

structure generated by hydrological conditions is very conservative because plants grown in the absence of interspecific competition have highly overlapping rather than randomly overlapping fundamental niches.

We used our field data to test for a trade-off between SEV axes. A mean SEV for each species on each axis at each site was calculated as $(\sum_{i=1}^n SEV_i p_i) / n$, where n was the number of quadrats in which a species was present, SEV_i was the value at the location of quadrat i , and p_i was the proportion of the species' total recorded abundance found in quadrat i . The distribution of mean SEV values in niche space (Fig. 2) shows a highly significant negative correlation between soil drying and waterlogging tolerance across species at both sites (Tadham, $r = 0.82$, $n = 64$, $P < 0.0001$ (Fig. 2a); Cricklade, $r = 0.98$, $n = 51$, $P < 0.0001$ (Fig. 2b)), indicating a trade-off between tolerances.

We used the method of phylogenetically independent contrasts, as implemented in the computer program CAIC¹⁹, to check the robustness of the trade-off between drought and waterlogging tolerance (Fig. 2). A composite phylogeny (available from the authors), with branch lengths set equal, was constructed for the 83 species in the study by using the most up-to-date molecular phylogenies available. Regression through the origin of aeration and dryness SEV contrasts gave a highly significant negative relationship at both sites (Tadham, $y = -1.20x$, $F_{(1,52)} = 87.12$, $P < 0.0001$, adjusted $R^2 = 0.62$; Cricklade, $y = -1.68x$, $F_{(1,44)} = 1,279$, $P < 0.0001$, adjusted $R^2 = 0.966$). The trade-off between soil-drying and waterlogging tolerance is therefore not only strong, but has shaped the evolution of tolerances in many independent cases²⁰.

For at least two reasons, meadows are unlikely to be the only species-rich communities that are structured by segregation of species along niche axes of soil drying and soil aeration. First, segregation across topographic gradients has been observed in many plant communities, and we have shown that the spatial variation in hydrological conditions thought to cause this might occur in the absence of any obvious topographic variation (as at Tadham) and that plants are sensitive to hydrology at a fine scale. Second, the trade-off between drought and aeration tolerance that we have demonstrated here is so strong and phylogenetically robust that it cannot be confined to our set of species alone and must reflect a general physiological constraint with wide occurrence. The hitherto largely vain search for plant niches in the established phase of the plant life cycle has been confined mainly to axes of nutrients and light availability, but our findings suggest that investigations of variation in soil hydrology at a fine spatial scale and over longer time-spans might well reveal a potent force that structures many types of plant community. The precise mechanism by which this force acts now requires investigation. □

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Ectoparasite infestation and sex-biased local recruitment of hosts

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Dispersal patterns of organisms are a fundamental aspect of their ecology, modifying the genetic and social structure of local populations^{1–4}. Parasites reduce the reproductive success and survival of hosts and thereby exert selection pressure on host life-history traits^{4–6}, possibly affecting host dispersal^{7–9}. Here we test experimentally whether infestation by hen fleas, *Ceratophyllus gallinae*, affects sex-related recruitment of great tit, *Parus major*, fledglings. Using sex-specific DNA markers, we show that flea infestation led to a higher proportion of male fledglings recruiting in the local population in one year. In infested broods, the proportion of male recruits increased with brood size over a three year period, whereas the proportion of male recruits from uninfested broods decreased with brood size. Natal dispersal distances of recruits from infested nests were shorter than those from uninfested nests¹⁰. To our knowledge, this study provides the first evidence for parasite-mediated host natal dispersal and local recruitment in relation to sex. Current theory needs to consider parasites as potentially important factors shaping life-history traits associated with host dispersal.

As part of a long-term study on the evolutionary and ecological aspects of host–ectoparasite interactions^{11–13}, we randomly infested half the nests in a population of great tits with adult hen fleas¹¹ over three breeding seasons. The remaining nests were kept free of fleas (see Methods). Similar to findings in another Swiss population¹⁴, flea infestation reduced the body mass of nestlings (mean mass (\pm s.e.) of 16-day-old nestlings: infested, 15.19 ± 0.16 g; uninfested, 15.84 ± 0.15 g; two-way ANOVA: flea treatment, $F(1, 283) = 10.1$, $P = 0.002$; year, $F(2, 283) = 26.7$, $P < 0.0001$; interaction, NS). Furthermore, the number of young fledged was lower in flea-infested than in uninfested broods (infested, 4.0 ± 0.2 , $N = 162$ broods; uninfested, 4.7 ± 0.2 , $N = 169$; two-way ANOVA for ranks: fleas, $\chi^2_1 = 7.28$, $P = 0.007$; year, $\chi^2_2 = 4,015$, $P < 0.0001$; interaction, NS). Thus, flea infestation had detrimental effects on great tit reproduction during the nestling period.

During the three years of the experiment, uninfested broods ($N = 150$) fledged 797 young of which 63 (7.9%) were recaptured as first-time breeders (that is, recruits; see Methods). Infested broods ($N = 137$) fledged 654 young of which 48 (7.3%) were recruited. Flea infestation had no significant effect on the total proportion of broods recruiting young (log likelihood ratio: fleas, $\chi^2_1 = 0.34$,

Table 1 Logistic regression on the proportion of fledglings per brood recruited locally

	(Change in) d.f.	(Change in) deviance	<i>P</i>
Null model	280	300.4	
Full model	275	204.4	
Year	2	75.5	< 0.0001
Nesting mass	1	11.8	< 0.001
Year*nesting mass	2	6.0	0.05
Rejected terms			
Flea infestation	1	0.07	0.79
Laying date	1	2.80	0.10
Year*flea infestation	2	0.12	0.90

Logistic regression²⁰ on the number of young recruited with the number of young fledged as the binomial denominator. Degrees of freedom in the null model indicate the number of broods. The effect of fleas remains nonsignificant when nesting mass is excluded from the model ($P > 0.50$).

$P = 0.55$; year, $\chi^2_2 = 57.53$, $P < 0.0001$; interaction, NS), on the number of recruits per brood (Wilcoxon two-sample test: $Z = -0.81$, $P = 0.42$) or on the proportion of fledglings recruited per brood (Table 1). As found in other studies on passerines, the probability of recruitment of fledglings was positively correlated with their mass¹⁵ (Table 1). In our study, flea infestation reduced the body mass of nestlings and the number of fledglings, but there was no evidence that fleas affected overall local recruitment. The relatively low reproductive performance of our great tit population compared with other Swiss populations indicates that our study area is a rather poor habitat^{14,16}. One possible explanation for the absence of an effect of fleas on local recruitment could be that more fledglings from uninfested nests dispersed away from our study area^{17,18}.

It has been suggested that the detrimental effects of parasites on adults depends on the sex of the host¹⁹. To examine whether flea infestation affected the recruitment of fledglings in relation to gender, we used sex-specific DNA-markers to determine the sex of young from 64 broods in one year (see Methods). Results showed that the proportion of males in the brood at fledging did not differ between flea treatments ($Z = 0.14$, $P = 0.9$; Fig. 1), and did not differ significantly from parity (both $P > 0.5$). However, we found that the proportion of male recruits differed in relation to flea infestation ($Z = 2.15$, $P = 0.03$). A greater proportion of male fledglings was recruited from flea-infested broods, whereas recruitment in uninfested broods was not significantly sex-biased (Fig. 1). Thus, flea infestations resulted in a significant bias in the proportion of male fledglings recruited, which could result from sex-related

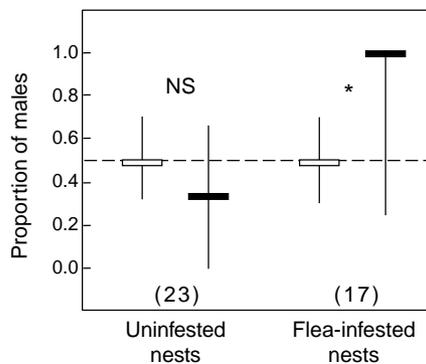


Figure 1 Flea infestation and proportion of males in great tit broods at fledging (white bars) and recruitment (black bars). Median values and interquartile ranges are shown. Number of broods recruiting young are in brackets. In infested broods, there was a significant difference in the proportion of males between fledging and recruitment (paired t -test: $t = -2.2$, d.f. = 16, $P = 0.04$; indicated by *). In uninfested broods the difference was not significant ($t = 1.8$, d.f. = 22, $P = 0.09$; indicated by NS). The change in the proportion of males between fledging and recruitment was significantly different between treatments (t -test: $t = 2.81$, d.f. = 38, $P = 0.007$).

differences in dispersal and/or mortality of fledglings after leaving the nest^{7,17,20}.

We analysed the data on all the recruits from the three years of experimental infestation to determine whether enhanced nestling competition within broods associated with flea infestation²¹ and the number of young in the brood^{22,23} affected the proportion of male recruits. We found a significant interaction between brood size at hatching and flea treatment on the proportion of male recruits in a brood (Fig. 2). In infested nests the proportion of male recruits tended to increase with brood size, whereas in uninfested broods the proportion of male recruits tended to decrease with brood size (Fig. 2). Our results indicate that increasing competition among nestlings in larger and infested broods lead to higher male local recruitment. Another study on great tits showed that an experimental enlargement of brood size also led to male-biased local recruitment²². In our study, variation in the effect of fleas with brood size on the proportion of male recruits could explain the fact that there was no overall significant effect of fleas on the total number of male and female recruits (uninfested, 29 males and 34 females; infested, 29 males and 19 females; $\chi^2_1 = 2.27$, $P = 0.13$).

We found no significant effect of fleas on the proportion of male fledglings when we analysed all broods sexed with DNA-markers ($Z = -0.53$, $P = 0.60$, $N = 37$ and 27), showing that fleas did not lead to sex-ratio biases in broods at fledging. In broods where we determined the sex of nestlings, males were heavier than females (mean difference at 14 days old: $0.7 \text{ g} \pm 0.1$; $N = 64$, $P < 0.001$). The sexual dimorphism in nestling body mass was not significantly affected either by fleas or by the number of young in the brood (fleas: $F(1, 61) = 0.32$, $P = 0.57$; brood size: $F(1, 61) = 0.03$, $P = 0.86$). Thus, differences in the proportion of males recruited were apparently not mediated by sex-dependent effects of fleas, or brood size on nestling body mass. There was no significant difference in the relative body mass of recruits in the two treatments (body mass deviation from the brood mean on day 14 (controlling for year and sex): $F(1, 106) = 0.77$, $P = 0.38$). This result indicates that young recruiting in the two treatments occupied similar relative positions in the body mass hierarchy within their broods²³.

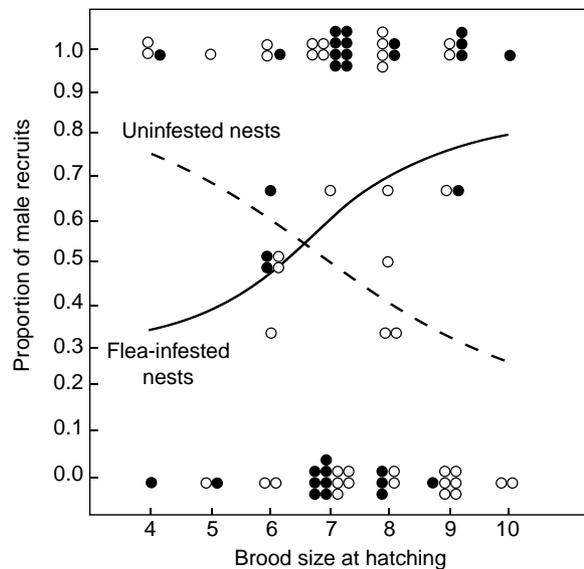


Figure 2 Interaction between flea infestation and brood size at hatching on the proportion of male recruits. Open symbols are for uninfested, and filled symbols for infested broods ($N = 75$). Fitted lines are from a logistic regression model on the number of male recruits (nominator) relative to the total number of recruits (denominator)²⁰, with year, flea treatment, brood size and their interactions as predictor variables. Only the interaction between flea treatment and brood size was significant (change in deviance of 5.49, d.f. = 1, $P = 0.02$; full model deviance was 101.8, d.f. = 71); all other effects were nonsignificant ($P > 0.20$).

We found that recruits from infested broods dispersed shorter natal distances (see Methods) than recruits from uninfested broods (mean for broods: infested, 532 ± 57 m; uninfested, 641 ± 44 m; generalized linear model: fleas, $F(1, 67) = 4.52$, $P = 0.04$; controlling for the effects of year, nestling mass and proportion of males (all $P > 0.10$). In contrast to other studies on great tits, which showed greater natal dispersal distances in females^{17,18,22}, the difference between the sexes was not significant in our study (mean for females, 660 ± 45 m, $N = 53$; mean for males, 547 ± 43 , $N = 58$; $F(1, 106) = 1.96$, $P = 0.16$; controlling for year and flea effects). The interaction between flea treatment and sex was not significant ($F(1, 105) = 0.27$, $P = 0.60$), indicating that fleas affected the natal dispersal distance of recruits independently of sex. Fleas could influence natal dispersal distances through an effect on nestling body mass^{18,22}, hormonal levels in nestlings²⁴ or through maternal effects^{8,12}. These different mechanisms suggest that fleas could have affected the competitive ability of individuals and their cost-benefit balance of dispersal^{3,25}. By dispersing shorter distances after growing in flea-infested nests, great tits remain closer to their natal territory where they could be better adapted or show higher tolerance to local parasites^{12,26,27}. This effect could be particularly important for females, as they face more frequent contacts with nest-based ectoparasites¹².

Current hypotheses for sex-biased dispersal propose that, in monogamous species with male resource defence like the great tit, males could gain greater benefits from their familiarity with essential local resources by remaining in their natal area^{3,10,28}. Our results of a male-biased recruitment in one year, and the interaction between flea treatment and brood size over three years, indicate that benefits of remaining in the natal area could be higher for males growing in large, flea-infested broods. A male-biased dispersal away from our study area from uninfested broods could also potentially explain lower local recruitment of males (Fig. 1). However, such male-biased dispersal would contrast with the female-biased dispersal pattern found in most monogamous birds^{3,10,17,28}.

To our knowledge, our study shows for the first time that parasite infestations affect host natal dispersal distances and can modify the sex-related probability of fledgling recruitment. Conditional sex-biased dispersal is not predicted by current theoretical models that focus mainly on inbreeding avoidance or local resource competition^{2,3,10,25,28}. Key concepts in sex-ratio theory and host-parasite coevolution have been developed by considering the effects of host dispersal^{1,4,26,27}. Our results indicate that, in certain organisms, hosts could modify their sex-allocation decisions in response to parasite infestations when parasites modify host sex-biased recruitment and dispersal. □

Methods

Experimental protocol. The study was performed in a population of great tits breeding in a mixed forest near Bern, Switzerland. Breeding pairs were assigned randomly to experimental treatments in each of three breeding seasons (1994–1996). In all three years, parasites were killed in all nests on the day the birds laid their second egg^{11–13}. Half the nests in the population were infested by a fixed number of adult fleas from the laying of the second egg or from the start of incubation onwards, whereas the other half were left uninfested. Uninfested nests in 1994 and 1995 were kept free of fleas by heat treatment in a microwave appliance every ten days; in 1996 nests were heat treated only once. Laying date and clutch size did not differ significantly between birds with flea-infested or uninfested nests (Wilcoxon two-sample test: laying date, $Z = -0.09$, $P = 0.93$; clutch size, $Z = 0.38$, $P = 0.71$; $N = 175$ and 168).

Data collection. For each breeding pair we recorded the date when the first egg was laid, clutch size, brood size at hatching, and the number of young fledged. Nestling body mass was measured to the nearest 0.1 g with an electronic balance on days 14 and 16 after hatching. On day 9, all nestlings were ringed with numbered aluminium rings. A local recruit was defined as a fledgling that was recaptured as a first-time breeder in the population until spring 1998. The linear distance between the nest where a young fledged to the nest where it was first re-captured as a breeder was taken as the natal dispersal distance¹⁰. In 1995,

nestlings of 64 broods were sexed using random amplified polymorphic DNA (RAPD) markers applied to the DNA extracted from blood collected in capillary tubes by venipuncture on 14-day-old nestlings²⁹. Mean values are shown \pm standard errors. Analysis was performed in JMP and GLMStat.

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Motion streaks provide a spatial code for motion direction

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Although many neurons in the primary visual cortex (V1) of primates are direction selective¹, they provide ambiguous information about the direction of motion of a stimulus^{2,3}. There is evidence that one of the ways in which the visual system resolves this ambiguity is by computing, from the responses of V1 neurons, velocity components in two or more spatial orientations