Dispersal of introduced house sparrows *Passer domesticus*: an experiment

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An important issue concerning the introduction of non-indigenous organisms into local populations is the potential of the introduced individuals to spread and interfere both demographically and genetically with the local population. Accordingly, the potential of spatial dispersal among introduced individuals compared with local individuals is a key parameter to understand the spatial and temporal dynamics of populations after an introduction event. In addition, if the variance in dispersal rate and distance is linked to individual characteristics, this may further affect the population dynamics. We conducted a large-scale experiment where we introduced 123 house sparrows from a distant population into 18 local populations without changing population density or sex ratio. Introduced individuals dispersed more frequently and over longer distances than residents. Furthermore, females had higher probability of dispersal than males. In females, there was also a positive relationship between the wing length and the probability of dispersal and dispersal distance. These results suggest that the distribution and frequency of introduced individuals may be predicted by their sex ratio as well as their phenotypic characteristics.

Keywords: invasive; *ex situ* conservation; morphological characters; movement pattern; reintroduction; transgenic organisms

1. INTRODUCTION

Owing to human activity, the introduction of alien species and individuals of deviant genotypes into wild populations is one of the major threats to global biodiversity (Lodge 1993; Clavero & Garcia-Berthou 2005). Numerous examples are available where introduced individuals have established viable populations (e.g. Blackburn & Duncan 2001). In many cases, such introductions have led to changes in local population structure, which may have pronounced effects both ecologically (Tiedje *et al.* 1989; Simberloff *et al.* 2005) and economically (Born *et al.* 2005). Furthermore, if alien and native individuals interact reproductively, this may alter the genetic composition and lead to changes of locally co-adapted gene complexes or establishment of deleterious alleles (Lynch & Walsh 1998), which may influence the growth rate of the population (McGinnity *et al.* 2003). On the contrary, for a population or a species that balances on the brink of extinction, a supply of introduced individuals may rescue the population and even the species from extinction (Ebenhard 1995). Hence, introductions may be an important management tool in the conservation of threatened or vulnerable populations (Griffith *et al.* 1989; Hedrick 1995; Madsen *et al.* 1999).

An important consequence of introducing individuals into an area is that they will often spread into surrounding areas. Thus, identifying the factors that influence the rate and spatial scale of spread should be considered when evaluating the ecological consequences of introducing individuals into an area (Puth & Post 2005). For example,

in two sympatric species of crayfish (*Pacifastacus leniusculus* and *Austropotamobius pallipes*), one resident and one invasive, the invasive species was shown to move substantially longer distances within the study area than the local species (Bubb *et al.* 2006). It has also been shown that relocated individuals of the tiger snake (*Notechis scutatus*) dispersed longer distances than the residents, although the frequency of movement was the same for both groups (Butler *et al.* 2005). These studies indicate that the spread of alien individuals may be faster than expected from theoretical models which only assume a linear rate of spread with time (Hastings 1996). The spatial scaling of movements, especially during the period just after an introduction episode, also varies substantially among species (Duncan *et al.* 1999, 2003). Thus, identifying the factors affecting the movement patterns during this period seems important for understanding the spread of introduced individuals into surrounding areas.

In vertebrates, there is now substantial empirical evidence that individual characteristics can explain a considerable proportion of the variation in both natal and breeding dispersal (Clobert *et al.* 2001; Aragón *et al.* 2006). For instance, in birds, females generally disperse over larger distances than males (e.g. Greenwood & Harvey 1982; Clarke *et al.* 1997), whereas the reverse pattern is found in mammals (e.g. Dobson 1982). Furthermore, evidence from a variety of taxa also suggests that the dispersal distance is associated with individual phenotypic characteristics. For instance, individuals with higher flight metabolic rate showed more frequent dispersal in the Glanville fritillary butterfly (*Melitaea cinxia*; Haag *et al.* 2005). Similarly, other physiological traits, such as individual ability of the immune system to

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Figure 1. Maps showing geographical locations of populations included in the introduction experiment of house sparrows in northern Norway. (a) The regional positions of the study areas in northern Norway and (b) the Vikna archipelago, where each local population (i.e. farm) is indicated by a triangle.

respond to novel antigens, have also been shown to be related to dispersal behaviour (Snøeijns *et al.* 2004).

Although many mechanisms that influence dispersal behaviour under natural conditions are known, few studies have experimentally examined the factors affecting the movement patterns of introduced individuals under natural conditions. In the present study, we intended to experimentally examine whether general dispersal patterns, as recorded in unmanipulated natural populations, can be applied to predict the dispersal pattern of individuals introduced into local populations. However, if introduced individuals have a more extensive dispersal behaviour, this may have important consequences both demographically and genetically, as well as for the management of introduction programmes (Puth & Post 2005).

We relocated alien individuals of house sparrows from a distant population at the island Vega, 95 km away, into a metapopulation consisting of 24 local house sparrow populations in the Vikna archipelago in northern Norway. Since the house sparrows in this area are exclusively associated with human settlements, we were able to cover a large study area with a high probability of detecting long-distance movements (Koenig *et al.* 1996; Clobert *et al.* 2001). In particular, we investigated whether the probability of dispersal and the dispersal distance differed between introduced and native individuals. Furthermore, we investigated whether variation in dispersal behaviour (i.e. probability of dispersal and dispersal distance) was related to individual sex or morphological characteristics. The analyses were performed using a model extending the gamma-binormal model, which is based on multisite capture-recapture data and accounts for the underlying continuous bivariate distribution of dispersal displacements, as proposed by Tufto *et al.* (2005). Using such a model is important because not accounting for unobserved long-distance dispersers may bias the results. In the current paper,

we extend the model to also account for various phenotypic characteristics of the different individuals as covariates.

2. MATERIAL AND METHODS

(a) *Experimental design*

We translocated house sparrows from the island Vega (66° N, 12° E; figure 1) into a metapopulation about 95 km south, which consisted of 244 individuals distributed among 24 local house sparrow populations in the Vikna archipelago (65° N, 11° E; figure 1) in northern Norway. The translocation experiment was conducted in February and March 2002.

The study area at Vikna covers 360 km² (figure 1) and consists of an agricultural landscape dominated by hills, lakes and fjords sparsely populated with dairy farms, where the house sparrows live within and around cattle sheds and barns. The mean distance between a farm and the nearest neighbouring farm was approximately 2 km.

In this experiment, we did not want to alter the original sex ratio or the absolute population sizes of the local populations at Vikna, thus avoiding the potential influence of changes in population structure on the movement patterns (see Sæther *et al.* 1999 and references therein). Initially, we captured all the individuals at Vikna, which were then kept with ad libitum food inside an abandoned barn. Eight individuals were observed, but not captured, at the start of the experiment. These individuals were accounted for in the estimation of population sizes and sex ratios, but were not included in the further analysis. Then, out of a total of 244 original individuals, we removed 50% of the females and 50% of the males from each of 18 out of the 24 farms in the Vikna archipelago. They were transported by car in special transport cages with a separate room for each individual bird to a distant location near the city Steinkjer (64° N, 11° E; figure 1), approximately 110 km to the southeast. None of these individuals later returned to Vikna. The same day, the

remaining 50% of the Vikna individuals were replaced in their original farms. Some hours later, the bisected farm populations at Vikna were supplemented by the introduction of 123 individuals from the island of Vega (figure 1), and thus brought back to the original population sizes and sex ratios. These birds had been captured approximately two weeks ago on Vega, and kept with ad libitum food in a barn prior to being transported to Vikna by car. Thus, both resident individuals from Vikna and introduced birds from Vega were given the same experimental treatment.

We know from previous work (Krogstad *et al.* 1996) that house sparrows survive such treatments very well. Accordingly, only approximately 1% of the birds died during the experiment. The introduced birds from Vega did not differ significantly from the native birds at Vikna with respect to tarsus length (*t*-test, $t = -0.285$, d.f. = 123.561, $p > 0.05$). However, genotypes at 17 presumably neutral microsatellite loci sampled from the Vikna ($n = 49$) and the Vega ($n = 48$) populations before the experiment demonstrated an overall difference in allele frequencies between the two populations (Fisher's method: d.f. = 34, $p < 0.001$, $F_{st} = 0.017$, GENETOP v. 3.4; H. Jensen & R. Moe unpublished data), which implies genetic divergence.

A bird was classified as a disperser if, during the period from April to October 2002, it was recaptured or observed at a different farm compared with the farm it was released on at the start of the experiment.

(b) Measuring phenotypic traits

The house sparrows were caught by mist netting and marked with numbered aluminium rings and plastic colour rings of unique individual combination; in addition several morphological traits were measured (§2c). Individual body condition index was estimated as the unstandardized residual from a linear regression of body mass on tarsus length, where sex and the interaction between sex and body mass were included. We also collected a small blood sample from each bird the first time it was caught (see Ringsby *et al.* (2002) and Jensen *et al.* (2004) for further description).

(c) Statistical analyses

The data were analysed using a model extending the gamma-binormal model proposed by Tufto *et al.* (2005), taking into account various characteristics of the different individuals as covariates. Note that individuals that remained resident during the study period were given a dispersal distance of 0 m, whereas individuals that dispersed away from the local population were given the respective distance in metres as dispersal distance. Consider an individual that migrated from patch i to j . We assumed that the dispersal displacements followed a bivariate gamma-binormal probability density,

$$f_{X,Y}(r; \sigma, \alpha) = \frac{2\left(\frac{\alpha}{2}\right)^{(\alpha+1)/2}}{\Gamma(\alpha)\pi\sigma^2} \left(\frac{r}{\sigma}\right)^{\alpha-1} K_{1-\alpha}\left(\sqrt{2\alpha}\frac{r}{\sigma}\right), \quad (2.1)$$

where σ is the s.d. of the dispersal displacements in either x or y direction and α is a shape parameter specifying the degree of leptokurtosis (for details, see Tufto *et al.* 2005). The probability of dispersing from some point inside patch j to some point inside patch i will then be approximately proportional to $f_{X,Y}(r_{ij}; \sigma, \alpha)A_i$, where r_{ij} is the distance from patch j to patch i and A_i is the area of the recipient patch i . In addition, to incorporate the effect of local heterogeneity, we assumed that the probability of dispersing to a particular

patch i was proportional to the habitat quality h_i^1 of the recipient patches i .

Only individuals that were recaptured in one of the study patches were included in the analysis (i.e. $n = 135$). The total likelihood of the data, therefore, depends on the probability of observing an individual dispersing from j to i condition on being recaptured, which becomes

$$m_{ij} = \frac{q_{ij}^1}{\sum_{i=1}^n q_{ij}^1}, \quad (2.2)$$

where

$$q_{ij}^1 = f_{X,Y}(x, y; \sigma, \alpha)h_i, \quad (2.3)$$

and $h_i = h_i^1 A_i$.

Characteristics of different individuals may influence the probability of dispersal and expected dispersal distances. Both of these quantities depend on σ . A simple model for how the probability of dispersal and expected dispersal distances is influenced by the characteristics of each individual is therefore to assume that σ , or $\ln \sigma$ (to ensure that σ can take only positive values), is linked to a linear predictor of regression coefficients and individual covariates of interest. The morphological traits body condition index (BC), tarsus length (TA), wing length (WI), bill depth (BD), bill length (BL), visible badge size (VB) and total badge size (TB) were included as possible covariates as well as SEX and STAT (i.e. dispersal status; resident or introduced). Interaction terms between morphological traits and SEX or STAT, respectively, and between SEX and STAT were also considered. Models with interaction terms were considered only if main effects were also present. SEX and STAT were set to $-1/2$ and $+1/2$ for males and females and residents and non-residents, respectively. All morphological traits were log transformed and standardized.

The total log likelihood of the data for a particular model is given by the sum of $\ln m_{ij}$ taken over all individuals, where the m_{ij} s are computed using equations (2.1), (2.2), (2.3). Unknown parameters of the model are the average dispersal s.d. σ_0 , the shape parameter α , patch quality parameters $h_2, h_3, \dots, h_n$ and the β s in the linear predictor for $\ln \sigma$. Maximum-likelihood estimates of the parameters were computed using the standard numerical methods, i.e. the optimum function in R, using a quasi-Newton optimization method. Approximately, asymptotic standard errors were computed from the inverse of the Hessian matrix at the maximum likelihood. Model selection was based on the Akaike information criteria (AIC; Burnham & Anderson 2002). A subset of all possible models including up to five covariates were simultaneously fitted to the data.

Statistical analyses were carried out using the software R v. 2.2.1 (R Development Core Team 2004). All statistical tests are two-tailed, and estimates are given ± 1 s.d.

3. RESULTS

During the summer and autumn after the introduction experiment was carried out (§2), we recaptured or resighted 135 of the 244 birds involved in the experiment. The resident individuals had a higher probability of being recaptured compared with the introduced individuals ($\chi_1^2 = 6.038$, $p < 0.05$), but there was no intersexual difference in the probability for recapture ($\chi_1^2 = 0.02$, $p > 0.05$). This may indicate higher survival rates of the residents compared with the introduced individuals, but it is

Figure 2. Histogram showing distribution of dispersal among (a) male and female house sparrows and (b) resident and introduced individuals of house sparrows in the Vikna archipelago.

also possible that this observation is a consequence of more frequent long-distance dispersal among introduced individuals (§4). Accordingly, an almost equal number of males ($n=67$) and females ($n=68$) were included in the further analyses, where 59 (43.7%; 28 males and 31 females) were introduced individuals and 76 (56.3%; 39 males and 37 females) were resident individuals.

Out of the recaptured birds, a large proportion, 75%, ($n=101$) remained in their original local population or in the local population they were released when introduced, whereas 25% ($n=34$) of the individuals dispersed to another local population during the study period and were thus defined as dispersers. Two translocated individuals, one male and one female, returned to their island of origin, Vega, and were thus excluded from the following analyses.

The distribution of dispersal distances in this population followed a leptokurtic pattern (figure 2). The majority of individuals did not disperse (i.e. they were included in the analyses with a dispersal distance of 0 m) or dispersed only short distances, whereas few individuals dispersed long distances (see also Tufto *et al.* 2005).

Based on the extended gamma-binormal model proposed by Tufto *et al.* (2005), we composed a set of 194 candidate models, representing relevant hypotheses that could potentially explain the observed dispersal pattern (see §2 for details). The best model, selected according to the Akaike weight criteria (table 1), showed that the estimated dispersal s.d. for an average individual

Table 1. Ten highest ranked models according to AIC, out of 194 in total, explaining the variation in dispersal behaviour, according to a gamma-binormal model (see §2 for further description) in a spatially distributed metapopulation of house sparrows at Vikna in northern Norway. STAT, status (i.e. introduced or resident); BC, body condition index; TA, tarsus length; WI, wing length; BL, bill length; VB, visible badge size; TB, total badge size. Interactions between two variables are denoted with parentheses and an asterisk between the focal variables.

model rank	explanatory variable	AIC	Δ AIC	AIC _w
1	STAT, SEX, WI, (WI*SEX)	268.56	0	0.034
2	STAT, SEX, WI, (WI*SEX), (WI*STAT)	269.23	0.67	0.025
3	STAT, SEX, WI, TB, (WI*SEX)	269.28	0.72	0.024
4	STAT, SEX, WI, BC, (WI*SEX)	269.48	0.92	0.022
5	STAT, SEX, WI, (WI*SEX), (STAT*SEX)	269.66	1.1	0.020
6	STAT, SEX, WI, BL, (WI*SEX)	269.94	1.38	0.017
7	STAT, SEX, WI, VB, (WI*SEX)	270.06	1.5	0.016
8	STAT, SEX, BL, (STAT*SEX)	270.16	1.6	0.015
9	STAT, SEX, BL, (STAT*SEX), (BL*STAT)	270.24	1.69	0.015
10	STAT, SEX, WI, TA, (WI*SEX)	270.34	1.79	0.013

Table 2. Parameter estimates of the best model according to AIC_w (table 1), describing the relationship between dispersal s.d. as response variable and explanative variables; STAT, SEX, WI and WI*SEX (abbreviations are as given in table 1) in an experimental introduction study of house sparrows in northern Norway. Here, β assigns the regression coefficients, s.e. the standard errors and p the level of significance according to a likelihood ratio test.

explanatory variable	β	s.e.	p
STAT	1.26	0.35	<0.001
SEX	0.87	0.43	<0.05
WI	0.26	0.21	>0.1
WI*SEX	0.88	0.41	<0.05

was 13.1 ± 7.6 km. For the estimated value of $\alpha=0.56$, this corresponds to a median dispersal distance of 9.56 ± 5.4 km. Estimates of parameters included in the selected model are given in table 2.

The best model revealed that the probability of dispersal and expected dispersal distances was influenced by individual status (STAT), i.e. introduced individuals had a higher probability of dispersing and higher expected dispersal distances (tables 1 and 2). Furthermore, females had a higher probability of dispersal and longer expected dispersal distances than males, differing by a factor of

Figure 3. Predicted s.d.s of dispersal distances (*y*-axis) among (a) resident individuals and (b) introduced individuals in a population of house sparrows in northern Norway. The relationships between predicted s.d.s of dispersal distances and standardized wing length are shown for females (dotted lines), males (dashed lines) and both sexes combined (solid lines). The relationships presented are based on the highest ranked model according to AIC_w (table 1) and its parameter estimates (table 2). Observed dispersal distances (metres) for (c) resident and (d) introduced males (solid circles) and females (open circles) versus standardized wing length.

$e^{0.87} = 2.38$ (table 2). The best model also included a positive interaction between wing length (WI) and sex (tables 1 and 2), whereas the main effect of wing length was not significant (table 2). This suggests that females with long wings had a higher probability of dispersal. Accordingly, the best model indicated that the probability of dispersing was higher and the dispersal distance longer, if the individual was introduced, if it was a female and, especially, if the female had long wings.

The best model had an evidence ratio of 1.36 ($w_1/w_2 = 0.034/0.025$) compared with the second best model, which included the same variables as the best ranked model, but in addition included an interaction term between wing length and status (table 1). Even though the evidence ratio in favour of the highest ranked model was moderate, the validity of the model seems substantial, considering that all of the 10 best models included the variables status and sex. In addition, 7 of the 10 top models included wing length and the interaction term wing length and sex. Accordingly, we feel confident that the best model identifies parameters that have considerable influence on the probability of dispersing and the dispersal distances observed.

4. DISCUSSION

In a metapopulation of house sparrows in northern Norway, we have shown that experimentally introduced individuals had a higher probability of dispersing and dispersed longer distances than residents (figures 2b and 3; tables 1 and 2). Furthermore, females dispersed, on average, more frequently and over longer distances than males (figures 2a and 3; tables 1 and 2). In females, but not in males, we also found that longer wings were associated with longer dispersal distances (figure 3; tables 1 and 2). Only 36 out of 123 introduced individuals (29%) were recaptured at the same place as they were released. This finding is in accordance with an earlier transplant experiment carried out by Krogstad *et al.* (1996), where reproductive success among inland and coastal populations of house sparrows was investigated. The recapture rate of these introduced individuals was 38% and thus corresponded well with our results. The total rate of recapture in our study was biased towards resident individuals. This could either indicate a higher mortality among the introduced individuals or alternatively that a higher proportion of introduced individuals moved out of our study area. The latter may be likely considering the

higher dispersal frequency demonstrated among the introduced individuals compared with the residents (§3), as well as regarding that the two individuals were resighted at the island of their origin.

Predicting the patterns of spread of introduced individuals into natural populations is becoming increasingly important owing to introduction incidences of non-indigenous organisms that frequently occur as a result of human activities. Examples of such incidences are escapes of cultured individuals from fish farms (Hindar *et al.* 1991), and spread of transgenic plants into natural populations (Williamson 1992; Saltonstall 2002), which may threaten the existence of local populations. Accordingly, there is a great need for knowledge about the spatial movements of such organisms in order to successfully control and perform risk assessment of invasive species and organisms.

Measuring organism expansions has been carried out opportunistically after historical introduction events (Duncan *et al.* 2003) or reintroductions, but there is a lack of ad hoc studies treating issues connected to introduction of non-native individuals (Seddon *et al.* 2007). In contrast, numerous theoretical investigations aiming to predict the spatial spread of introduced organisms as a function of time are available (Hastings 1996; Kot *et al.* 1996; Hastings *et al.* 2005). Many of these models are based on the assumption that the distances of spread increase linearly with time (Hastings 1996) and are mainly concerned about the spread of the organism through subsequent generations (Hastings *et al.* 2005). Our results show that a considerable amount of movement among such introduced organisms may occur just immediately after an introduction event. This effect should therefore be accounted for in the predictions of intergeneration spatial propagation.

Studies that have identified and quantified important patterns of spread on a large scale among both artificially introduced and resident individuals in a natural vertebrate population are rare (but see e.g. Calvete & Estrada 2004). This may partly be due to methodological problems concerning the identification of dispersal rates (Koenig *et al.* 1996).

Our results demonstrate the importance of correctly predicting the patterns of spread in endangered populations in which translocations are conducted in order to rescue populations or species suffering from low population sizes, low genetic variability or inbreeding depression (Ebenhard 1995; Hedrick 1995). When successful, the intended introductions can save populations from extinction (Madsen *et al.* 1999), and hence be a major management tool for conserving biological diversity. Such translocations, however, do show a low rate of success (Griffith *et al.* 1989; Seddon 1999; Teixeira *et al.* 2007). One of the factors that are of central importance in the probability of settlement and reproduction is how the individuals that are released into the new area distribute themselves after the introduction event (Tweed *et al.* 2003). In this respect, our results show that a large proportion of introduced organisms may end up in a place different from the one they were intended to, and that these may not be a random sample of the introduced individuals. A consequence of this may be a decreased rate of success of reintroductions, as it makes the population less viable because individuals may settle in unsuitable habitats or move away from their potential mates.

This may be substantiated by the fact that highly mobile organisms like birds are generally less successful at establishing self-sustaining populations after translocations (Wolf *et al.* 1996). On the other hand, introduction success may also depend upon the high spatial dispersal of the released organism in order to distribute the individuals with novel alleles over a broader range and thus more effectively in the receiver population.

Possible proximate causes of more rapid spread among introduced individuals than among residents may involve social mechanisms where resident individuals behave intolerantly to new individuals (Matthysen 2005). Furthermore, the introduced individuals may also disperse because they cannot find proper shelter or places to forage at the locality they are released (Greenwood & Harvey 1982; Cilimburg *et al.* 2002). However, the design of our experiment, where half of the native population was replaced by introduced individuals, i.e. no increase in population density, implies that our experimental design did not alter the natural access to food and shelter. Both groups of individuals (residents and introduced) were subject to the same experimental treatment, only differing in the distance between the place of capture and release. Still it is possible that one component of the variation in the observed increase in dispersal behaviour among translocated individuals was due to confusion initiated by the sudden release in unfamiliar surroundings (Teixeira *et al.* 2007). Accordingly, this additional factor could have potentially influenced translocated individuals in their decisions over settlement or dispersal (Stamps & Swaisgood 2007).

Our results show that females disperse more frequently and over longer distances than males (figures 2 and 3; tables 1 and 2). This is commonly found in avian studies (Clarke *et al.* 1997), and is partly thought to be a consequence of inbreeding avoidance (Pusey 1987) as male offspring often return to their natal area for breeding. Interestingly, the generally known patterns of sex-biased dispersal in birds seem to prevail both among individuals that are translocated and in populations experiencing large-scale immigration. Thus, this enables prediction of spread among individuals in introduced and natural populations based on general patterns.

Variation in dispersal patterns has previously been shown to be correlated with different physiological (Snoejis *et al.* 2004; Haag *et al.* 2005), behavioural (Clobert *et al.* 1994; Dingemanse *et al.* 2003) and morphological traits (Sinervo & Clobert 2003; Sinervo *et al.* 2006). At the most extreme, there are present, in some species (e.g. crickets and aphids), two distinct morphs, one dispersal morph with wings and another wingless non-dispersing morph (Roff & Fairbairn 1991; Braendle *et al.* 2006). Although the pattern of distinct dispersal morphs does not apply to birds, it is possible that longer wings contribute to better flying ability (Fitzpatrick 1998), and thus that longer wings should be of higher adaptive value for dispersers. Accordingly, it is possible that the longer-winged individuals are more frequent dispersers under natural conditions as well as under manipulated circumstances.

Dispersal determines the level of gene flow in a population and thus affects local adaptation. When dispersing individuals consist of a non-random sample of the population, this process may have a major impact on

population dynamics and evolutionary trajectories (Garant *et al.* 2005; Postma & van Noordwijk 2005). In a previous study on house sparrows in northern Norway, wing length showed high heritability in females ($h^2 = 0.633$), but less in males ($h^2 = 0.327$; Jensen *et al.* 2003). This implies that dispersing females produce daughters possessing long wings which, according to present results, are also likely to disperse more frequently and over longer distances. Furthermore, wing length is shown to be genetically correlated with other fitness-related traits (Jensen *et al.* in preparation), suggesting that dispersing individuals may affect the genetic composition and average fitness in recipient populations. The observed dispersal bias towards long-winged individuals may be a consequence of a better physical condition among these individuals. There is now extensive evidence that dispersal may be condition dependent (Ims & Hjermann 2001; Massot *et al.* 2002), which implies that dispersal decisions may be triggered by different cues, such as population density, resource availability and conspecific dominance. However, even under such circumstances, the individuals that are leaving the resident habitat may have certain phenotypic characteristics, determined by genetic (Sinervo *et al.* 2006), maternal and environmental effects.

To conclude, we have shown that in a population of both resident and introduced house sparrows, the translocated individuals possessed a greater ability of spatial spread in the environment. In addition, females dispersed to a greater extent and the length of their wings was an important trait for predicting the rate at which they dispersed.

Other factors that might also be important in predicting the spread of introduced individuals in such populations are density or resource availability in each patch and the age structure in each subpopulation (Robert *et al.* 2004). This has not been tested in our study, but should be considered for future research. The model allows different degrees of densities to affect dispersal pattern, but these effects are not tested explicitly. Nevertheless, our results emphasize the fact that translocated individuals may have wider dispersal pattern than expected, which may have important implications for management. For instance, in cases in which a group of individuals are unintentionally released into the wild, immediate efforts should be made to hinder dispersal, as their spread may be faster and wider than expected. On the other hand, in management programmes where individuals are reintroduced into an area in order to rescue populations from extinction, the present study indicates that larger female-biased groups should be released in order to ensure that a viable population size remains in the area. Altogether, this suggests that dispersal should not be considered as a random process.

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