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Settlement in empty versus occupied habitats: an experimental study on bank voles

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Abstract Despite the recognised importance of colonisation (settlement in empty habitats) and immigration (settlement in an established population) to species persistence and evolution few have investigated these processes in territorial mammals and how they affect species' traits. We translocated female bank voles (*Myodes glareolus*) onto an island (2.58 ha) in a two-stage experiment (stage 1: *colonisation* of empty population space and stage 2: *immigration* into an established population) to test (1) if colonisers and immigrants differ in probability of settlement and pregnancy, and (2) if settlement is affected by cues of conspecifics, i.e., simulated deserted home ranges (SDHR) and resident presence. Density was kept well below saturation in 8 temporally distinct population replicates over 3 years. SDHR and resident presence neither attracted nor repelled colonisers and immigrants, respectively, and settlement was not different from a random model. Probability of settlement tended to be higher in colonisers than immigrants and the probability of pregnancy was significantly higher in colonisers; immigrants settling within the home range of residents had nearly zero probability of pregnancy. Colonisation of empty habitat patches selected based on physical or resource based habitat features is apparently the optimal settlement strategy of dispersing voles, because cues from conspecifics may provide ambiguous information and social factors may inhibit settlement or delay reproduction in immigrants even at low population density.

Keywords Conspecific attraction · Habitat selection · *Myodes* · Social fence · Translocation

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Introduction

The viability of species in a patchy environment at risk of extinction is positively affected by two processes: (1) colonisation (settlement in empty habitats), which buffers against local extinctions (Hanski 1998); and (2) immigration (settlement in an established population), which counteracts random demographic events and loss of genetic variation (Brown and Kodric-Brown 1977). These two processes, colonisation and immigration, also characterise the final phase of a successful dispersal process (Ims and Yoccoz 1997). However, the scientific literature on dispersal has focused mostly on factors that determine emigration and less on the settlement processes of colonisation and immigration (Bowler and Benton 2005). The costs of search and settlement are high, and the benefits are paid when successful reproduction is achieved during residency (Stamps 2001). Since the individual settlement decision affects future reproductive success it should generate a strong selective pressure for optimal strategies. Hence, it is critical to determine the ecological factors that affect settlement, and whether colonisers and immigrants differ in settlement and reproductive success because this understanding will inform us in how to manage successfully populations of territorial organisms.

Behavioural ecologists working with habitat selection have recognised that dispersing animals select habitat non-randomly and that the decision to settle is determined by different external cues (e.g., Hildén 1965; Stamps 1988). In territorial species with natal dispersal, habitat quality should be a particularly important cue since acquisition of high quality resources within a defendable area has a direct effect on future survival and reproduction. However, in heterogeneous landscapes gathering information about habitat quality consumes time and energy, and is risky (e.g., increased risk of predation). Therefore, search time may be negatively correlated with survival, habitat selectivity and fitness after settlement (Ward 1987; Stamps et al. 2005). Species dependent on patchily distributed resources for settlement, with a limited time available for dispersal, should benefit from cues that indicate habitat quality that are easy to assess. Cues of resident conspecific presence (e.g., visual observation, odour marks and vocalisation) may function as such an indirect signal of habitat quality, especially if the cue signals reproductive success (Danchin et al. 1998). Attraction to conspecifics may also arise from fitness gains related to residency among conspecifics (Courchamp et al. 1999). Consequently, conspecific attraction is a common phenomenon documented in many species, especially in colonial birds (Danchin et al. 1998), but also in territorial lizards (Stamps 1987). Experimental simulation of conspecific cues has been used to attract and establish breeding populations in otherwise abandoned patches (e.g., Ward and Schlossberg 2004).

Even though using conspecific cues for settlement may yield benefits, such benefits must be stronger than the costs associated with intraspecific competition if it is to determine settlement (Greene and Stamps 2001; Donahue 2006). In territorial species, presence of residents in a patch may function as a beneficial cue if neighbouring locations are vacant and of high quality (e.g., abundant food resources), while relying on conspecific presence in more saturated patches might be costly if competition from aggressive residents form a social fence inhibiting movement and settlement attempts (e.g., Gundersen et al. 2001). Accordingly, negative density dependent immigration success is common in many territorial species (e.g., Andreassen and Ims 2001).

We used experimental translocations of bank voles *Myodes glareolus* to test determinants of settlement and reproductive success of colonising and immigrant females. *Myodes* voles are highly territorial during pregnancy and lactation, with high site fidelity between successive breeding attempts, while immature females depend on territory acquisition for maturation and breeding (Bondrup-Nielsen and Karlsson 1985). In contrast, males show extensive home range overlap with other males and several females territories (Bondrup-Nielsen and Karlsson 1985).

Experimental studies have shown that home range locations in males are determined by the spatial distribution of females, whereas female home ranges are independent of those of males (Ims 1988). Active habitat selection in bank voles based on physical structure and vegetation type in boreal forest has been demonstrated in several previous studies (e.g., Lofgren 1995; Ecke et al. 2002), whereas we are not aware of previous studies that have assessed the effect of cues from conspecific as potential habitat selection/settlement rule parameter in any rodent species. However, as in other rodent species (Brennan and Kendrick 2006; Arakawa et al. 2008), odour marking of reproducing bank vole females is considered as part of their spacing behaviour (Viitala and Hoffmeyer 1985; Rozenfeld and Denoel 1994). *Myodes* species show aggregated distributions in heterogeneous landscapes (Mazurkiewicz 1994), but also large density fluctuations with phases of very low densities including local extinctions (Hansson and Henttonen 1985). During peak densities, maturation of immature females is inhibited by the spacing behaviour and social dominance of reproducing females (Prevot-Julliard et al. 1999). It is assumed that when a reproducing female disappears (dies) from a saturated patch the available home range is rapidly occupied by a immature female, which then matures and establish her own territorial boundaries for breeding within the home range (Bondrup-Nielsen and Ims 1986).

Based on the social system and population dynamics of bank voles, three, non-mutually exclusive, settlement scenarios in immature females are possible. First, since local extinctions are common and females depend on exclusive resources for reproduction, colonisation of empty high quality habitats should be beneficial. Second, due to high search costs and habitat heterogeneity, using resident conspecific presence as a habitat cue might be advantageous. Third, at peak densities the best tactic may be "to sit and wait" until receiving a cue signalling that a home range is deserted (owner has died). One such cue could be the gradual disappearance of odour markings and the absence of physical defence.

In this experiment we test if (1) colonisers and immigrants differ in probability of settlement and pregnancy, and (2) if settlement is affected by cues of conspecifics [i.e., simulated deserted home ranges (SDHR) and resident presence].

Methods

Study site and animals

The study site was an island, in a lake in Kynndalen, Hedmark county, south-east Norway (60°52′N, 11°56′E).

The island was 2.58 ha and situated 68 m from the nearest mainland shore and 58 meters from a narrow peninsula. The island has typical bank vole habitat, with Scotch pine (*Pinus silvestris*) as the dominant overstory vegetation layer and with bilberry (*Vaccinium myrtilus*) and moss (*Pleurozium schreberi*) as the dominant field and ground layers, respectively. In a few open spots, lichen (e.g., *Cladonia rangiferina*) were common. An earlier experiment on the island showed that this habitat was representative of mainland habitats because of a relatively dense native population of bank voles (Ims 1987). We used 71 pitfall live-traps to monitor bank voles, with each trap approximately 15 meters apart (Fig. 1). Traps were baited with carrot and oatmeal.

Study animals (125 immature females, 58 mature males) were randomly chosen among suitable candidates captured in a nearby forest on the mainland and individually marked by toe-clipping. Females were held under laboratory

Fig. 1 Map of the island (study site) and pitfall live-traps used to monitor bank voles *Myodes glareolus*. The petri dishes contained urine soaked sawdust from reproducing females to simulate deserted home ranges (SDHR). Placement was randomised between replicates. The figure shows SDHR in replicate 1

conditions for a few days to make sure that they were not pregnant. During the study natural immigration from the mainland or the peninsula was low (females $n = 3$, males $n = 3$), and these individuals are not accounted for in the analyses.

Experimental design

The experiment was replicated 8 times over 3 years and 3 seasons (see Table 1 for details). Prior to each replicate all resident individuals were removed and the island was left undisturbed for 10 days. Each replicate consisted of two stages; colonisation and immigration, both lasting for 12 days. At the onset of the colonisation stage 15 petri dishes with urine soaked sawdust (a few hours old) from reproductive females were placed in each of 4 distinct areas to simulate odour marks from deserted home ranges (SDHR; Fig. 1). The SDHR size (mean $\pm$ SD = 791 m^2 $\pm$ 75 m^2) was approximately the same size as the average female home range quantified in other studies (e.g., Bujalska and Grum 1989, also confirmed in the present study). Each of the 4 SDHR used in the same replicate was designed to cover 4 pitfalls and randomised between replicates to break any confounding effects of habitat quality defined by the physical environment and the vegetation. Immediately after the placement of the 4 SDHR 5–6 immature females were released individually at random locations and left undisturbed for 9 days to colonise the island. A 3-day live trapping period ended the colonisation stage and the petri dishes were removed after the trapping. Traps were checked 5 times a day during the trapping period to determine the home ranges of the females that had settled and thus colonised the island. These animals are hereafter termed residents and they were left on the island for the following immigration stage. At each trap occasion we noted for each individual trap location, weight and reproductive status.

The immigration stage was initiated immediately after the colonisation stage by the release of 9–10 additional immature females. These immigrants were given 9 days to establish, before a new 3-days trapping period ended the immigration stage. The trapping was done as described above with 5 trap checks a day and was done to locate the home ranges of both residents and immigrants that had settled on the island.

Five mature males were released at the onset of each replicate. Additional males were released to replace dead or dispersed individuals and to secure a sex ratio sufficient for mating opportunities in both stages (Klemme et al. 2007; later confirmed: 71% of the colonisers and 75% of the immigrants had overlapping home ranges with one or more males). The replicate was terminated by removing all individuals from the island. The island was then left undisturbed for 10 days before we started the next replicate.
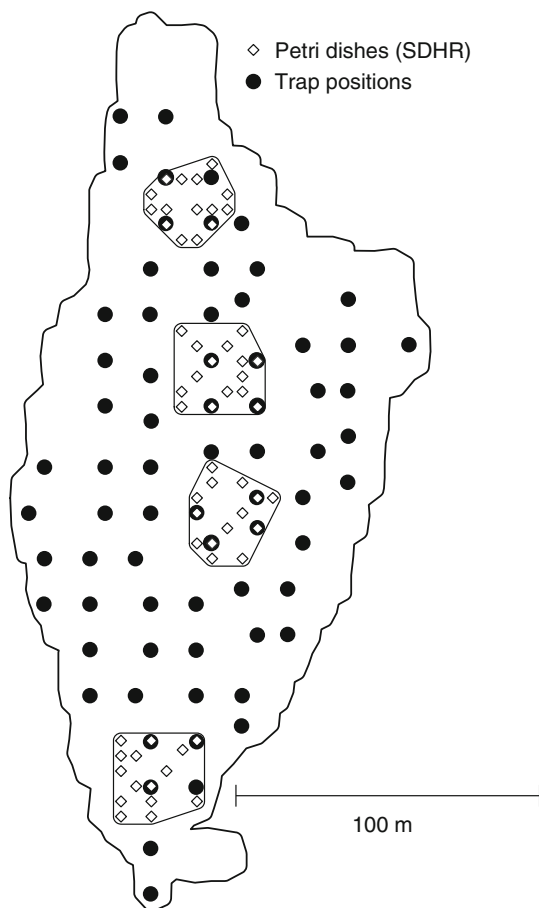
Table 1 Time table of the experiment, number of female bank voles in each category at the beginning and at the end of each stage, and number of pregnant females

Replicate	Year	Season	Stage	Female category	Number of females		
					Beginning	End	Pregnant
1	1991	July	Colonisation	Coloniser	5	4	2
			Immigration	Resident	4	4	3
				Immigrant	10	8	2
2	1991	Aug	Colonisation	Coloniser	5	3	2
			Immigration	Resident	3	3	3
				Immigrant	10	2	1
3	1991	Sept	Colonisation	Coloniser	6	2	0
			Immigration	Resident	2	2	0
				Immigrant	10	5	0
4	1992	July	Colonisation	Coloniser	6	4	3
			Immigration	Resident	4	3	3
				Immigrant	10	3	1
5	1992	Aug	Colonisation	Coloniser	6	0	0
			Immigration	Resident	0	0	0
				Immigrant	10	2	0
6	1992	Sept	Colonisation	Coloniser	6	2	1
			Immigration	Resident	2	1	0
				Immigrant	9	4	0
7	1994	July	Colonisation	Coloniser	6	6	4
			Immigration	Resident	6	6	6
				Immigrant	10	3	1
8	1994	Aug	Colonisation	Coloniser	6	3	2
			Immigration	Resident	3	2	2
				Immigrant	10	2	1

A low number of released females in each replicate was used to ensure a density well below saturation (maximum density colonisation stage = 2.3/ha; immigration stage = 6.2/ha; e.g., compared to 21/ha in Ims 1987) providing unoccupied habitats for both colonisers and immigrants in the settlement decision.

Settlement and space use descriptors

Settlement was defined as presence on the island. Hence, colonisers had settled if they were captured at the end of the colonising stage; immigrants had settled and residents had continued their residency if they were captured at the end of the immigration stage. Animals that were not captured in these trapping periods were not captured on the island later in the study either, and were assumed to be dead or emigrated from the island.

Replicate number five was excluded because none of the colonisers persisted to become residents and consequently, released females in the immigration stage could not be categorised as immigrants.

Home range size, home range overlap with other females and home range centres were calculated for all females in the colonisation and immigration stages. Home range size was calculated using minimum convex polygon (MCP) of each individual's capture coordinates. Home range centre was calculated as the arithmetic mean point of a home range and the distance between home ranges was measured as the distance between home range centres. All space use descriptors were estimated in Arc GIS 9.3 (Environmental Systems Research Institute, Inc. ESRI).

Identification of pregnancy

All females removed from the island after the immigration stage (residents and immigrants) were autopsied to determine pregnancy and embryo length. Embryo length in residents (after 24 days) was used to identify individuals that were already pregnant after the first 12 days, i.e., became pregnant as colonisers. Residents with embryos longer than 1.7 cm (indicating foetuses >12 days; Ożdżeński and Mystkowska 1976) or "birth scars" were deemed pregnant as colonisers (i.e., before immigrants were introduced). Using this criterion makes pregnancy rate comparison between colonisers and immigrants valid as both categories had then the same temporal exposure (i.e., 12 days) to mature males.

Probability of settlement and pregnancy analyses

Probabilities of settlement (presence or absence on the island 12 days after introduction to the island) and pregnancy (pregnant or not) were compared between colonisers and immigrants by means of mixed logistic models with binomial error implemented by the GLIMMIX macro in SAS version 9.1 (Littell et al. 2006). Release weight, season (month) and year were used as covariates in the models. If year and season did not contribute significantly ($P < 0.05$) to the models in interaction with female category, they were included in the model as random intercept.

Determinants of settlement analyses

We analysed the probability for colonisers to be captured within SDHR and for immigrants to be captured within resident home ranges in mixed logistic models in the same way as described above for settlement and pregnancy.

Even though settling individuals might be repelled from home ranges, they may still use cues of conspecifics and settle in the neighbourhood. In order to investigate aggregation we measured the distances from (1) the coloniser's home range centre to the nearest SDHR centre and (2) the immigrant's home range centres to the nearest resident home range centre, and compared these nearest neighbour distances with the expectations from random dispersion. The expected distribution for the nearest neighbour distances was found by randomly distributing 1000 home range centres in the available space outside SDHR and resident home ranges, respectively, and measuring the distance to the nearest SDHR or resident home range centre. The median of the 1000 distances was used as the expected nearest neighbour distance for a female. For each replicate this process was repeated until the number of median random distances was equal to the number of female immigrants in the replicate. The mean of the replicate medians was used as the expected replicate specific settlement distance to the nearest neighbour (i.e., SDHR or resident home range centre) given that settlement location was independent of conspecific cues. The randomisation process was repeated for all replicates. Finally, observed nearest neighbour distances could be compared with the sample obtained from the randomised home range centres and was used to test the hypothesis of conspecific attraction with a one-tailed t test.

Results

Probability of settlement and pregnancy

A total of 109 females (40 colonisers and 69 immigrants) were released during the 7 replicates used in the analyses.

Out of the 40 colonisers, 24 were present at the end of the colonisation stage and could be classified as residents at onset of the immigration stage. A total of 21 residents and 27 immigrants were present at the end of the immigration stage.

Across female category the probability of settlement (presence on the island) did not differ between years ($F_{2,2} = 1.34$, $P = 0.43$) or seasons ($F_{2,4} = 2.72$, $P = 0.18$) and settlement was not correlated with release weight of the individual females ($F_{1,111} = 1.99$, $P = 0.16$). The probability of settlement tended to be higher in colonisers than immigrants (contrast: $F_{1,12} = 4.12$, $P = 0.065$; Fig. 2). Number of colonisers settling on the island varied between replicates resulting in varying number of residents at the onset of the immigration stage. However, the number of residents did not correlate with the probability of settlement in immigrants ($F_{1,5} = 0.02$, $P = 0.89$).

The probability of pregnancy was significantly lower in immigrants compared with colonisers (contrast: $F_{1,12} = 6.20$, $P = 0.029$; Fig. 3). Across individual category the probability of pregnancy was significantly lower in September than July and August [July: 0.65 (95% CL 0.46, 0.81); August: 0.68 (95% CL 0.37, 0.89); September: 0.06 (95% CL 0.01, 0.35); contrast: $F_{1,4} = 8.56$, $P = 0.043$]. Year and release weight had no effect on pregnancy (both $P > 0.37$), neither did number of residents ($F_{1,5} = 1.98$, $P = 0.26$). Immigrants that settled within the home range of resident females had a lower probability of being pregnant [0.04 (95% CL 0.01, 0.34)] than immigrants that established home ranges that did not overlap with resident females [0.38 (95% CL 0.22, 0.76); $F_{1,19} = 4.46$,
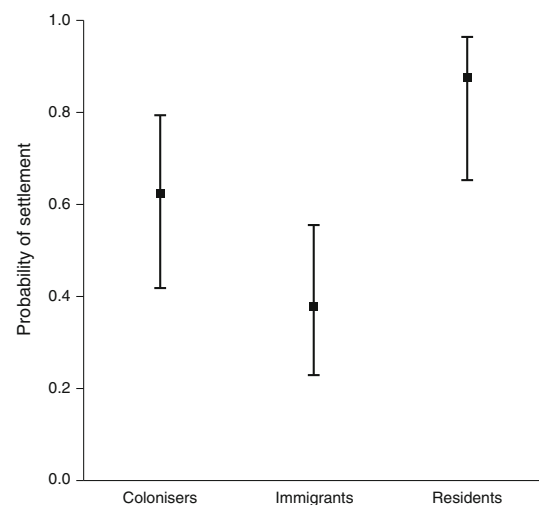

Fig. 2 Probability of settlement (mean $\pm$ 2 SE) on the island for the three female categories: colonisers ($n = 40$), immigrants ($n = 69$) and residents ($n = 24$). The resident category consists of present individuals from the colonisation stage (i.e., previously successful colonisers) and the probability estimate refers to continued residency, i.e., to remain on the island during the immigration stage
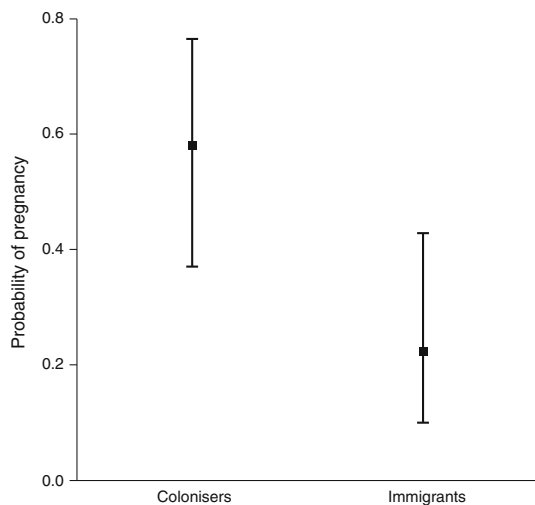
Fig. 3 Probability of pregnancy (mean ± 2 SE) in colonisers ($n = 21$) and immigrants ($n = 27$) during their first 12 days on the island

Fig. 4 Comparison between observed settlement distance (*open bars*) and the expectations from a random settlement distance (*filled bars*) from colonisers home range centres to SDHR centres, and the same comparison between observed and random distance from immigrants to residents (mean meters; minimum, maximum). The low variability in random settlement distance of colonisers is caused by randomisation in placement of SDHR between replicates

$P = 0.048$). In contrast, the overlap between immigrants and residents had no effect on the probability of pregnancy in residents ($F_{1,13} = 1.57$, $P = 0.23$).

Determinants of settlement

There was no difference in home range size between the female categories ($F_{2,12} = 1.79$, $P = 0.21$; linear mixed model with year and season as random effects). However, there was a tendency of smaller home ranges in residents [mean size = 493 m^2 (95% CL 174, 813)] compared with immigrants [831 m^2 (95% CL 539, 1123); contrast: $F_{1,12} = 3.43$, $P = 0.088$].

As the release weight of females was not a significant covariate in the logistic model predicting the probability of settlement this potential covariate was not included in the following statistical analyses ($P > 0.16$). In addition, the covariates year and season never added significantly in the models predicting the probabilities of capturing colonisers and immigrants, respectively (all $P > 0.34$). SDHR did not affect the probability of capturing colonisers [outside SDHR: 0.20 (95% CL 0.09, 0.39), inside: 0.16 (0.07, 0.36); $F_{1,6} = 0.61$, $P = 0.47$] and there was no effect of resident home ranges on the probability of capturing immigrants [outside resident home range: 0.26 (95% CL 0.11, 0.51), inside: 0.30 (0.12, 0.59); $F_{1,6} = 0.15$, $P = 0.71$]. Observed distances between home range centres of colonisers and the nearest SDHR centre was not different from randomised sample of nearest neighbour distance ($t_6 = 0.01$, $P = 0.50$; Fig. 4), and neither did observed distances between immigrant and resident home range centres differ from the random settlement distance ($t_{12} = 0.19$, $P = 0.43$; Fig. 4).
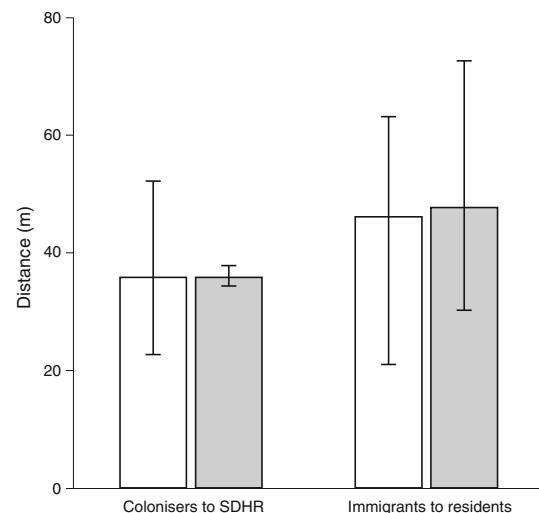
Discussion

We examined experimentally the outcome of transfer (sensu Ims and Yoccoz 1997) of individuals in empty and occupied habitat to decide whether resident conspecifics affected the settlement processes and subsequently the reproductive success of settlers. There was no evidence that females used the presence of conspecific cues as determinants of settlement. Thus, the spatial organisation of female bank voles appears to be mainly determined by territoriality (Bondrup-Nielsen and Karlsson 1985) and habitat selection based on physical and vegetation parameters (Lofgren 1995; Ecke et al. 2002; Keitt et al. 2002).

Colonisers tended to have a higher probability of settlement and were more likely to become pregnant than immigrants. However, even though colonisers and immigrants differed in their success the probability of settlement and pregnancy in immigrants was not correlated to resident density at the spatial scale of the island. Apparently, preference for the physical environment and the vegetation caused social interaction independent of density in the recipient population. Hence, these results add support for presence of social fences around high quality habitats at low population density, rather than conspecific attraction.

There was no difference in the probability of capturing colonisers within and outside SDHR, and settlement in the neighbourhood was no different than expected from a random settlement. We used fresh urine (some hours old) from reproductive females and based our test on the assumption that the gradual disappearance of urine

components could signal vacancy of high quality habitats (Bondrup-Nielsen and Ims 1986). The absence of any effect may reflect that this type of cue alone does not function as an indicator of habitat quality due to opposing forces working on selection; (1) the attraction to a location where urine indicates previous successful reproduction and (2) the repulsion to a location where the cue is negatively correlated to survival, e.g., if the cue signals high predation chances. However, we make this interpretation somewhat cautiously as odour recognition has previously found to be part of the spacing behaviour in many microtine species including the bank vole (Rozenfeld and Denoel 1994; Brennan and Kendrick 2006; Arakawa et al. 2008).

We did not explicitly test longevity and discrimination of urine from reproductive females in immature females. Substantial evidence from other rodent studies on relatively non-volatile urine components indicates discrimination for at least some period of time (Brennan and Kendrick 2006; Arakawa et al. 2008). However, if only highly volatile components of urine affect settlement we may have missed the effect since we estimated the response after 10–12 days of habituation on the island. Although our experiment is not well suited for exploring short-term behavioural effects of odour marking we were able to address fitness consequences.

While urine components alone do not appear to affect settlement and reproduction, physical presence and close contact with conspecifics might. However, even though resident females are highly aggressive towards intruders (Koskela et al. 1997) immigrants settled both inside and outside resident home ranges. In addition, immigrants settled no differently than expected from a random settlement in the neighbourhood. Although females were neither repelled nor attracted by residents, they may have been affected by the physical environment and the vegetation. In a previous methodological study using the same dataset (all replicates and both sexes pooled) with the purpose of comparing different statistical methods linking intensity of bank vole space use to habitat variables, while correcting for spatial autocorrelation, Keitt et al. (2002) found habitat selection based on variables representing cover and food. Since neither SDHR nor resident presence affected settlement, it is reasonable to conclude that direct assessment of habitat quality (i.e., the physical environment and vegetation) rather than conspecific attraction causes aggregated distributions in heterogeneous landscapes (Mazurkiewicz 1994).

Settlement probability tended to be higher in colonisers than immigrants, although immigrant settlement was not affected by resident density. In general, the nearly significant difference between colonisers and immigrants was in accordance with the social fence scenario which predicts the repulsive effect of residents to be relaxed and

settlement of subordinate individuals to increase at low densities (Hestbeck 1982; Gundersen et al. 2001). Thus, it appears to be more advantageous being a coloniser of an empty area rather than an immigrant into populated space (review in Lambin et al. 2001). In a comparable experiment with prairie voles (Microtus ohrogaster) Danielson and Gaines (1987) found a difference between colonisers and immigrants but no effect of resident conspecific density on settlement in immigrants. The absence of any effect of resident density on settlement in immigrants might be explained by the small range of population densities (0.4–2.3/ha) employed at the island scale in our experiment. However, social interactions may still be important if the per capita rate of social interactions within a small population is not simple linear functions of population density (McGuire and Getz 1998) as would be if individuals are competing for a few high quality patches. Andreassen and Ims (2001) found that immigration probabilities did not only depend on population density, but on the demographic structure of the recipient population. Thus, the demonstration of social fence effects, expressed as a difference in probability of settlement and reproduction between colonisers (competing only with unsettled immature individuals) and immigrants (also competing with mature residents, independent of density) need other study approaches than simply making linear correlations between such response variables and population density.

Some previous immigration experiments on small rodents report comparable performance between settled immigrants and residents (Danielson and Gaines 1987; Johannesen and Andreassen 1998), which suggest that assimilated immigrants may do well in the face of competition. We found that immigrants suffer from lower probability of pregnancy compared with individuals settling in empty habitats, which shows that resident presence may at least delay reproduction in immigrants. In contrast with experiments in fenced populations where movement is constrained, our open system allowed for rejection of the whole habitat at the island scale in the settlement decision. Previous experiments with Myodes voles on the same island have indicated that voles that do not settle emigrate form the island by swimming (Ims 1989). During our study a total of 6 of the absent individuals from the island (colonisers; $n = 2$, immigrants; $n = 4$) were captured in traps which were placed on the peninsula for other purposes. In theory, time spent searching for suitable habitat may reduce selectivity and force transient individuals to accept lower quality habitats (Stamps et al. 2005). Accordingly, leaving the island would induce additional search costs because of increased time spent as transient individual in a hostile environment as well as drowning. Our translocated individuals simulate a population subset with high dispersal probability (Bondrup-Nielsen and Karlsson 1985).

However, individual variation within this subset (Gundersen et al. 2002; Korpela et al. 2011) and the following difference in responses to costs and benefits associated with "swimming" or settlement on the island may explain why some females left the island, while others chose to settle even though pregnancy might be delayed. Even a short delay of maturation and pregnancy in females may negatively affect performance in such short lived species, because number of potential litters might be reduced, and offspring born later in season may suffer from decreased maturation and survival probabilities (Prevot-Julliard et al. 1999; also in our study the probability of pregnancy decreased with season). Despite the low density in our study, social components seem to be important when immigrants are likely to encounter dominant residents and vacant habitats exists.

Due to the habitat preferences it is likely that our immigrants first attempted to settle in locations already occupied by residents. Nearly 60% of the residents were pregnant at the onset of the immigration stage and immigrants were met by aggressive residents which they had to challenge to get access to the highest quality habitats. Such encounters establish a dominance hierarchy and subordinate immigrants could be rejected from large parts of resident home ranges (Mappes et al. 1995; Koskela et al. 1997). In our study 37% of the immigrants had overlapping home ranges with residents, but nearly none of them got pregnant. The absence of any repelling effect of resident home ranges and the low probability of pregnancy in immigrants confirms that some immigrants share home ranges with residents and do not reproduce, while others establish independent territories in lower quality habitats and reproduce (Jonsson et al. 2002). The tendency of larger home ranges in immigrants may also reflect settlement in such lower quality habitats (Ims 1987). It is reasonable to assume that residents occupying the highest quality habitats within a suitable patch may increase settlement costs in immigrants by rejection or depression of reproduction even at such low densities as reported here, i.e., social interactions independent of density (McGuire and Getz 1998).

Small mammals may serve as model organisms for many species facing habitat degradation, population lows and local extinctions (e.g., Ims et al. 1993). In a conservation perspective our experiment highlights the common challenge faced by most translocation experiments since approximately 60% of all females disappeared within the short time frame of a replicate (Stamps and Swaisgood 2007). In addition our study emphasises the importance of careful considerations when choosing between translocations onto vacant suitable patches or into small populations, since translocated immigrants might be more likely to emigrate from the patch and suffer delayed reproduction due to social interactions with residents.

In conclusion, in species showing large density fluctuations search and identification of high quality patches are likely crucial adaptations (Ehrich et al. 2009). When empty habitat is periodically available dispersal and colonisation based on direct assessment of habitat quality may confer significant advantages. In territorial species with natal dispersal colonisation of vacant high quality patches is apparently the optimal settlement strategy, because social factors may inhibit settlement and delay reproduction in immigrants even at low densities.

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