals may display a nonideal breeding habitat selection. Observed deviation from ideal habitat selection in wheatears could be caused, for example, by limited knowledge about alternatives or conflicting demands (see *Introduction*). However, our results suggest that a major cause is the mismatch between territorial characteristics linked to preference and those linked to reproductive performance.

One cause for nonideal habitat selection may be a within-season temporal mismatch between the cue used and reproductive performance (Orians and Wittenberger 1991). 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. Habitats with tall field layers at the time of establishment (e.g., long-term fallow fields, abandoned pastures, and residual grassland habitats) were clearly avoided (T. Pärt, D. Arlt, and A. Qvarnström, *unpublished manuscript*). However, ~50% of all sites with a short field layer in April grew tall field layers later on. Obviously, the information of field layer height at the time of establishment poorly predicted field layer height at the critical time when nestlings were being fed. Thus, there was a poor temporal correlation between the conditions at the time of selection and conditions when young were reared. Such an uncoupling of preference and habitat quality may be caused by rapid habitat alterations (as, for example, in agricultural landscapes), causing past cues of habitat quality to be independent of present habitat quality (Kokko and Sutherland 2001, Schlaepfer et al. 2002, Battin 2004). At present we do not have historical data on whether field layer height at the time of establishment better predicted within-season variation in field layers in the past. Several other studies suggest that cues available at the beginning of the breeding season may only poorly predict reproductive success in patches, whereas cues collected in the previous year may be more reliable (Boulinier et al. 1996, Reed et al. 1999). In wheatears, at least failed breeders and floaters make their choice of the subsequent breeding site by prospecting other conspecific breeding pairs (T. Pärt, D. Arlt, and A. Qvarnström, *unpublished manuscript*). Because territory field layer height is temporally correlated across years, these prospecting individuals could potentially collect reliable information on field layer height a year ahead of their next breeding attempt. Although this fraction of the population (probably <20%) prefers sites with permanently short field layers (T. Pärt, D. Arlt, and A. Qvarnström, *unpublished manuscript*), there is no apparent preference for permanently short field layers when all individuals, with different types of histories, are analyzed together. Thus, our results suggest that many males failed to prefer territory sites with permanently short field layers despite the fact that this characteristic strongly affects reproductive performance.

The second mismatch between territory preference and reproductive performance, the observed preference of territory aggregations (territory cluster size), is more ambiguous. Several studies suggest that individuals frequently prefer patches with many conspecifics in the previous or current year of breeding (see Stamps 1988, Reed and Dobson 1993, Lima and Zollner 1996), but it is not clear whether one should expect a positive relationship between such a preference of breeding aggregations and individual fitness. This is because fitness may be locally density dependent (e.g., Sillett et al. 2004), causing individual reproductive performance to be independent or negatively related to the size of breeding aggregations. The weak negative relationship between male survival and territory cluster size may potentially reflect such effects of local density.

Other potential explanations for the apparent nonadaptive preference for territory aggregations include: (1) nonselective individuals in a landscape dominated by low-quality habitats (Stamps and Krishnan 2005) using territory cluster size as detection cue, (2) effects of recent habitat alterations changing former relationships between cue and fitness (sensu Kokko and Sutherland 2001), or (3) cryptic benefits related to the size of territory clusters such as increased probability to establish a territory or to shift to a better site in a subsequent year. The first hypothesis seems unlikely, since the landscape in our study area contains a relatively high proportion of high-quality habitat (60% of all established territories have short field layers), whereas the other two are still open to future tests. Most importantly, the last explanation points to two previously neglected aspects of habitat selection, the probability to establish a territory and to improve the site selection in the future. Although this hypothesis is largely untested, territory clusters reflecting larger patches of breeding habitat may have a higher potential for territory compression and packing (see Adams 2001, Ridley et al. 2004), thus increasing probability of successfully establishing a territory in spite of an increased local competition for sites. Early male wheatears often defend a larger territory at arrival than later when other males have settled in the neighborhood (see *Methods*), because late-arriving males are often able to establish a territory in parts of, or between, the original territories of earlier-arriving males. Conversely, an attraction to aggregations of conspecifics may also reduce the risk of territory crowding and compression by encroachment of late-settling individuals (Getty 1981). Furthermore, breeding in a territory cluster may facilitate prospecting of alternative sites in the same neighborhood and thus increase the probability to shift to a better site in the subsequent year. In fact, a majority (>60%) of all between-year shifts of territories by male wheatears are made within clusters (D. Arlt and T. Pärt, *unpublished data*).

To summarize, the enigmatic preference for territory aggregations suggest that studies of habitat selection, and ecological traps in specific, require detailed data not only on reproduction and survival but also on the probability of establishing a territory and the effects of subsequent choices on lifetime reproductive performance. The frequent findings of, for example, floaters (individuals failing to establish a territory [Zack and Stutchbury 1992]) suggest that territory establishment and future choices may be important to investigate if we are to fully understand observed patterns of habitat preference and its relationship to individual fitness.

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APPENDIX

Variation of territory sites with respect to potential predictors and estimators of territory quality (*Ecological Archives* E088-049-A1).