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1 **Settlement in empty vs. occupied habitats: An**
2 **experimental study on bank voles**

3

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22

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

42

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

45

46 **Introduction**

47

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

64 Behavioural ecologists working with habitat selection have recognised that
65 dispersing animals select habitat non-randomly and that the decision to settle is
66 determined by different external cues (e.g., Hildén 1965; Stamps 1988). In territorial
67 species with natal dispersal, habitat quality should be a particularly important cue since
68 acquisition of high quality resources within a defensible area has a direct effect on
69 future survival and reproduction. However, in heterogeneous landscapes gathering
70 information about habitat quality consumes time and energy, and is risky (e.g.,

71 increased risk of predation). Therefore, search time may be negatively correlated with
72 survival, habitat selectivity and fitness after settlement (Ward 1987; Stamps et al. 2005).
73 Species dependent on patchily distributed resources for settlement, with a limited time
74 available for dispersal, should benefit from cues that indicate habitat quality that are
75 easy to assess. Cues of resident conspecific presence (e.g., visual observation, odour
76 marks and vocalisation) may function as such an indirect signal of habitat quality,
77 especially if the cue signals reproductive success (Danchin et al. 1998). Attraction to
78 conspecifics may also arise from fitness gains related to residency among conspecifics
79 (Courchamp et al. 1999). Consequently, conspecific attraction is a common
80 phenomenon documented in many species, especially in colonial birds (Danchin et al.
81 1998), but also in territorial lizards (Stamps 1987). Experimental simulation of
82 conspecific cues has been used to attract and establish breeding populations in
83 otherwise abandoned patches (e.g., Ward and Schlossberg 2004).

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

93 We used experimental translocations of bank voles *Myodes glareolus* to test
94 determinants of settlement and reproductive success of colonising and immigrant

95 females. *Myodes* voles are highly territorial during pregnancy and lactation, with high
96 site fidelity between successive breeding attempts, while immature females depend on
97 territory acquisition for maturation and breeding (Bondrup-Nielsen and Karlsson 1985).
98 In contrast, males show extensive home range overlap with other males and several
99 females territories (Bondrup-Nielsen and Karlsson 1985). Experimental studies have
100 shown that home range locations in males are determined by the spatial distribution of
101 females, whereas female home ranges are independent of those of males (Ims 1988).
102 Active habitat selection in bank voles based on physical structure and vegetation type in
103 boreal forest has been demonstrated in several previous studies (e.g., Lofgren 1995;
104 Ecke et al. 2002), whereas we are not aware of previous studies that have assessed the
105 effect of cues from conspecific as potential habitat selection/settlement rule parameter
106 in any rodent species. However, as in other rodent species (Brennan and Kendrick 2006;
107 Arakawa et al. 2008), odour marking of reproducing bank vole females is considered as
108 part of their spacing behaviour (Viitala and Hoffmeyer 1985; Rozenfeld and Denoel
109 1994). *Myodes* species show aggregated distributions in heterogeneous landscapes
110 (Mazurkiewicz 1994), but also large density fluctuations with phases of very low
111 densities including local extinctions (Hansson and Henttonen 1985). During peak
112 densities, maturation of immature females is inhibited by the spacing behaviour and
113 social dominance of reproducing females (Prevot-Julliard et al. 1999). It is assumed that
114 when a reproducing female disappears (dies) from a saturated patch the available home
115 range is rapidly occupied by a immature female, which then matures and establish her
116 own territorial boundaries for breeding within the home range (Bondrup-Nielsen and
117 Ims 1986).

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

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

130

131 **Methods**

132

133 Study site and animals

134

135 The study site was an island, in a lake in Kynndalen, Hedmark county, south-east
136 Norway (60°52'N, 11°56'E). The island was 2.58 ha and situated 68 m from the nearest
137 mainland shore and 58 meters from a narrow peninsula. The island has typical bank
138 vole habitat, with Scotch pine (*Pinus silvestris*) as the dominant overstory vegetation
139 layer and with bilberry (*Vaccinium myrtillus*) and moss (*Pleurozium schreberi*) as the
140 dominant field and ground layers, respectively. In a few open spots, lichen (e.g.,
141 *Cladonia rangiferina*) were common. An earlier experiment on the island showed that

142 this habitat was representative of mainland habitats because of a relatively dense native
143 population of bank voles (Ims 1987). We used 71 pitfall live-traps to monitor bank
144 voles, with each trap approximately 15 meters apart (Fig. 1). Traps were baited with
145 carrot and oatmeal.

146 Study animals (125 immature females, 58 mature males) were randomly chosen
147 among suitable candidates captured in a nearby forest on the mainland and individually
148 marked by toe-clipping. Females were held under laboratory conditions for a few days
149 to make sure that they were not pregnant. During the study natural immigration from the
150 mainland or the peninsula was low (females $n = 3$, males $n = 3$), and these individuals
151 are not accounted for in the analyses.

152

153 Experimental design

154

155 The experiment was replicated 8 times over 3 years and 3 seasons (see Table 1 for
156 details). Prior to each replicate all resident individuals were removed and the island was
157 left undisturbed for 10 days. Each replicate consisted of two stages; colonisation and
158 immigration, both lasting for 12 days. At the onset of the colonisation stage 15 petri
159 dishes with urine soaked sawdust (a few hours old) from reproductive females were
160 placed in each of 4 distinct areas to simulate odour marks from deserted home ranges
161 (SDHR; Fig. 1). The SDHR size (mean \pm SD = $791 \text{ m}^2 \pm 75 \text{ m}^2$) was approximately the
162 same size as the average female home range quantified in other studies (e.g., Bujalska
163 and Grum 1989, also confirmed in the present study). Each of the 4 SDHR used in the
164 same replicate was designed to cover 4 pitfalls and randomised between replicates to
165 break any confounding effects of habitat quality defined by the physical environment

166 and the vegetation. Immediately after the placement of the 4 SDHR 5-6 immature
167 females were released individually at random locations and left undisturbed for 9 days
168 to colonise the island. A three-day live trapping period ended the colonisation stage and
169 the petri dishes were removed after the trapping. Traps were checked 5 times a day
170 during the trapping period to determine the home ranges of the females that had settled
171 and thus colonised the island. These animals are hereafter termed residents and they
172 were left on the island for the following immigration stage. At each trap occasion we
173 noted for each individual trap location, weight and reproductive status.

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

179 Five mature males were released at the onset of each replicate. Additional males
180 were released to replace dead or dispersed individuals and to secure a sex ratio
181 sufficient for mating opportunities in both stages (Klemme et al. 2007; later confirmed:
182 71% of the colonisers and 75% of the immigrants had overlapping home ranges with
183 one or more males). The replicate was terminated by removing all individuals from the
184 island. The island was then left undisturbed for 10 days before we started the next
185 replicate.

186 A low number of released females in each replicate was used to ensure a density well
187 below saturation (maximum density colonisation stage = 2.3/ha; immigration stage =
188 6.2/ha; e.g., compared to 21/ha in Ims 1987) providing unoccupied habitats for both
189 colonisers and immigrants in the settlement decision.

190

191 Settlement and space use descriptors

192

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

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

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

209

210 Identification of pregnancy

211

212 All females removed from the island after the immigration stage (residents and
213 immigrants) were autopsied to determine pregnancy and embryo length. Embryo length

214 in residents (after 24 days) was used to identify individuals that were already pregnant
215 after the first 12 days, i.e., became pregnant as colonisers. Residents with embryos
216 longer than 1.7 cm (indicating foetuses > 12 days; Ozdżeński and Mystkowska 1976) or
217 “birth scars” were deemed pregnant as colonisers (i.e., before immigrants were
218 introduced). Using this criterion makes pregnancy rate comparison between colonisers
219 and immigrants valid as both categories had then the same temporal exposure (i.e., 12
220 days) to mature males.

221

222 Probability of settlement and pregnancy analyses

223

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

231

232 Determinants of settlement analyses

233

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

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

255

256 **Results**

257

258 Probability of settlement and pregnancy

259

260 A total of 109 females (40 colonisers and 69 immigrants) were released during the 7

261 replicates used in the analyses. Out of the 40 colonisers, 24 were present at the end of
262 the colonisation stage and could be classified as residents at onset of the immigration
263 stage. A total of 21 residents and 27 immigrants were present at the end of the
264 immigration stage.

265 Across female category the probability of settlement (presence on the island) did not
266 differ between years ($F_{2,2} = 1.34, P = 0.43$) or seasons ($F_{2,4} = 2.72, P = 0.18$) and
267 settlement was not correlated with release weight of the individual females ($F_{1,111} =$
268 $1.99, P = 0.16$). The probability of settlement tended to be higher in colonisers than
269 immigrants (contrast: $F_{1,12} = 4.12, P = 0.065$; Fig. 2). Number of colonisers settling on
270 the island varied between replicates resulting in varying number of residents at the onset
271 of the immigration stage. However, the number of residents did not correlate with the
272 probability of settlement in immigrants ($F_{1,5} = 0.02, P = 0.89$).

273 The probability of pregnancy was significantly lower in immigrants compared with
274 colonisers (contrast: $F_{1,12} = 6.20, P = 0.029$; Fig. 3). Across individual category the
275 probability of pregnancy was significantly lower in September than July and August
276 (July: 0.65 [95% CL: 0.46, 0.81]; August: 0.68 [95% CL: 0.37, 0.89]; September: 0.06
277 [95% CL: 0.01, 0.35]; contrast: $F_{1,4} = 8.56, P = 0.043$). Year and release weight had no
278 effect on pregnancy (both $P > 0.37$), neither did number of residents ($F_{1,5} = 1.98 P =$
279 0.26). Immigrants that settled within the home range of resident females had a lower
280 probability of being pregnant (0.04 [95% CL: 0.01, 0.34]) than immigrants that
281 established home ranges that did not overlap with resident females (0.38 [95% CL:
282 $0.22, 0.76$]; $F_{1,19} = 4.46, P = 0.048$). In contrast, the overlap between immigrants and
283 residents had no effect on the probability of pregnancy in residents ($F_{1,13} = 1.57, P =$
284 0.23).

285

286 Determinants of settlement

287

288 There was no difference in home range size between the female categories ($F_{2,12} = 1.79$,
289 $P = 0.21$; linear mixed model with year and season as random effects). However, there
290 was a tendency of smaller home ranges in residents (mean size = 493 m² [95% CL: 174,
291 813]) compared with immigrants (831 m² [95% CL: 539, 1123]; contrast: $F_{1,12} = 3.43$, P
292 = 0.088).

293 As the release weight of females was not a significant covariate in the logistic model
294 predicting the probability of settlement this potential covariate was not included in the
295 following statistical analyses ($P > 0.16$). In addition, the covariates year and season
296 never added significantly in the models predicting the probabilities of capturing
297 colonisers and immigrants, respectively (all $P > 0.34$). SDHR did not affect the
298 probability of capturing colonisers (outside SDHR: 0.20 [95% CL: 0.09, 0.39], inside:
299 0.16 [0.07, 0.36]; $F_{1,6} = 0.61$, $P = 0.47$) and there was no effect of resident home
300 ranges on the probability of capturing immigrants (outside resident home range: 0.26
301 [95% CL: 0.11, 0.51], inside: 0.30 [0.12, 0.59]; $F_{1,6} = 0.15$, $P = 0.71$). Observed
302 distances between home range centres of colonisers and the nearest SDHR centre was
303 not different from randomised sample of nearest neighbour distance ($t_6 = 0.01$, $P = 0.50$,
304 Fig. 4), and neither did observed distances between immigrant and resident home range
305 centres differ from the random settlement distance ($t_{12} = 0.19$, $P = 0.43$; Fig. 4).

306

307 **Discussion**

308

309 We examined experimentally the outcome of transfer (*sensu* Ims and Yoccoz 1997) of
310 individuals in empty and occupied habitat to decide whether resident conspecifics
311 affected the settlement processes and subsequently the reproductive success of settlers.
312 There was no evidence that females used the presence of conspecific cues as
313 determinants of settlement. Thus the spatial organization of female bank voles appears
314 to be mainly determined by territoriality (Bondrup-Nielsen and Karlsson 1985) and
315 habitat selection based on physical and vegetation parameters (Lofgren 1995; Ecke et al.
316 2002; Keitt et al. 2002).

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

325 There was no difference in the probability of capturing colonisers within and outside
326 SDHR, and settlement in the neighbourhood was no different than expected from a
327 random settlement. We used fresh urine (some hours old) from reproductive females
328 and based our test on the assumption that the gradual disappearance of urine
329 components could signal vacancy of high quality habitats (Bondrup-Nielsen and Ims
330 1986). The absence of any effect may reflect that this type of cue alone does not
331 function as an indicator of habitat quality due to opposing forces working on selection;
332 (1) the attraction to a location where urine indicates previous successful reproduction

333 and (2) the repulsion to a location where the cue is negatively correlated to survival,
334 e.g., if the cue signals high predation chances. However, we make this interpretation
335 somewhat cautiously as odour recognition has previously found to be part of the spacing
336 behaviour in many microtine species including the bank vole (Rozenfeld and Denoel
337 1994; Brennan and Kendrick 2006; Arakawa et al. 2008).

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

346 While urine components alone do not appear to affect settlement and reproduction,
347 physical presence and close contact with conspecifics might. However, even though
348 resident females are highly aggressive towards intruders (Koskela et al. 1997)
349 immigrants settled both inside and outside resident home ranges. In addition,
350 immigrants settled no differently than expected from a random settlement in the
351 neighbourhood. Although females were neither repelled nor attracted by residents, they
352 may have been affected by the physical environment and the vegetation. In a previous
353 methodological study using the same dataset (all replicates and both sexes pooled) with
354 the purpose of comparing different statistical methods linking intensity of bank vole
355 space use to habitat variables, while correcting for spatial autocorrelation, Keitt et al.
356 (2002) found habitat selection based on variables representing cover and food. Since

357 neither SDHR nor resident presence affected settlement, it is reasonable to conclude that
358 direct assessment of habitat quality (i.e., the physical environment and vegetation)
359 rather than conspecific attraction causes aggregated distributions in heterogeneous
360 landscapes (Mazurkiewicz 1994).

361 Settlement probability tended to be higher in colonisers than immigrants, although
362 immigrant settlement was not affected by resident density. In general, the nearly
363 significant difference between colonisers and immigrants was in accordance with the
364 social fence scenario which predicts the repulsive effect of residents to be relaxed and
365 settlement of subordinate individuals to increase at low densities (Hestbeck 1982;
366 Gundersen et al. 2001). Thus, it appears to be more advantageous being a coloniser of
367 an empty area rather than an immigrant into populated space (review in Lambin et al.
368 2001). In a comparable experiment with prairie voles (*Microtus ohrogaster*) Danielson
369 and Gaines (1987) found a difference between colonisers and immigrants but no effect
370 of resident conspecific density on settlement in immigrants. The absence of any effect
371 of resident density on settlement in immigrants might be explained by the small range
372 of population densities (0.4 - 2.3/ha) employed at the island scale in our experiment.
373 However, social interactions may still be important if the *per capita* rate of social
374 interactions within a small population is not simple linear functions of population
375 density (McGuire and Getz 1998) as would be if individuals are competing for a few
376 high quality patches. Andreassen and Ims (2001) found that immigration probabilities
377 did not only depend on population density, but on the demographic structure of the
378 recipient population. Thus, the demonstration of social fence effects, expressed as a
379 difference in probability of settlement and reproduction between colonisers (competing
380 only with unsettled immature individuals) and immigrants (also competing with mature

381 residents, independent of density) need other study approaches than simply making
382 linear correlations between such response variables and population density.

383 Some previous immigration experiments on small rodents report comparable
384 performance between settled immigrants and residents (Danielson and Gaines 1987;
385 Johannesen and Andreassen 1998), which suggest that assimilated immigrants may do
386 well in the face of competition. We found that immigrants suffer from lower probability
387 of pregnancy compared with individuals settling in empty habitats, which shows that
388 resident presence may at least delay reproduction in immigrants. In contrast with
389 experiments in fenced populations where movement is constrained, our open system
390 allowed for rejection of the whole habitat at the island scale in the settlement decision.
391 Previous experiments with *Myodes* voles on the same island have indicated that voles
392 that do not settle emigrate from the island by swimming (Ims 1989). During our study a
393 total of 6 of the absent individuals from the island (colonisers; $n = 2$, immigrants; $n = 4$)
394 were captured in traps which were placed on the peninsula for other purposes. In theory,
395 time spent searching for suitable habitat may reduce selectivity and force transient
396 individuals to accept lower quality habitats (Stamps et al. 2005). Accordingly, leaving
397 the island would induce additional search costs because of increased time spent as
398 transient individual in a hostile environment as well as drowning. Our translocated
399 individuals simulate a population subset with high dispersal probability (Bondrup-
400 Nielsen and Karlsson 1985). However, individual variation within this subset
401 (Gundersen et al. 2002; Korpela et al. 2011) and the following difference in responses
402 to costs and benefits associated with “swimming” or settlement on the island may
403 explain why some females left the island, while others chose to settle even though
404 pregnancy might be delayed. Even a short delay of maturation and pregnancy in females

405 may negatively affect performance in such short lived species, because number of
406 potential litters might be reduced, and offspring born later in season may suffer from
407 decreased maturation and survival probabilities (Prevot-Julliard et al. 1999; also in our
408 study the probability of pregnancy decreased with season). Despite the low density in
409 our study, social components seem to be important when immigrants are likely to
410 encounter dominant residents and vacant habitats exists.

411 Due to the habitat preferences it is likely that our immigrants first attempted to settle
412 in locations already occupied by residents. Nearly 60 % of the residents were pregnant
413 at the onset of the immigration stage and immigrants were met by aggressive residents
414 which they had to challenge to get access to the highest quality habitats. Such
415 encounters establish a dominance hierarchy and subordinate immigrants could be
416 rejected from large parts of resident home ranges (Mappes et al. 1995; Koskela et al.
417 1997). In our study 37% of the immigrants had overlapping home ranges with residents,
418 but nearly none of them got pregnant. The absence of any repelling effect of resident
419 home ranges and the low probability of pregnancy in immigrants confirms that some
420 immigrants share home ranges with residents and do not reproduce, while others
421 establish independent territories in lower quality habitats and reproduce (Jonsson et al.
422 2002). The tendency of larger home ranges in immigrants may also reflect settlement in
423 such lower quality habitats (Ims 1987). It is reasonable to assume that residents
424 occupying the highest quality habitats within a suitable patch may increase settlement
425 costs in immigrants by rejection or depression of reproduction even at such low
426 densities as reported here, i.e., social interactions independent of density (McGuire and
427 Getz 1998).

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

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

444

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448

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450

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557

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

559 Figure legends

560

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

565

566 **Fig. 2** Probability of settlement (mean \pm 2SE) on the island for the three female categories:
567 colonisers ($n = 40$), immigrants ($n = 69$) and residents ($n = 24$). The resident category consists
568 of present individuals from the colonisation stage (i.e., previously successful colonisers) and the
569 probability estimate refers to continued residency, i.e., to remain on the island during the
570 immigration stage

571

572 **Fig. 3** Probability of pregnancy (mean \pm 2SE) in colonisers ($n = 21$) and immigrants ($n = 27$)
573 during their first 12 days on the island.

574

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

Figure 1

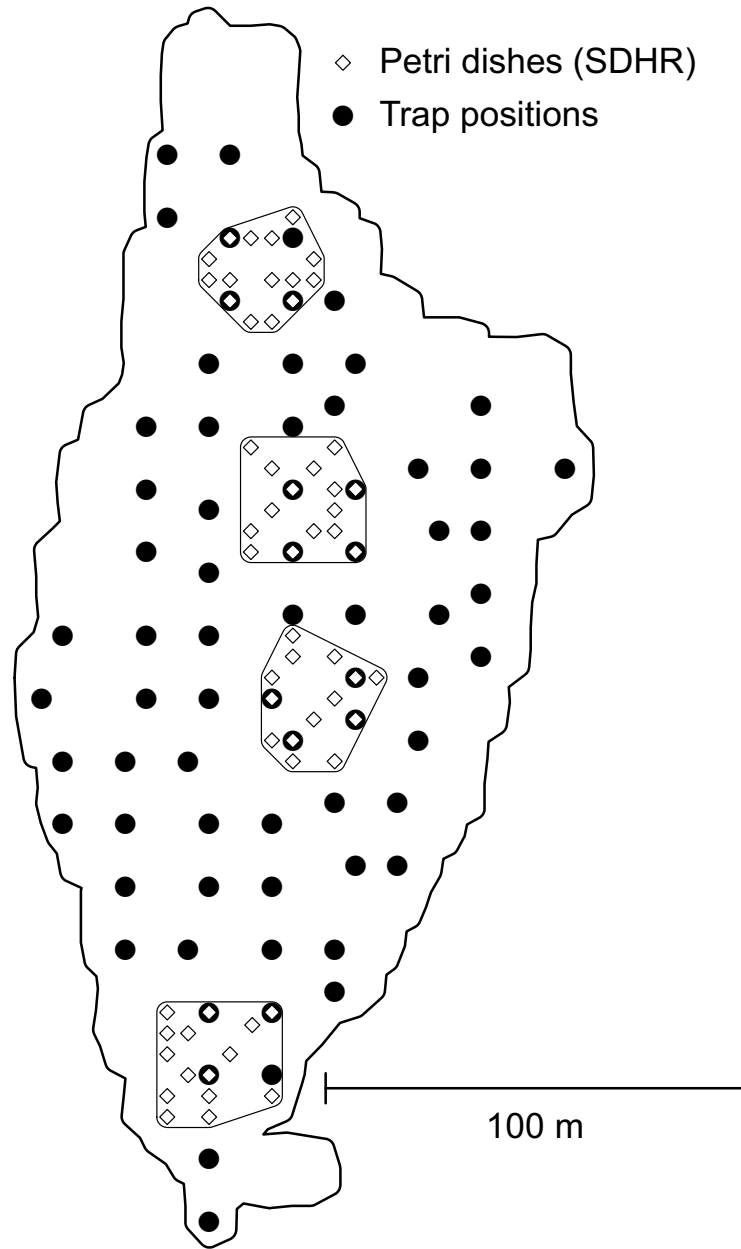


Figure2

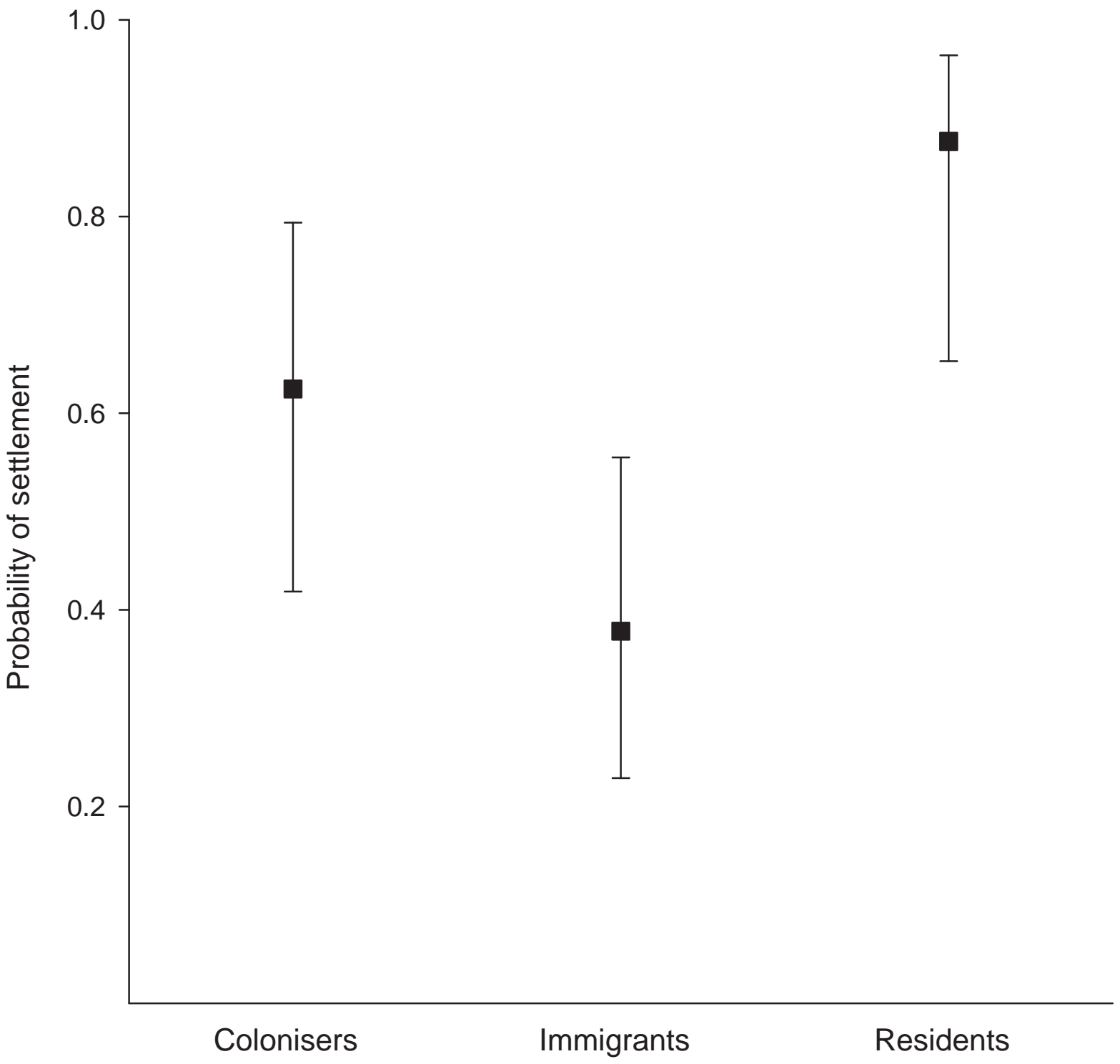


Figure3

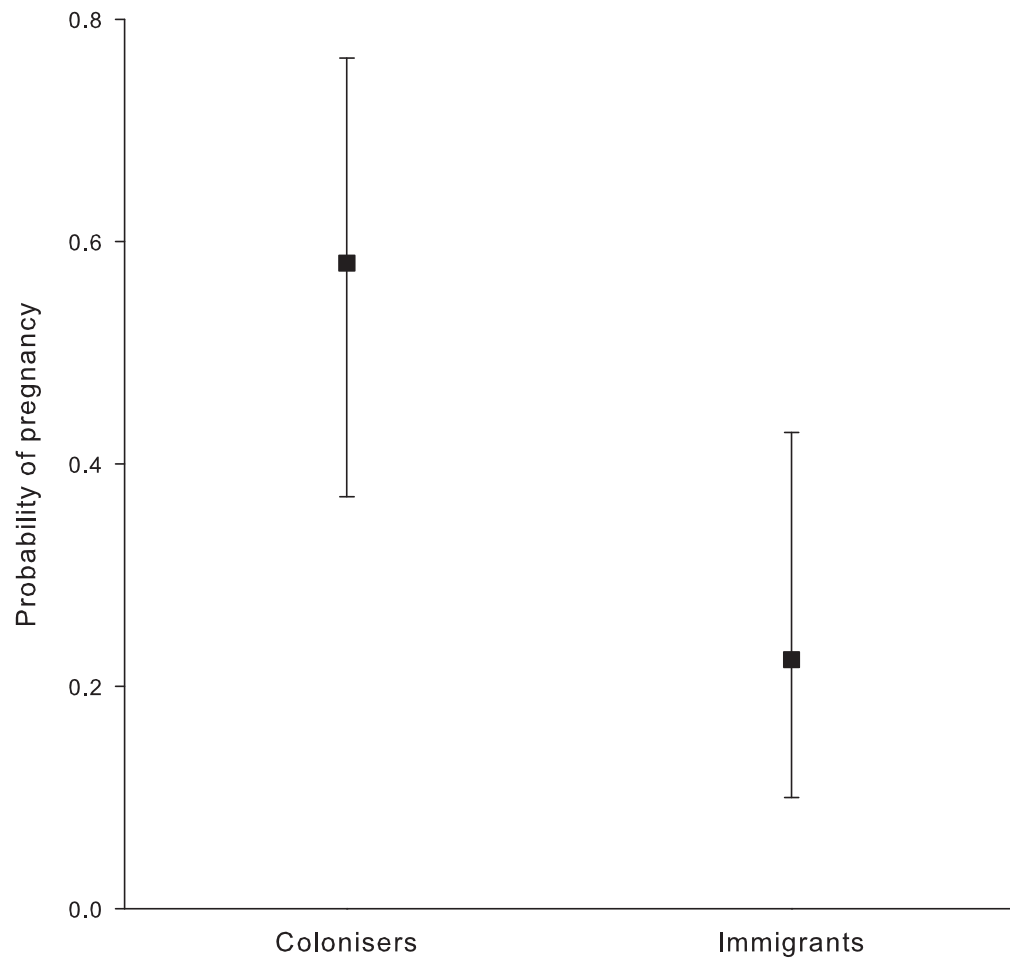


Figure4

