SPATIAL SCALE OF LOCAL BREEDING HABITAT QUALITY AND ADJUSTMENT OF BREEDING DECISIONS

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Abstract. Experimental studies provide evidence that, in spatially and temporally heterogeneous environments, individuals track variation in breeding habitat quality to adjust breeding decisions to local conditions. However, most experiments consider environmental variation at one spatial scale only, while the ability to detect the influence of a factor depends on the scale of analysis. We show that different breeding decisions by adults are based on information about habitat quality at different spatial scales. We manipulated (increased or decreased) local breeding habitat quality through food availability and parasite prevalence at a small (territory) and a large (patch) scale simultaneously in a wild population of Great Tits (*Parus major*). Females laid earlier in high-quality large-scale patches, but laying date did not depend on small-scale territory quality. Conversely, offspring sex ratio was higher (i.e., biased toward males) in high-quality, small-scale territories but did not depend on large-scale patch quality. Clutch size and territory occupancy probability did not depend on our experimental manipulation of habitat quality, but territories located at the edge of patches were more likely to be occupied than central territories. These results suggest that integrating different decisions taken by breeders according to environmental variation at different spatial scales is required to understand patterns of breeding strategy adjustment.

Key words: breeding investment, timing, and habitat quality; environmental variability in time and space; Great Tit; individual breeding strategies; Parus major; sex-biased natal dispersal.

INTRODUCTION

Life history trade-offs impose constraints on individuals in the use of resources, and thus the need for optimizing decisions in order to maximize expected fitness benefits (Roff 1992, Stearns 1992). In spatially and temporally heterogeneous environments, strong selective pressures should favor the use of information about breeding habitat quality by individuals to adjust breeding decisions to local conditions (Reed et al. 1999, Dall et al. 2005). Many studies have attempted to identify environmental factors affecting individual breeding decisions, most of them by manipulating a given factor expected to affect decisions and observing subsequent changes in individuals' responses. These studies provide evidence that individuals gather and use information on local environmental quality in decision-making processes such as breeding habitat selection (e.g., Clobert et al. 2001, Doligez et al. 2002, Eggers et al. 2006) or breeding investment (e.g., Boutin 1990, Doligez and Clobert 2003,

Eggers et al. 2006). Nevertheless, most experimental studies are based on manipulations at a single spatial scale. The ability to detect the influence of a factor, however, depends on the scale at which the analysis is performed (Orians and Wittenberger 1991, Mitchell et al. 2001). An absence of response may reflect either a lack of use of information or a scale problem, if individuals use information on the factor considered but at a lower or higher scale (Orians and Wittenberger 1991). The scale at which information is gathered and used can shape the costs of adjusting a decision, since individuals' knowledge of the environment is likely to be limited by time, energy, and mobility constraints (Reed et al. 1999, Dall et al. 2005). Therefore, scale issues are crucial in understanding the optimization of breeding decisions by individuals according to local conditions. However, they remain largely ignored (Orians and Wittenberger 1991, Mitchell et al. 2001). In particular, experimental studies rarely investigate which scale would be appropriate before conducting a manipulation. This may, however, lead to different results between populations or species facing different spatiotemporal patterns of environmental variation (e.g., Paradis 1998, Mitchell et al. 2001). Furthermore, the issue of whether individuals use information at different spatial scales to adjust different breeding decisions independently remains poorly investigated.

Offspring sex ratio adjustment according to local habitat quality offers an illustration of this scale issue. Several types of models considering different spatial scales have been proposed to explain offspring sex ratio adjustment patterns. According to classical models of sex allocation (Hamilton 1967, Trivers and Willard 1973, Clark 1978, Charnov 1982, Schwarz 1988), the relative fitness of male and female offspring may vary depending on factors acting at a small spatial scale (i.e., natal territory or family group; Hamilton 1967, Trivers and Willard 1973, Clark 1978, Schwarz 1988, Frank 1990). Parents are expected to bias offspring sex ratio toward the sex that benefits most from parental investment depending on territory quality, maternal condition or social rank, paternal attractiveness or competitive ability (Trivers and Willard 1973, Charnov 1982, Frank 1990), and kin interactions within the group (Hamilton 1967, Clark 1978, Schwarz 1988). Recently, however, a model showed that parents are also expected to adjust offspring sex ratio according to local breeding habitat quality at a larger spatial scale than natal territory (i.e., the scale of average natal dispersal) to maximize the probability that their offspring settle in high-quality habitats (Julliard 2000). According to this "natal dispersal" model, when (1) natal dispersal is sex biased, and (2) breeding habitat quality varies in space at the natal dispersal scale, but (3) is temporally predictable, parents are expected to bias offspring sex ratio toward the philopatric sex when breeding in a high-quality habitat, and toward the dispersing sex when breeding in a low-quality habitat (Julliard 2000).

In the case of offspring sex ratio, the multiplicity of factors that may influence sex ratio adjustment was suggested to partly explain the low frequency of offspring sex ratio biases observed in vertebrate species (Komdeur and Pen 2002, West and Sheldon 2002). Surprisingly, however, most theoretical and empirical studies have investigated sex ratio as an isolated trait on which a factor is acting at one spatial scale only. In particular, the "natal dispersal" model, which deals with selective pressures potentially acting at large spatial scales (Julliard 2000), has never been tested experimentally. Trade-offs resulting from conflicting environmental factors acting at various spatial scales could explain the absence of coherent patterns of sex ratio biases among years, populations, or species (Palmer 2000, Radford and Blakey 2000, Krackow 2002, Ewen et al. 2004, West et al. 2005). More generally, such trade-offs are likely to influence the extent to which individuals will adjust different breeding decisions (such as offspring sex ratio) and the direction of these adjustments, depending on the scales of habitat quality variation (Orians and Wittenberger 1991).

To test the influence of environmental factors acting at different spatial scales on early breeding decisions, we manipulated local breeding habitat quality at two spatial scales simultaneously in a wild population of Great Tits (*Parus major*), a small hole-nesting passerine bird. We increased or decreased both territory (small scale) and patch (large, natal dispersal scale) habitat quality and investigated responses on early breeding decisions: laying date, primary clutch sex ratio, clutch size, and occupancy rate (i.e., small-scale territory choice). We thus tested whether breeding Great Tits adjusted various early breeding decisions according to small-scale habitat quality, large-scale habitat quality, or both.

METHODS

Study site and manipulation of habitat quality

The study was performed in spring 2003, in a Great Tit population breeding in nest boxes in three forests composed of an heterogeneous mixture of deciduous and pine trees (low-quality breeding habitat), near the city of Bern, Switzerland. Great Tits represent 85% of breeding attempts in nest boxes in these forests. Each box was manipulated to either increase or decrease territory quality. Territory quality was increased by supplementing nest boxes every third day with food (Boutin 1990, Rytkonen 2002) comprising live maggots and seeds and hazelnuts embedded in fat balls. Food supplementation has been shown in many studies to advance the onset of breeding and to increase clutch size, juvenile growth rate, and fledgling condition (Boutin 1990), which reflects an increase in breeding-site quality. Food was placed in cups at a distance of 1–5 m from each nest box, within a 5 × 5 cm grid cage to restrict access to small forest birds. This avoided attracting larger animals (corvids, squirrels), which are potential egg or fledgling predators (Cramp and Perrins 1993). Alternatively, territory quality was decreased by infesting nest boxes with 80 hen fleas, *Ceratophyllus gallinae*, collected from old nests in the same population. Fleas are very common tit ectoparasites (Tripet and Richner 1997), and strongly affect current and future breeding success, leading, in particular, to a reduction of fledgling number by 30% for parents (Richner et al. 1993), and of lifetime number of recruits by 36% for individuals raised in infested nests (Fitze et al. 2004b), for the same level of infestation as here. The presence of fleas in a nest box has been shown to decrease the probability of box occupancy, to delay laying (Oppliger et al. 1994), to decrease fledgling condition (Richner et al. 1993), and also tends to decrease clutch size (Richner et al. 1993), thus reflecting a strong reduction in nest box quality. Forty fleas were added to nest boxes at the beginning of the experiment, and another 40 fleas were added after two weeks in all decreased-quality boxes (including those already occupied). Previous results on flea demography within nests show that 40 adult fleas are enough to establish a parasite population in a nest (Tripet and Richner 1999). We manipulated two factors of habitat quality simultaneously in order to maximize the difference in quality between high-quality and low-quality territories. The fact that individuals may respond differently to different factors (here, food availability and presence of para-

sites) for each breeding decision does not affect our predictions based on comparing spatial scales of habitat quality (see *Predictions and analyses*), and thus does not affect our results.

We created 21 forest patches comprising 30 uniformly distributed nest boxes each (neighboring boxes were located 80–100 m from each other; see Appendices E and F). Area and nest box density were thus kept constant across patches. All territories within a patch were either manipulated in the same way, or alternatively received different treatments. Thus, we created three types of patches: high-quality patches (HP) containing high-quality territories only; medium-quality patches (MP) containing 50% high-quality and 50% low-quality territories alternated in space; and low-quality patches (LP) containing only low-quality territories (Appendix E). A territory of a given quality was surrounded either by territories of the same quality (in high-quality and low-quality patches) or by territories of the opposite quality (in medium-quality patches). In total, four types of territories were thus created: high-quality (HT) and low-quality (LT) territories surrounded by either high-quality or low-quality territories on a local scale. In this tit population as in others (Verhulst et al. 1997, Tinbergen 2005), natal dispersal distance is sex biased ($F_{1,113} = 20.80$, $P < 0.0001$ for 115 Great Tit natal dispersal events recorded between 1998 and 2000): females dispersed longer distances (797 ± 64 m [mean ± SE], $N = 50$) than males (495 ± 39 m, $N = 65$). Patch area (19.7 ± 0.6 ha [mean ± SE]) and interpatch distance were, therefore, chosen based on sex-specific natal dispersal distance distributions in this population, so as to maximize the probability that (1) juveniles of the philopatric sex (i.e., males) would stay within their natal patch, and (2) juveniles of the dispersing sex (i.e., females) would disperse outside their natal patch to breed in the next year (Julliard 2000; see Appendices A–D for details and tests of the other assumptions of the "natal dispersal" model).

Experimental manipulation of habitat quality was initiated between 15 and 30 March (i.e., as late as possible; about two to four weeks before the peak of laying), because we aimed at manipulating breeding habitat choice at the patch scale (i.e., large scale) as little as possible. While individuals had already chosen their breeding habitat at a large spatial scale (i.e., patch or subpatch scale) at that time, our manipulation could still have affected small-scale habitat (i.e., territory or nest box) choice, in particular in medium-quality patches. This, however, does not affect our predictions when comparing responses at different scales (see *Predictions and analyses*). We created six high-quality patches, nine medium-quality patches, and six low-quality patches. The higher number of medium-quality patches compared to high-quality and low-quality patches allowed us to balance number of territories (and thus nests) in each treatment.

Breeding data, DNA sampling, and molecular sexing of chicks and embryos

Nest boxes were monitored regularly for occupancy and breeding data. Daily visits when nests were ready allowed us to record exact laying date, clutch size, and hatching date. Blood was sampled from nestlings for molecular sexing soon after hatching (in most cases on the hatching day or the following day), and unhatched eggs were collected for embryos after a few days, allowing us to investigate primary clutch sex ratio. Blood samples of 2–10 µL were taken from the superficial plantar metatarsal vein of chicks and transferred to 200 µL of EDTA buffer for molecular sexing. The samples were frozen at −20°C on the same day. Unhatched eggs were dissected and dead embryos were transferred to EtOH abs (absolute ethanol) and stored at −20°C for sexing. Sexing was performed using a DNA test following Griffiths et al. (1998) (see Appendix H). For practical reasons, breeding adults could not be caught. Thus, parental characteristics (age, size, body condition) could not be included in the analyses. However, our predictions and, in particular, the expected differences with spatial scale remain unchanged whether habitat quality leads to breeding decisions adjustment directly or via parental quality or condition.

We monitored 292 experimental Great Tit nests (13.8 ± 0.9 nests per patch, mean ± SE). Small variations in sample sizes between analyses are due to some nests being deserted during laying and missing laying dates for a few nests. Sexing was performed for 277 nests and for 95.5% of the 2289 eggs (i.e., 2187 eggs). The remaining eggs could not be sexed because: (1) eggs were sterile and contained no embryo, or no embryo could be found (61 eggs, 2.7%); (2) eggs were broken before the start of incubation, or nestlings had died before sampling (i.e., no sample could be obtained; 33 eggs, 1.4%); (3) molecular sexing did not work out (eight eggs, 0.3%). Results on offspring sex ratio were unchanged when excluding broods where at least one embryo/nestling could not be sexed.

PREDICTIONS AND ANALYSES

The predicted pattern of early breeding decisions in response to our manipulation of breeding habitat quality at two spatial scales depends on which selective pressures act in our population, and on which scale is consequently used by parents to adjust decisions (Fig. 1). If individuals use information on habitat quality, the level of habitat quality perceived should decrease from high-quality territories in high-quality patches (i.e., HT-HP territories), to low-quality territories in low-quality patches (i.e., LT-LP territories; Fig. 1). Differences in responses (1) between high-quality territories in high-quality and medium-quality patches (i.e., HT-HP and HT-MP territories) and low-quality territories in medium-quality and low-quality patches (i.e., LT-MP and LT-LP territories), respectively, and (2) between high-quality and low-quality territories within medium-
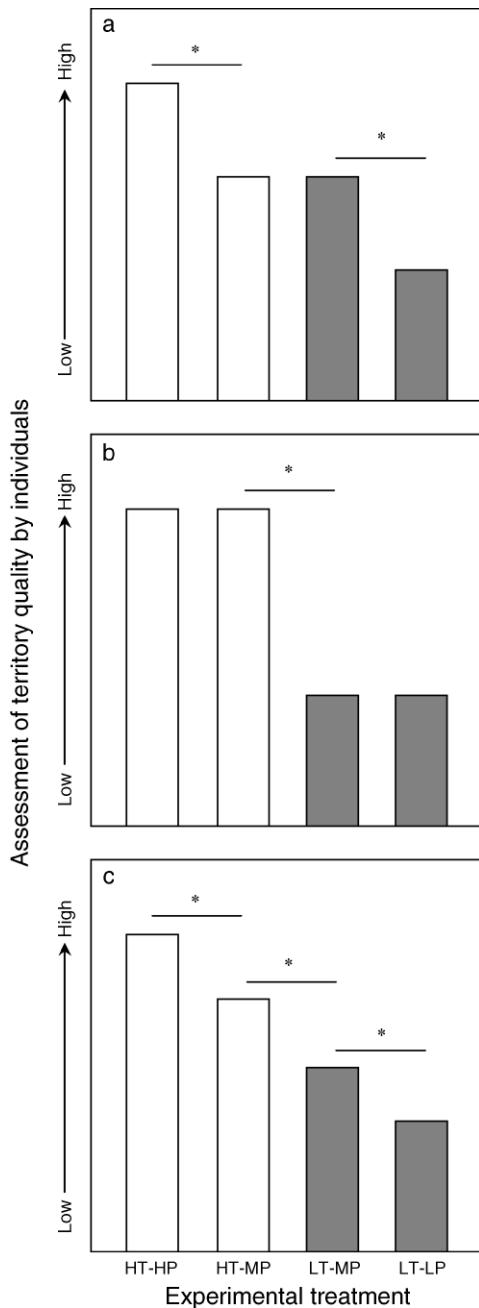
FIG. 1. Expected responses in early breeding variables according to experimental treatment and spatial scale of habitat quality acting on adjustment of individual breeding decisions: (a) large-scale (patch) habitat quality (natal dispersal scale) only; (b) small-scale (territory) quality only; (c) both large and small spatial scales (patch and territory). Territory assessment is based on qualitative predictions (unitless). Open and gray fills represent high-quality (increased food availability) and low-quality (nest parasites added) territories, respectively. Treatments: high-quality territories in high-quality patches (HT-HP; 180 nest boxes in six patches); high-quality territories in medium-quality patches (HT-MP; 135 nest boxes in nine patches); low-quality territories in medium-quality patches (LT-MP; 135 nest boxes in nine patches); and low-quality territories in low-quality patches (LT-LP; 180 nest boxes in six

quality patches (i.e., HT-MP and LT-MP territories), will reveal at which scale(s) information is used by parents. If Great Tit parents adjust a breeding decision according to patch quality only, they should increase the value of the corresponding breeding variable in high-quality patches and decrease it in low-quality patches, compared to medium-quality patches (relative biases), but no difference in the corresponding breeding variable should be observed between increased and decreased quality territories within medium-quality patches (Fig. 1a). If parents adjust a decision according to territory quality only, they are expected to increase the breeding variable in high-quality (HT) compared to low-quality (LT) territories, but the quality of surrounding territories should not affect the corresponding breeding variable. Thus there should be no difference between high-quality territories in high-quality and medium-quality patches (HT-HP and HT-MP territories) on the one hand, and between low-quality territories in medium-quality and low-quality patches (LT-MP and LT-LP territories) on the other hand (Fig. 1b). Finally, if parents adjust a decision according to both territory and patch quality, an intermediate situation should be observed with a higher value of breeding variable in high-quality compared to low-quality patches and, additionally, a higher value in high-quality compared to low-quality territories, corresponding to a gradual decrease in perceived habitat quality (Fig. 1c).

Habitat quality is expected to affect early breeding decisions by individuals. On high-quality habitat, Great Tit pairs are expected to (1) advance the onset of breeding (i.e., laying date), because of a strong seasonal decline in breeding success (Verhulst et al. 1995), (2) lay larger clutches, and (3) bias offspring sex ratio toward males, since residual reproductive value of high-quality males should be higher than females due to sexual selection (Charnov 1982, Kölliker et al. 1999, Sheldon et al. 1999, Oddie and Reim 2002). Although food supplementation and parasite infestation were not previously shown to directly affect clutch sex ratio in birds, they strongly affect fledgling condition and future breeding prospects (Richner and Tripet 1999, Rytkonen 2002, Fitze et al. 2004a), and parents are thus expected to adjust sex ratio accordingly. Furthermore, in this population, local breeding habitat quality varied in space at the scale of natal dispersal, but was temporally autocorrelated (Appendices C and D). Therefore, pairs breeding in high-quality patches (i.e., at the scale of natal dispersal) are also expected to bias offspring sex ratio toward the philopatric sex (i.e., males; Julliard 2000). Finally, pairs should settle preferentially on high-quality territories. Because the manipulation of habitat quality was conducted in early spring when breeders

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patches). See *Methods: Study site and manipulation of habitat quality* for the manipulation of habitat quality. Asterisks indicate expected significant differences ($P < 0.05$).
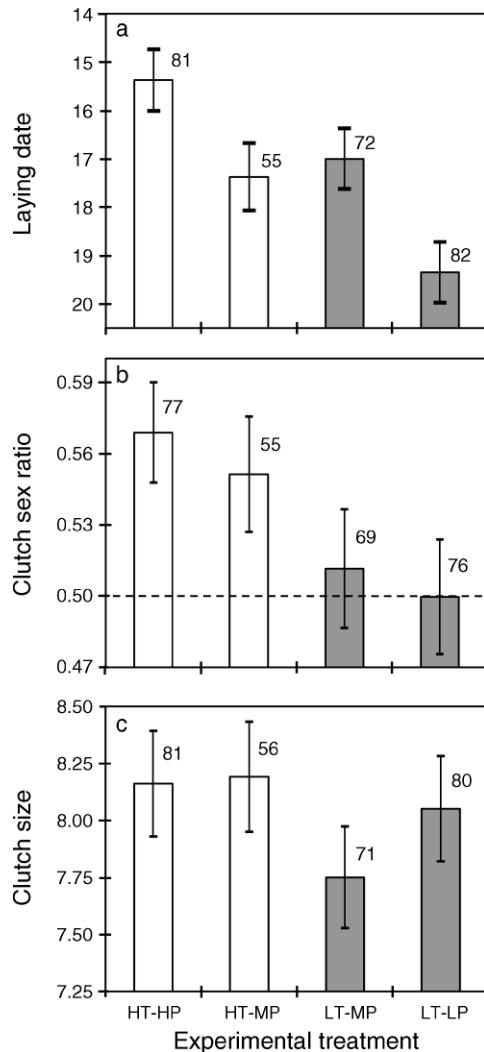
FIG. 2. Effect of the experimental manipulation of local habitat quality at the territory and patch scales on (a) laying date, (b) offspring primary sex ratio (here, proportion of males in the clutch), and (c) clutch size. Values are mean ± SE with sample sizes (number of broods) given above the bars. See Fig. 1 for the description of experimental treatments, and *Predictions and analyses: Statistical analyses* for statistics. Laying date depended on habitat quality at the patch (large) scale, while clutch sex ratio depended on quality at the territory (small) scale. Laying date values on the *y*-axis indicate the date in April (i.e., starting with 14 April). Clutch size did not depend on treatment, despite the lower value in LT-MP territories. The *y*-axis has been reversed for laying date (low values up on the axis) for the sake of coherence between graphs (low values of laying dates indicate higher quality).

have already started to secure a breeding area, it is unlikely to have affected patch choice, and preference should be limited to within-patch (i.e., small-scale) territory choice.

Statistical analyses

Sex ratio and nest box occupancy were analyzed with logistic regressions, laying date, clutch size, and fledgling body condition with GLM, using mixed models (proc mixed in SAS; Littell et al. 1996). Patch and territory treatment were included as one fixed factor with four modalities (HT-HP, HT-MP, LT-MP, and LT-LP) in all analyses, together with laying date and clutch size when applicable. The relative location of territory within the patch was also included as a binary explanatory variable (nest box located on the edge row of territories or in the center of the patch); more specifically, at least one side of territories located on the edge was bounded by the patch border, while all sides of territories in the center of the patch were bounded by other territories in the same patch (Appendix G). Territory location may indeed affect both the perceived quality of the territory and the probability for the offspring to change patch (see Appendix G). Therefore, we also tested the influence of territory location on the effect of treatment on the variable considered by including the territory location × treatment interaction. Finally, models included forest and patch replicate (nested within forest) as random variables. Statistical tests were two-tailed except for the effect of treatment, for which there is a clear a priori prediction for the direction of effects (see *Predictions and analyses*, and Fig. 1). The statistical significance of treatment was adjusted using ordered heterogeneity tests to gain statistical power (Rice and Gaines 1994), and the corresponding statistic ($r_S P_c$) and P values (denoted by P_{OH}) are given in each case. The alternative hypothesis (H_1) tested in this case was: $v(\text{HT-HP}) \geq v(\text{HT-MP}) \geq v(\text{LT-MP}) \geq v(\text{LT-LP})$, where $v(X)$ is the value of the breeding variable on territory type X (see *Predictions and analyses*, and Fig. 1). Differences between treatment modalities revealing the spatial scale of habitat quality involved were identified in a second step using orthogonal contrasts.

RESULTS

Laying date: effect of large-scale habitat quality

Laying date depended on the experimental treatment of habitat quality ($N = 290$, $F_{3,268} = 6.66$, $r_S P_c = 0.800$, $P_{OH} = 0.010$; Fig. 2a). Great Tits laid 2.0 days earlier in high-quality territories in high-quality patches (i.e., HT-HP territories), compared to high-quality territories in medium-quality patches (i.e., HT-MP territories; orthogonal contrast, $F_{1,268} = 4.49$, $P = 0.035$), and they laid 2.3 days earlier in low-quality territories in medium-quality patches (i.e., LT-MP territories), compared to low-quality territories in low-quality patches (i.e., LT-LP territories; $F_{1,268} = 7.00$, $P = 0.009$). However, within medium-quality patches, laying dates did not differ between high-quality and low-quality territories (i.e., between HT-MP and LT-MP territories; $F_{1,268} = 0.20$, $P = 0.656$; Fig. 2a). In other words, laying date was affected by large-scale patch quality, but not by small-scale territory quality. Because a delay of two days in laying may lead to a decrease in juvenile recruitment rate of >10% (Verhulst et al. 1995), such differences confirm that our manipulation affected patch quality in the

expected way. The location of territory within a patch influenced neither the effect of treatment on laying date (location $\times$ treatment interaction, $F_{3,264} = 1.29$, $P = 0.277$) nor laying date itself ($F_{1,267} = 0.01$, $P = 0.933$).

Offspring sex ratio: effect of small-scale habitat quality

Offspring primary sex ratio was also affected by treatment ($N = 277$, $F_{3,255} = 1.14$, $r_S P_c = 0.667$, $P_{OH} = 0.035$; Fig. 2b). Sex ratio was biased toward males in high-quality territories, compared to low-quality territories, whatever the quality of surrounding territories (marginally significant orthogonal contrast, $F_{1,255} = 3.19$, $P = 0.075$). However, offspring sex ratio did not differ between high-quality territories in high-quality and medium-quality patches (i.e., between HT-HP and HT-MP territories; $F_{1,255} = 0.05$, $P = 0.824$), or between low-quality territories in medium-quality and low-quality patches (i.e., between LT-MP and LT-LP territories; $F_{1,255} = 0.01$, $P = 0.927$; Fig. 2b). In other words, sex ratio was affected by small-scale territory quality, but not by large-scale patch quality. Offspring sex ratio did not depend on clutch size ($F_{1,254} = 1.55$, $P = 0.215$) or laying date ($F_{1,252} = 0.01$, $P = 0.940$). Territory location within the patch influenced neither the effect of treatment on sex ratio (location $\times$ treatment interaction, $F_{3,251} = 1.74$, $P = 0.159$) nor sex ratio itself ($F_{1,254} = 0.04$, $P = 0.851$).

Clutch size: no effect of local habitat quality

Clutch size ranged from 5 to 12 eggs. Clutch size was not affected by treatment ($N = 284$, $F_{3,262} = 0.96$, $r_S P_c = 0.354$, $P_{OH} > 0.10$; Fig. 2c). It did not depend on laying date either ($F_{1,260} = 0.54$, $P = 0.464$). Territory location within the patch influenced neither the effect of treatment on clutch size (location $\times$ treatment interaction, $F_{3,258} = 0.23$, $P = 0.872$) nor clutch size itself ($F_{1,262} = 0.23$, $P = 0.634$). In other words, none of the variables measuring habitat quality tested here explained clutch size variation.

Occupancy probability: effect of territory location

Finally, the probability for a nest box to be occupied did not depend on treatment ($N = 60$, $F_{3,37} = 1.32$, $r_S P_c = 0.430$, $P_{OH} = 0.10$; Fig. 3a), and territory location within the patch did not influence the effect of treatment on occupancy probability (location $\times$ treatment interaction, $F_{3,34} = 1.45$, $P = 0.245$). However, occupancy probability depended on the location of the territory within the patch ($F_{1,38} = 11.57$, $P = 0.002$). Nest boxes in territories on the edge of patches were nearly twice as likely to be occupied as nest boxes in the center of patches (Fig. 3b).

DISCUSSION

Environmental factors affecting different components of breeding success will often vary at different spatio-temporal scales (Orians and Wittenberger 1991, Boulinier and Lemel 1996). Therefore, individuals have to track multiscale variations in breeding habitat quality to
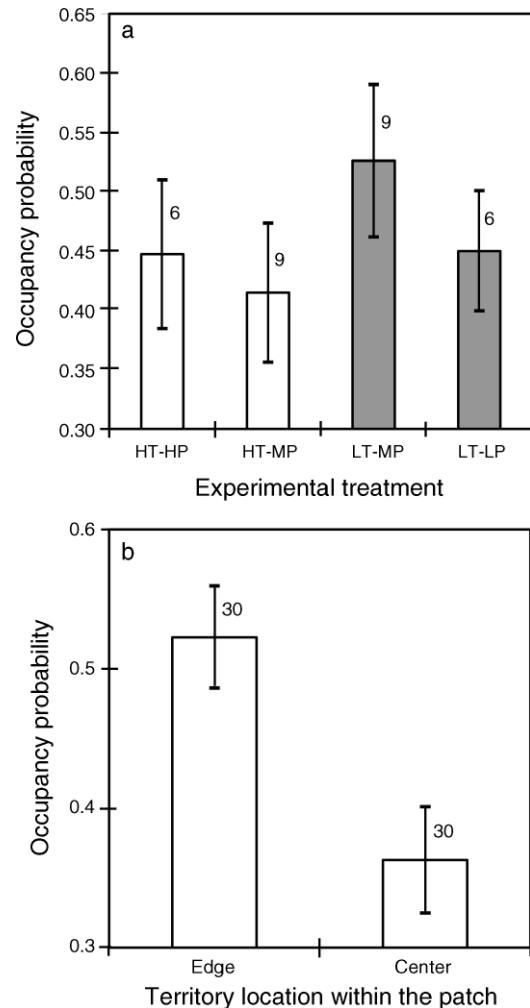
FIG. 3. Effect of (a) experimental manipulation of habitat quality, and (b) location of the territory within the patch on the probability of territory occupancy (mean $\pm$ SE). See Fig. 1 for the description of experimental treatments, and *Predictions and analyses: Statistical analyses* for statistics. Sample sizes: (a) number of patches of each type containing the territories considered (six high-quality and low-quality patches, and nine medium-quality patches; the medium-quality patches contain territories of two types), and (b) total number of patches, since each patch contains both edge and center territories. See *Methods: Study site and manipulation of habitat quality*, and Appendices E and F.

adjust different breeding decisions. So far, only correlative studies have accounted for scale issues in describing observed patterns of individual decisions in different taxa (e.g., Henschel and Lubin 1997, Stapp 1997, Huhta et al. 1998). Our study provides experimental evidence that individuals perceive local breeding habitat quality at different spatial scales and adjust different breeding decisions independently using information gathered at these different scales. Here we investigated four different early breeding decisions: when to breed (laying date); where to breed (small-scale

territory choice); how many offspring to produce (clutch size); and how to allocate resources between sexes (clutch sex ratio). These probably constitute a hierarchical series of tightly linked and simultaneous decisions. Nevertheless, they involved different types of information at different scales.

The absence of clutch sex ratio and clutch size adjustment according to large-scale patch quality was not due to Great Tit parents being unaware of the quality of other territories in the same patch, or using territory quality as a proximate for patch quality through the natural spatial autocorrelation in habitat quality (Appendix C). The adjustment of laying date according to patch quality indeed revealed that parents explore their environment at a larger scale than their territory at the beginning of the breeding season, and perceived and used large-scale habitat quality in deciding when to breed, while they used small-scale habitat quality to adjust offspring sex ratio. It is possible that, in deciding when to breed, Great Tits perceived all territories within the medium-quality patches (i.e., HT-MP and LT-MP territories) as intermediate quality territories if they forage outside their territory before laying. However, this still implies that they perceive habitat quality and use information at a larger scale than the territory for making decisions, and thus does not change our conclusions. The difference in response to treatment between laying date and clutch sex ratio unambiguously shows that individuals use information at different spatial scales to make different breeding decisions. The nonsignificant interaction between territory location and treatment on laying date and sex ratio may also suggest that individuals perceive their patch as one entity. Furthermore, our experimental manipulation of habitat quality affected some breeding decisions (laying date, offspring sex ratio), but not others (clutch size, small-scale territory choice). Despite the fact that adjusting offspring number to local conditions should be advantageous, food supplementation was not often found to influence clutch size (Boutin 1990). Moreover, contrary to previous findings in this species, flea infestation did not affect clutch size, although clutch size difference between HT-MP and LT-MP territories was of the same order of magnitude as previously found (Fitze et al. 2004b; Fig. 2c). Because many environmental and social factors affect breeding success, individuals should also integrate other factors of habitat quality into their decisions than those manipulated here. For instance, nest predation risk has been suggested to explain clutch size variation between (Martin 1995) and within (Doligez and Clobert 2003) populations. Individuals are likely to have accounted for factors, and possibly also spatial scales, not considered here in making decisions about clutch size. This is illustrated by territory occupancy probability, which did not directly depend on our manipulation of habitat quality, but depended on territory location within the patch, which

resulted from our manipulation of local nest box availability and distribution. Thus small-scale territory choice involved habitat quality measured by cues other than food availability and parasitism, at an intermediate spatial scale (edge vs. center of patches). Great Tit pairs may have perceived territories located at the edge of patches as higher quality territories and been more likely to settle there because individuals in edge territories could secure larger territories (since nest boxes located at the edge of patches had less neighboring nest boxes). Thus they would face lower intraspecific competition for food resource during nestling rearing and lower risk of extra-pair copulations for males. Furthermore, edge territories may have been more heterogeneous because many of the patches were located on the edge of the forests (see Appendix F), or were bordered by fragments of forest that were devastated by the Lothar storm in the winter of 1999–2000 (indeed, patches did not encompass large devastated areas), and breeding Great Tits seem to prefer heterogeneous habitats (B. Doligez, *personal observation*), probably because of the higher food diversity available in such habitats.

In this tit population, the level of offspring sex ratio adjustment according to habitat quality was weak (as in many other bird studies; see Radford and Blakey 2000, West and Sheldon 2002, Ewen et al. 2004), and selective pressures for offspring sex ratio adjustment seem to act mainly at a small scale (i.e., natal territory). Sex ratio adjustment according to local habitat quality at the scale of natal dispersal (Julliard 2000) did not apply. One explanation may be that the "natal dispersal" model implicitly assumes that parents exert control over the dispersal behavior of their offspring (Julliard 2000). However, natal dispersal behavior has been found to depend on local environmental quality in different species (e.g., Verhulst et al. 1997, Clobert et al. 2001). Tit juveniles may have the opportunity to assess their environment directly until settlement in the next year and thus choose their future breeding site accordingly. Thus the "natal dispersal" model may better apply to species where information gathering on local quality by juveniles is strongly constrained (e.g., migratory bird species under strong time constraints; Slagsvold 1987). Conversely, biasing sex ratio toward males in high-quality compared to low-quality territories (i.e., at a small scale) should be adaptive because of (1) the higher quality of offspring (as measured by body condition at fledging) produced in high-quality compared to low-quality territories ($N = 1364$, $F_{3,1155} = 2.96$, $r_S P_c = 0.775$, $P_{OH} = 0.014$; accounting for nest as a random variable; orthogonal contrast between high-quality and low-quality nests, $F_{1,1155} = 8.79$, $P = 0.003$; B. Doligez, *unpublished data*), and (2) the higher negative impact of nest parasites on male offspring in this population (Tschirren et al. 2003). Finally, we cannot rule out that the observed offspring sex ratio bias may also be the result of physiological constraints rather than parental

decisions, since our manipulation of territory quality may have affected parental condition. Additional experimental work would be needed to test whether offspring sex ratio was actively adjusted or constrained. The constraint hypothesis, however, does not explain the large-scale adjustment pattern of laying date, or the difference in patterns of variation between breeding decisions (laying date vs. clutch sex ratio) depending on treatment.

Our results show that understanding how individuals optimize breeding strategies requires consideration of multiscale environmental variation. To investigate breeding decisions by individuals, the choice of scale in experimental manipulations of environmental factors should be driven by previous detailed descriptions of spatial variation patterns. Due to the multiplicity of selective pressures, and the variability of spatial scales involved within and between species, it may otherwise be difficult to predict the adaptive value of a set of breeding decisions. For instance, when natal dispersal occurs at the scale of the territory, different models will make the same predictions based on different selective pressures (Clark 1978, Schwarz 1988, Julliard 2000). The task will even be complicated when selective pressures act in a context-dependent or phenotypic-dependent way, resulting in different use of information by different individuals.

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APPENDIX A

Testing the "natal dispersal" model assumptions (*Ecological Archives* E089-086-A1).

APPENDIX B

Natal dispersal distance of Great Tits in the study population (*Ecological Archives* E089-086-A2).

APPENDIX C

Spatial variation in breeding habitat quality in the study area (*Ecological Archives* E089-086-A3).

APPENDIX D

Temporal autocorrelation of local breeding habitat quality in the study area (*Ecological Archives* E089-086-A4).

APPENDIX E

Setup of experimental patches (*Ecological Archives* E089-086-A5).

APPENDIX F

Map of the experimental patches (*Ecological Archives* E089-086-A6).

APPENDIX G

Territory location within patch and constraints on natal dispersal distances (*Ecological Archives* E089-086-A7).

APPENDIX H

Methods for molecular sexing of chicks and embryos (*Ecological Archives* E089-086-A8).

Ecological Archives **E089-086-A1**

Blandine Doligez, Anne Berthouly, Damien Doligez, Marion Tanner, Verena Saladin, Danielle Bonfils, and Heinz Richner. 2008. Spatial scale of local breeding habitat quality and adjustment of breeding decisions. *Ecology* **89:1436–1444.**

Appendix A. Testing the "natal dispersal" model assumptions.

We checked the three assumptions of the "natal dispersal" model, i.e., (i) sex-biased natal dispersal, (ii) spatial variation in breeding habitat quality at the scale of natal dispersal, and (iii) temporal predictability of habitat quality (Julliard 2000).

We used natal dispersal data collected between 1997 and 2000 in the main study area, the Bremgartenwald, on our study species, the great tit, obtained from records of ringed nestlings that recruited within the local breeding population. Within the Bremgartenwald until year 2000, nest boxes were distributed continuously in space, thus allowing us to obtain unconstrained dispersal distances. The dispersal distance was computed as the straight distance (in m) between the natal nest box and the first breeding attempt nest box. We tested whether this distance differed between sexes, after accounting for natal conditions (year, hatching date, fledgling mass and body condition, and brood size at fledging). See Appendix B.

To investigate spatial and temporal variability in local breeding habitat quality, we used the main breeding characteristics as measures of habitat quality: nest box occupancy rate, clutch size, laying date, probability of breeding failure, fledgling number for successful nests, and fledgling body mass and condition (defined as the ratio of body mass over tarsus length at day 14). We used breeding data collected on great tits in the Bremgartenwald during the period 1993–2000 in these analyses. Within the Bremgartenwald, we defined square zones based on the mean natal dispersal distance of the most philopatric sex (i.e., approximately 450 m × 450 m; see below). We then checked spatial and temporal variation in breeding characteristics by (i) testing the influence of zone, year and their interaction (defined as random factors) on these values, and (ii) measuring their temporal autocorrelation. Nest box occupancy rate and probability of breeding failure were analysed with logistic regressions, laying date, clutch size and fledgling number and body condition with GLMs, using mixed models (proc mixed in SAS - Littell et al. 1996). Autocorrelation coefficients (Moran's I) and significance (measuring temporal predictability) were obtained using the R software (Legendre and Vaudor 1991).

Spatial variation in breeding habitat quality: All measures of local breeding habitat quality varied in space at the scale of natal dispersal distances (see Appendix C), as reflected by significant effects of zone or zone × year interaction. More importantly, the zone × year interaction was significant for nearly all variables of reproductive success, showing that the relative quality of each zone varied through time at a large temporal scale (see below for year to year predictability), i.e. the same zones were not always the best or the worst quality zones. This implies that tits have to keep on sampling their environment and gathering information on where the best sites are at a given time.

Temporal predictability of breeding habitat quality: Occupation rate and clutch size were temporally autocorrelated (one-year time lag: occupation rate: $n = 168$, Moran's I = 0.712, $P < 0.001$; clutch size: $n = 162$, Moran's I = 0.284, $P = 0.004$ - see Appendix D). We found no temporal autocorrelation in fledgling number ($n = 162$, Moran's I = -0.1296, $P = 0.140$), and mean fledgling body mass ($n = 162$, Moran's I = -0.0540, $P = 0.348$) or condition ($n = 160$, Moran's I = -0.0026, $P = 0.530$). However, these variables measure late breeding success, and nesting attempts in this population have been largely manipulated during these years (brood size manipulations, artificial nest parasite infestations, etc.), which is likely to have blurred any temporal autocorrelation. From results on early breeding traits, i.e. nest site choice and clutch size, we can conclude that the environment is at least partially predictable at the spatial scale of natal dispersal in the main study area, the Bremgartenwald.

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Ecological Archives **E089-086-A2**

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Appendix B. Natal dispersal distance of Great Tits in the study population.
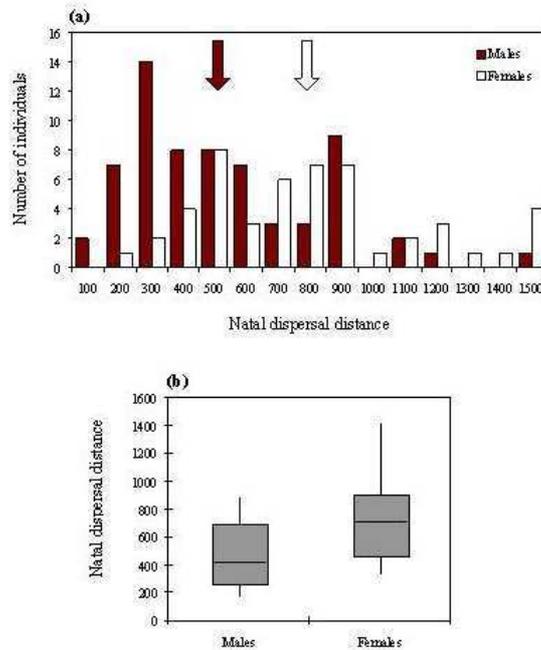
FIG. B1. Natal dispersal distance of male and female Great Tits hatched in the Bremgartenwald in the years 1997 to 1999. (a) Sex-specific natal dispersal distance distributions. Arrows indicate mean dispersal distance values for each sex. (b) Box plots of natal dispersal distances; limits of boxes represent 25% and 75% of dispersal distances, limits of lines represent 10% and 90%, and median dispersal distances are indicated with a line within the box.

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Ecological Archives **E089-086-A3**

Blandine Doligez, Anne Berthouly, Damien Doligez, Marion Tanner, Verena Saladin, Danielle Bonfils, and Heinz Richner. 2008. Spatial scale of local breeding habitat quality and adjustment of breeding decisions. *Ecology* **89:1436–1444.**

Appendix C. Spatial variation in breeding habitat quality in the study area.

Temporal changes in spatial variation of local breeding habitat quality at the scale of natal dispersal distance in the study population. Habitat quality was measured using the major breeding characteristics of great tits in the Bremgartenwald 1993–2000: (a) nest box occupation rate; (b) laying date; (c) probability of breeding failure; (d) number of fledglings in successful nests; (e) fledgling body mass; and (f) fledgling body condition.

TABLE C1. the value of the statistical test (Z) and associated probability (P) describe the effect of zone and interaction zone × year (random factors) on breeding characteristics, in a mixed logistic regression model (proc mixed, SAS - Littell et al. 1996). N: sample size. Unit of analysis: zone for occupation rate; nest for laying date, probability of failure and fledgling number (successful nests only); fledgling for body mass and condition. In the latter case, the nest was also included as a random variable in the analysis to account for the non-independence of siblings. The interaction zone × year could not be tested for occupation rate as only one value is obtained per zone per year. Significant results are shown in bold. Results do not qualitatively change when excluding data from year 2000, showing that the spatio-temporal variability in local breeding habitat quality was not due to the consequences of the 1999 Lothar storm.

Measure of habitat quality	N	Effect of zone		Effect of zone × year	
		Z	P	Z	P
(a) Occupation rate	96	**2.20**	**0.0138**	-	-
(b) Laying date	919	0.06	0.4775	**1.54**	**0.0613**
(c) Probability of failure	871	0.31	0.3798	**2.37**	**0.0089**
(d) Fledgling number	761	0.64	0.2605	**2.07**	**0.0195**
(e) Fledgling body mass	5021	0.92	0.1783	**3.56**	**0.0002**
(f) Fledgling body condition	5010	0.95	0.1705	**2.76**	**0.0029**
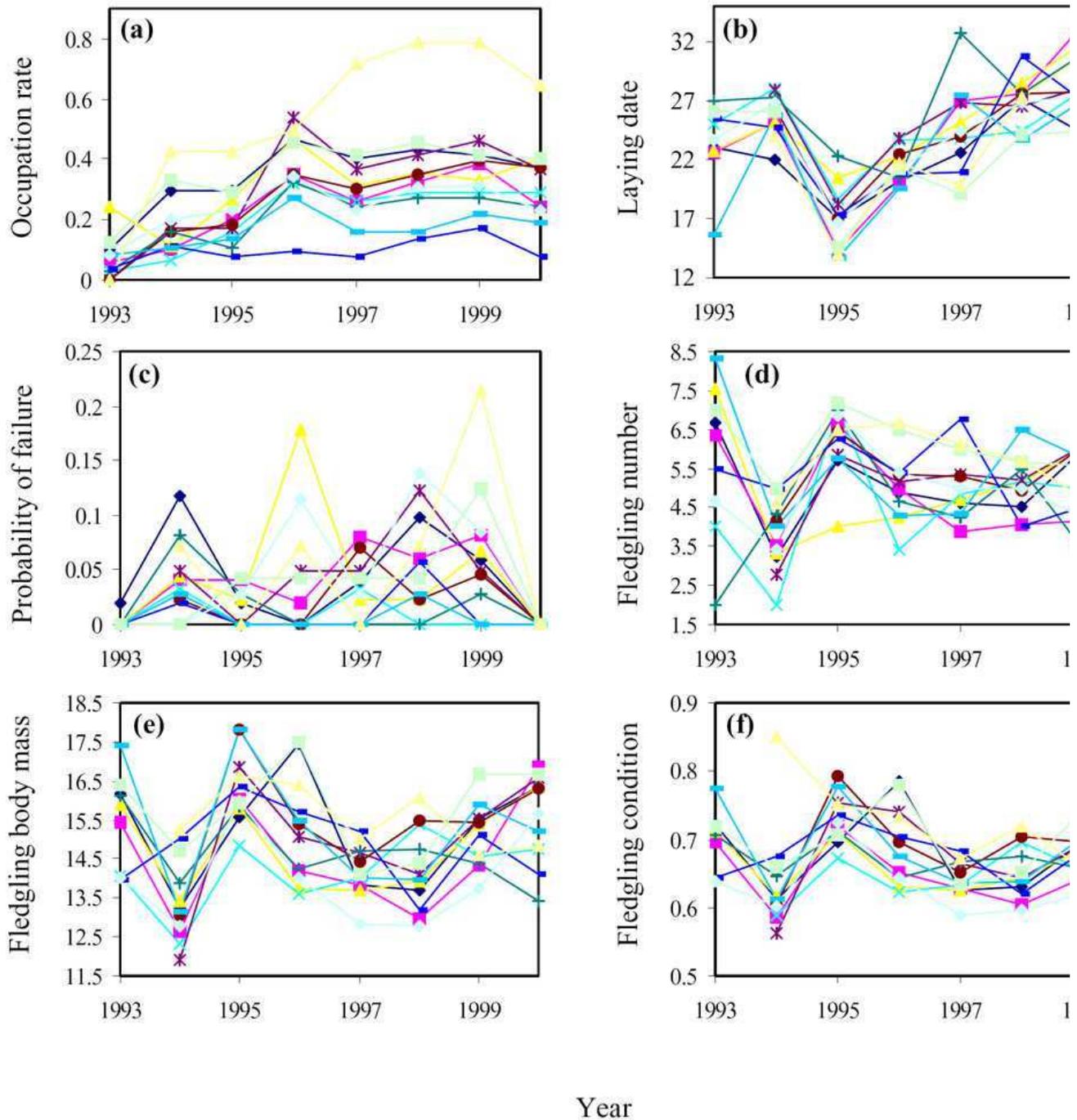
FIG. C1. Each color represents one zone. The significant effect of the interaction zone × year is visualised by the many line crossings, which indica[...] relative quality of a zone compared to others changed through time.

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Ecological Archives **E089-086-A4**

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Appendix D. Temporal autocorrelation of local breeding habitat quality in the study area.
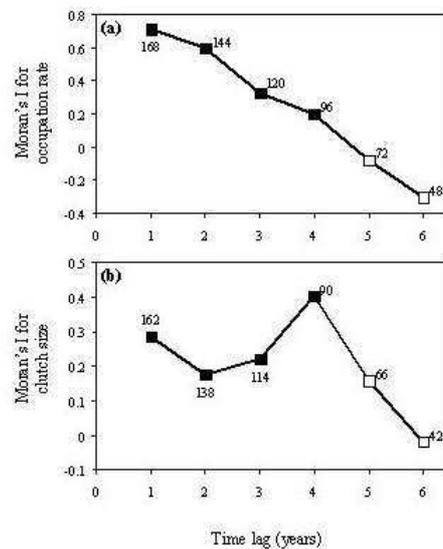
   FIG. D1. Temporal autocorrelation of local breeding habitat quality, as measured by (a) occupation rate and (b) clutch size. On the *x*-axis is given the time lag in years; on the *y*-axis is given the autocorrelation coefficient (Moran's I). Black squares: significant coefficients ($P < 0.05$); open squares: nonsignificant coefficients. Numbers indicate sample sizes. (The increase observed in Moran's I for clutch size for time lags of four years is probably an artefact.)

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Appendix E. Setup of experimental patches.
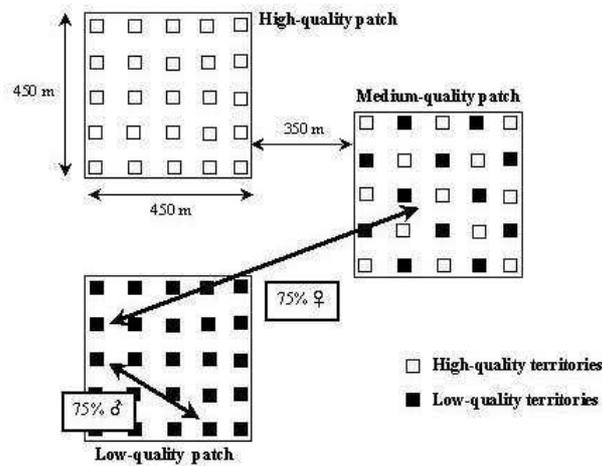
FIG. E1. Open squares: territories supplemented with food; black squares: nest boxes infested with ectoparasites. In high-quality patches, all territories were supplemented with food (HT-HP). In low-quality patches, all nest boxes were infested with ectoparasites (LT-LP). In medium-quality patches, half of the territories were supplemented with food (HT-LP) and half were infested with ectoparasites (LT-HP), alternatively in space. Each patch comprised 30 nest boxes uniformly distributed in space. Patch dimensions and inter-patch distance were chosen so as to maximise the difference in dispersal probability between male and female offspring. Each patch was a 450×450 m square (or had the equivalent area when a rectangular shape). Inter-patch distance was chosen so that the centre points of two adjacent patches were separated by the mean natal dispersal distance of females (i.e., 800 m). Together with the lack of available nest sites between patches, these distances should lead to approx. 75% of male offspring expected to stay in their natal patch and 75% of female offspring expected to leave their natal patch (under the hypothesis that natal dispersal probability does not depend on local habitat quality).

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Ecological Archives **E089-086-A6**

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Appendix F. Map of the experimental patches.
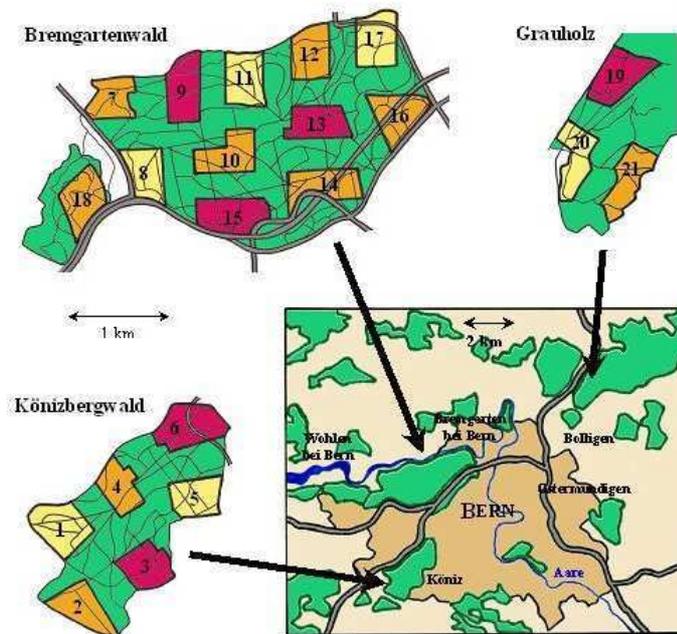
FIG. F1. Map of the 21 experimental patches in the three study forests around the city of Bern. Yellow patches: low-quality patches (patches 1, 5, 8, 11, 17, and 20); red patches: high-quality patches (patches 3, 6, 9, 13, 15, and 19); orange patches: medium-quality patches (patches 2, 4, 7, 10, 12, 14, 16, 18, and 21). See text for the description of the experimental manipulation of local breeding habitat quality. Mean patch area did not differ between patch treatments (mean area $\pm$ 1 SE in ha: high quality patches: 19.3 $\pm$ 1.1, medium quality patches: 19.8 $\pm$ 1.1, low quality patches: 20.0 $\pm$ 1.1, $F_{2,15} = 0.24$, $P = 0.791$. Spatial scale is identical for the three forests and is indicated).

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Ecological Archives **E089-086-A7**

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Appendix G. Territory location within patch and constraints on natal dispersal distances.

With regard to our test of the natal dispersal model of sex ratio adjustment (Julliard 2000), it is important to note that constraints on natal dispersal will slightly differ for offspring depending on the location of their natal territory within the patch (on the edge vs. in the center - see figure below). The probability of settling in the natal patch may differ between offspring from pairs breeding in the centre and on the edge of patches. Offspring from territories in the centre of patches would have to disperse distances larger than 575 m on average to change patch, while offspring from territories at the edge of patches would have to disperse only 350 m . However, the boxes available within a radius of 500 m are in both cases located in majority within the natal patch: 100% and 75% of boxes for offspring hatched in central and edge territories respectively. Furthermore, the large between-patch areas, which contain no nest boxes, should enhance the difference between males and females in the probability to settle in the natal patch. Dispersal distance distributions were recorded under a continuous distribution of nest boxes. When facing large zones with no available breeding sites, we expect that males would be more prone to stay in their natal patch while females would be more prone to leave.
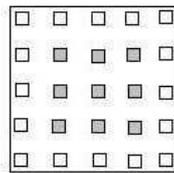
FIG. G1. Location of the different types of territories within a patch. White squares: nest boxes in edge territories; gray squares: nest boxes in central territories. The mean number of territories located on the edge of a patch is 17.9 ± 0.19 (each patch comprising 30 territories).

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Ecological Archives **E089-086-A8**

Blandine Doligez, Anne Berthouly, Damien Doligez, Marion Tanner, Verena Saladin, Danielle Bonfils, and Heinz Richner. 2008. Spatial scale of local breeding habitat quality and adjustment of breeding decisions. *Ecology* **89:1436–1444.**

Appendix H. Methods for molecular sexing of chicks and embryos.

To sex tit nestlings, we used a DNA test following the protocol of Griffiths et al. (1998). DNA was extracted from nestling's blood using commercial kits (Wizard Genomic DNA Isolation Kit, Promega, Switzerland; DNeasy Tissue Kit, Qiagen, Basel, Switzerland) following the manufacturers' protocols. For DNA extraction from dead embryo tissue, we used DNeasy Tissue Kit (Qiagen, Basel, Switzerland), following the protocol for rodent tail.

PCR amplification was carried out in a total volume of 10 µL. The final reaction conditions were as follows: 0.25 U HotStarTaq DNA polymerase (Qiagen, Basel, Switzerland), 1 µL Taq buffer, 2.5 mM $MgCl_2$, 0.2 mM of each dNTP (Amersham Pharmacia Biotech Inc.) and 1 µM each of primers P2 and P8. 1 µL of genomic DNA was used as template. PCR was performed in a GeneAmp 2400 or GeneAmp 9700 Thermocycler (Applied Biosystems, Rotkreuz, Switzerland) with the following temperature profile: initial denaturation at 95°C for 15 min; 40 cycles of 94°C for 30 sec, 52°C for 15 sec, and 72°C for 75 sec. The program was completed by an additional extension step at 72°C for 7 min.

PCR products were separated by electrophoresis at 8 V/cm on ethidium bromide stained 2% agarose gels and visualized by UV transillumination. The nestlings were sexed according to the presence of one (males) or two bands (females) (Tschirren et al. 2003).

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