Concurrent effects of age class and food distribution on immigration success and population dynamics in a small mammal

Alice Rémy[1]*, Jean-François Le Galliard[2,3], Morten Odden[1] and Harry P. Andreassen[1]

[1]*Faculty of Applied Ecology and Agricultural Sciences, Hedmark University College, Anne Evenstadsvei 80, No-2480 Koppang, Norway;* [2]*CNRS – UMR 7625, Laboratoire Ecologie-Evolution, Université Pierre et Marie Curie Case 237, 7 Quai St Bernard, 75005 Paris, France; and* [3]*CNRS/ENS UMS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78 rue du Château, 77140 St-Pierre-lès-Nemours, France*

Summary

1. During the settlement stage of dispersal, the outcome of conflicts between residents and immigrants should depend on the social organization of resident populations as well as on individual traits of immigrants, such as their age class, body mass and/or behaviour.

2. We have previously shown that spatial distribution of food influences the social organization of female bank voles (*Myodes glareolus*). Here, we aimed to determine the relative impact of food distribution and immigrant age class on the success and demographic consequences of female bank vole immigration. We manipulated the spatial distribution of food within populations having either clumped or dispersed food. After a pre-experimental period, we released either adult immigrants or juvenile immigrants, for which we scored sociability and aggressiveness prior to introduction.

3. We found that immigrant females survived less well and moved more between populations than resident females, which suggest settlement costs. However, settled juvenile immigrants had a higher probability to reproduce than field-born juveniles.

4. Food distribution had little effects on the settlement success of immigrant females. Survival and settlement probabilities of immigrants were influenced by adult female density in opposite ways for adult and juvenile immigrants, suggesting a strong adult–adult competition. Moreover, females of higher body mass at release had a lower probability to survive, and the breeding probability of settled immigrants increased with their aggressiveness and decreased with their sociability.

5. Prior to the introduction of immigrants, resident females were more aggregated in the clumped food treatment than in the dispersed food treatment, but immigration reversed this relationship. In addition, differences in growth trajectories were seen during the breeding season, with populations reaching higher densities when adult immigrants were introduced in a plot with dispersed food, or when juvenile immigrants were introduced in a plot with clumped food.

6. These results indicate the relative importance of intrinsic and extrinsic factors on immigration success and demographic consequences of dispersal and are of relevance to conservation actions, such as reinforcement of small populations.

Key-words: behavioural traits, demography, dispersal, food distribution, intrasexual competition

Introduction

It is often acknowledged that immigration has positive effects on population viability since it represents a gain of

individuals and can increase genetic diversity, thus causing a rescue effect in small, isolated populations (Brown & Kodric-Brown 1977; Bowne & Bowers 2004; Le Galliard, Ferrière & Clobert 2005). However, immigrants can also decrease the fitness of residents through exploitation of shared resources, territorial contests or infanticide, leading

*Correspondence author. E-mail: remy.alice@neuf.fr

to detrimental demographic effects (Clinchy 1997; Lin, Hayes & Solomon 2004; Bowler & Benton 2005; Andreassen & Gundersen 2006; López-Sepulcre, Norris & Kokko 2009; Andreassen *et al.* 2013). Such conflicts are more likely to arise in the territorial sex that depends most on an exclusive access to critical resources to achieve high fitness. Hence, as regards mammals, residents of the territorial sex usually behave aggressively towards same-sex immigrants (Boydston, Morelli & Holekamp 2001; Back *et al.* 2002) and may inhibit immigrants' reproduction to reduce future resource competition between resident and immigrant offspring (Solomon, Vandenbergh & Sullivan 1998; Stockley & Bro-Jørgensen 2011). As a counterstrategy, immigrants can commit infanticide to take over territories and increase their mating opportunities (Ebensperger 1998).

The degree and type of intraspecific competition between residents and immigrants can be, however, determined by environmental, extrinsic variables, such as population density and the spatial distribution of resources (Lott 1991; Maher & Lott 2000; Bowler & Benton 2005; López-Sepulcre, Kokko & Norris 2010). In particular, it has been observed in many vertebrate species that clumped resources can lead to an aggregation of individuals with overlapping home ranges, while more dispersed resources can favour a more pronounced territorial behaviour (Ims 1987; Wauters & Dhondt 1992; Maher & Lott 2000; Rémy *et al.* 2013). In turn, these differences in the social organization should influence immigration patterns (Brandt 1992). Aggregation of residents when resources are clumped can limit the access to resources for immigrants and increase settlement costs (East & Hofer 2001). On the other hand, size of populations with a territorial social system is often maintained below the carrying capacity of the habitat, because of the limited number of breeding territories (Fretwell & Lucas 1969). Lower immigration rates are thus expected in territorial than non-territorial populations, at least for the territorial sex (Brandt 1992).

The settlement success of an immigrant should also depend on individual traits of dispersing animals (intrinsic factors; Bowler & Benton 2005). More competitive individuals, such as larger individuals or those in better condition, should pay lower immigration costs and have a higher probability to establish a territory (Wauters & Dhondt 1993; Bowler & Benton 2005). In addition, depending on the ecological and social conditions, the submissive, aggressive or social behaviour of dispersers towards conspecifics could determine their settlement success (Cote *et al.* 2010). For example, Cote & Clobert (2007) showed that asocial common lizards (*Lacerta vivipara*) more often established in low-density populations, while social individuals preferentially settled in high-density populations. Age is one individual trait that should be associated with settlement success, as it is related to both body size and behaviours displayed by individuals. Adults are bigger and often more aggressive than juveniles (Korhonen & Alasuutari 1995; Hoset *et al.* 2011) and should have a higher settlement success. However, age

could also be linked to reproductive status, and adult immigrants might represent a higher threat for territory owners and experience higher levels of aggression from residents (Back *et al.* 2002).

A few studies have examined the concurrent effects of extrinsic and intrinsic factors on settlement success, including population density for the former, and individual sex, behaviour and motivation to disperse for the latter (Gundersen, Andreassen & Ims 2002; Clobert *et al.* 2009; Cote *et al.* 2010; Rémy *et al.* 2011). Yet, to our knowledge, only one investigated the concurrent effects of the characteristics of immigrants and the spatial distribution of food resources. In this study, Lurz, Garson and Wauters (1997) observed in red squirrels (*Sciurus vulgaris*) a lower proportion of adults among immigrant females in the habitat favouring a female territorial system instead of a non-territorial system. Here, we employed a two-by-two factorial design to investigate the success and subsequent impacts of immigration as a function of immigrant age class and spatial distribution of food. Food was either dispersed or clumped inside enclosed populations of bank voles, in order to obtain two different social organizations of adult females (Rémy *et al.* 2013). In addition, immigrants introduced into those populations were either juvenile or adult females, for which we measured mass, aggressiveness and sociability prior to release. We designed our experiment for female bank voles because they are territorial and need to secure an exclusive area to breed, but their social organization is flexible in response to the spatial distribution of food (Ylönen & Viitala 1991; Rémy *et al.* 2013). Moreover, unfamiliar females can commit infanticide (Ylönen, Koskela & Mappes 1997), and the resulting increase in breeding failure could impede the growth of the resident population.

We first predicted that immigration success should be determined by the spatial distribution of food, but in contrasting ways for the two age classes of immigrants. When food is clumped and resident females aggregate, settlement should be easier for adult immigrants than for young, potentially subordinate individuals, as the latter should suffer higher foraging costs (Goldberg, Grant & Lefebvre 2001). On the other hand, when food is dispersed and resident females more territorial, adult female immigrants should suffer more aggression and achieve lower immigration success than juvenile immigrants, as they represent more threatening competitors for breeding territories (Back *et al.* 2002). We further controlled whether differences in mass, aggressiveness and sociability between immigrants could also explain differences in their settlement success between and within age classes. Regarding population growth, we would expect populations with clumped food to reach higher size than populations with dispersed food, as we previously observed (Rémy *et al.* 2013). However, Andreassen & Gundersen (2006) showed in root voles (*Microtus oeconomus*) that the introduction of dominant, adult individuals decreased the survival rate of females having high degree of home range overlap with other

females. Thus, populations with clumped food and immigration of adult females should experience a higher turnover of breeding females, and we predicted that the associated deleterious demographic consequences would reverse the demographic advantage of a more social organization (López-Sepulcre, Kokko & Norris 2010).

Materials and methods

EXPERIMENTAL AREA

The experiment was carried out between 24 June and 9 October 2010 at Evenstad Research Station, south-east Norway. The experimental area consisted of 20 plots (50 × 34 m), fenced with a galvanized, steel sheet fence extending 0·4 m above-ground and 0·6 m below-ground. To prevent mammalian predation, a fence 1·5 m high topped with an electric wire surrounded the area. Vegetation cover within the plots consisted of a dense meadow dominated by Poaceae and Fabaceae spp. Plots were connected together by several tunnels dug deep into the ground by water voles (*Arvicola amphibius*) prior to our experiment, allowing some movements of voles among all plots. Vegetation along the fences was mowed on a 2·5-m-wide strip every 2 weeks (resulting patch size: 45 × 29 m), and all visible tunnels' entrances were regularly destroyed to reduce these interplot movements. We then considered the entire study area as a metapopulation of 20 subpopulations interconnected by flow of individuals. Snap traps were placed every 3 m on the outer side of the surrounding fence to ensure that animals disappearing during the experiment did not disperse to the surrounding area. Only two individuals from our experiment were found in these snap traps. Moreover, the number of disappearing individuals (presumably dead) did not differ between plots at the periphery and plots in the inner part of the experimental area (loglinear model: $Z = 0·64$, $P = 0·524$). So the bias in our mortality estimates resulting from escaping individuals not caught in the snap traps should be small and similar between plots.

MANIPULATION OF FOOD DISTRIBUTION

We manipulated the food distribution by supplementing enclosures with a mixture of sunflower and oat seeds in equal proportions. In the dispersed food treatment, seeds were manually spread out all over the plot, while in the clumped food treatment, seeds were placed in the centre of the plot in a food hopper covered by a galvanized metal sheet chimney, similar to the protocol in Rémy *et al.* (2013). Each treatment was replicated inside ten plots chosen randomly. Each plot was initially supplied with 5 kg of seed mixture and then with 2 kg of seeds every 2–3 weeks.

EXPERIMENTAL PROCEDURE

Bank voles released in the field, both founders and introduced females (hereafter called immigrants), were either individuals from a captive colony maintained during the winter at the Animal Division, University of Oslo, or overwintered animals captured in our experimental plots and maintained in captivity during late spring. During captivity, animals were provided with carrots, apples, sunflower seeds and water *ad libitum*. Before release, all individuals were sexed, weighed to the nearest 0·1 g

and individually marked by toe clipping (no more than one toe per foot) for future identification.

On 24 June, a founder population of four females and four males was released in the middle of each plot. Founders were juveniles; females had no visible nipples and males had no scrotal testes. Individuals of each sex were allocated to plots in a way to standardize the initial body mass between plots (ANOVA: $F_{19,139} = 0·79$, $P = 0·712$; range: 10–17 g). During the pre-immigration period, founder animals were left undisturbed for 34 days, when they could establish a stable social system and some of them could start to reproduce (Koskela, Mappes & Ylönen 1997). Female bank voles have a gestation period of *c.* 21 days and give birth to two to ten offspring per litter, which are weaned before the age of 3 weeks (Koivula *et al.* 2003). Fifty-eight out of 80 females and 40 out of 80 males survived this pre-immigration period, and the average density (40 animals.ha^{-1}) at the start of the immigration period was high enough to induce competition between residents and immigrants (Ylönen, Kojola & Viitala 1988). Average density and sex ratio did not differ between treatments when the immigration period started ($F_{3,16} = 1·17$, $P = 0·354$, and $F_{3,16} = 0·47$, $P = 0·706$, respectively). To check that food distribution influenced the social organization of founder females, we estimated roughly from trapping data the spatial organization of females within each population at the end of the pre-immigration period (30 days after release), using metrics similar to those described in Rémy *et al.* (2013). The average distance between the activity centre of females was greater in the dispersed than in the clumped food treatment (ANOVA; $F_{1,18} = 4·52$, $P = 0·048$; Fig. 1), and the proportion of traps shared among females (an index of spatial overlap) was smaller in the dispersed food treatment (Wilcoxon–Mann–Whitney test; $W = 14$, $P = 0·045$).

Regarding immigrants, individuals were allocated to one of the two age categories (juveniles vs. adults) according to their mass and breeding condition. Juvenile females weighted less than 17 g
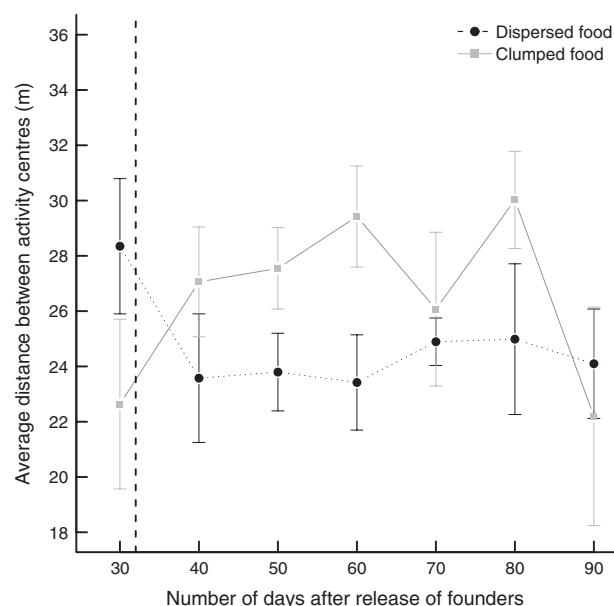

Fig. 1. Average distance (± SE) between the activity centres of resident founder females throughout the study in plots with dispersed food and with clumped food. The dashed vertical line indicates the start of the period during which immigrants were released inside each plot.

(range: 12–16 g) and had a closed vagina, while adult females weighted more than 17 g (range: 18–22 g) and had an open vagina. To investigate whether any potential difference in immigration success between juveniles and adults was due to age-related variation in behaviour, we scored the social and aggressive behaviours of each immigrant against unfamiliar females prior to introduction (see below). During the immigration period, one immigrant female, either juvenile or adult, was released into each plot and every 10 days, at one randomly chosen edge of the vegetation patch to mimic a natural immigration situation. Each plot received immigrants of the same age class throughout the experiment ($N = 5$ replicates per food distribution × immigrant age class combination).

LIVE TRAPPING

Populations were monitored by live trapping throughout the season. A grid of 4 × 5 Ugglan special livetraps (Grahnab, Marieholm, Sweden), spaced 10 m, was set in each plot. Traps were baited with carrots and sunflower and oat seeds, which were removed after each trapping session to avoid supplementation of food. Populations were live-trapped at intervals of 10 days until early October, totalling 10 trapping sessions. Each trapping session lasted for 3 days and consisted of seven trap checks. For each capture, we recorded individual identity, sex, body mass, trap location, and reproductive status for females (pregnant or lactating). Field-born individuals were individually marked by toe clipping when first captured. The high trappability during the trapping sessions (*c.* 97% per trapping session) allowed estimating survival and reproduction with precision.

BEHAVIOURAL TESTS ON IMMIGRANTS PRIOR TO RELEASE

Prior to the release of immigrants, dyadic encounters in a neutral arena (32 × 23 × 20 cm) were used to score the behaviour of juvenile and adult immigrants towards unfamiliar adult females from the captive breeding colony. Each immigrant female was tested twice against two different opponents with a minimum resting time of 8 h between each test. For the tests, females were placed in the opposite sides of the arena during an acclimation period of 1 min, and behavioural observations lasted 10 min during which the duration of four main behaviours described by Ims (1987) was recorded: amicable, approaching, aggressive (including both attacks and threats) and avoidance of approaching female. Observers were placed 2 m away from the arena and avoided moving during the observations to reduce disturbance of animals. Observers terminated the trial in case of violent fights, which happened only once. In total, we recorded the behaviour of 106 out of the 120 released immigrants (55 adults and 51 juveniles). Females without behavioural data were individuals used to replace immigrants that died shortly before their planned release.

The duration of each behaviour was averaged for each female (two trials per female), and a principal component analysis on standardized values of each behavioural trait was run to score inter-individual variation in behaviour. The first principal component (PC1; 31·3% variance) was positively correlated with amicable behaviour and approaching (factor loadings: 0·71 and 0·67, respectively; a sociability axis). PC2 (28·3% variance) was negatively correlated with avoidance behaviour and positively correlated with aggressive behaviour (factor loadings: −0·62 and 0·69,

respectively; an aggressiveness axis). Behavioural scores on PC1 were slightly, but not significantly, higher for adults (0·15 ± 0·17) than for juvenile immigrants (−0·16 ± 0·13; ANOVA: $F_{1,104} = 2·13$, $P = 0·148$). There was, however, a significant difference in PC2 scores between age classes (PC2; ANOVA: $F_{1,104} = 16·59$, $P < 0·0001$), with adults displaying more aggressive behaviours than juveniles (0·38 ± 0·15 for adults; −0·40 ± 0·12 for juveniles). No differences in PC scores were observed between immigrants released in the dispersed food plots and those released in the clumped food plots (ANOVA: $F_{1,104} = 0·04$, $P = 0·834$ for PC1 scores; $F_{1,104} = 0·49$, $P = 0·484$ for PC2 scores).

DATA ANALYSIS

Effects of immigrant age class, food distribution and their interaction on settlement success of immigrants and on the demographic parameters of residents were analysed using statistical procedures available in R 2.8.0 (http://cran.r-project.org/). Model terms were tested with an ANOVA procedure, and the most parsimonious model was selected by a backward elimination of non-significant terms. For all tests, $\alpha = 0·05$ was used for the significance level. Because most demographic traits of voles vary smoothly across the summer and fall seasons (Andreassen & Ims 2001), our models included a linear effect of trapping session number as a covariate. Models with a nonlinear effect of time did not better fit the data. Effects of adult male density and adult female density in each plot were also included in the models. Densities were estimated by the minimum number of individuals known to be alive. Number of animals within the plots during the immigration period ranged from 2 to 42 (mean ± SE = 13·9 ± 0·8). Number of adult resident males ranged from 0 to 4 (mean ± SE = 1·5 ± 0·1), while number of adult females (residents and settled immigrants) ranged from 0 to 7 (mean = 3·2 ± 0·1) and was only weakly correlated with adult male densities ($r = 0·15$, $t_{118} = 1·70$, $P = 0·092$). Our models also included the identity of the 20 plots as a random factor, unless otherwise stated. Results are reported as mean ± SE.

Immigrant females

Ten days after release, each immigrant female was either captured in the release plot (alive and not dispersing), captured in another plot (alive and dispersing) or never captured again (considered as dead; see the proportions in the Results section). Most dispersers (84%) settled in a plot within 10 days after release and did not move after this period. For the remainder 16%, all of them settled in another plot within the next 10-day period. The session of settlement was thus considered as the first trapping session an immigrant has been captured in its settlement plot. First, we tested for treatment effects on immigrants' survival and their probability of dispersing out of the release plot between the release session and the next trapping session using binomial generalized linear mixed models (GLMMs; $N = 120$ for survival analysis, $N = 71$ for dispersal analysis). Adult male and female densities were calculated in each plot at the time of release. We further analysed where immigrants preferentially settled with a binomial GLM (response variable '1' for dispersed food plots and '0' for clumped food plots; $N = 71$). Finally, reproductive success of immigrants was assessed with field observations of pregnancy followed by lactation and analysed with a binomial GLMM (1: success, 0: failure; $N = 71$), with a random effect

identifying the plot of settlement. We included effects of session of settlement, the average densities of adult males and females experienced by immigrants after settlement, and a categorical factor representing the dispersal status. For all these analyses, the interaction between adult female density and immigrant age class was tested, to check whether adult female density differentially influenced immigration success of juvenile and adult immigrants.

For the immigrant females for which we had behavioural data, we investigated whether body mass at release and social and aggressive behaviours could explain some of differences in immigrants' settlement success between and within age classes. To do so, we used the models selected from the previous analyses, to which we included the variables mass at release, PC1 score and PC2 score, either in addition to the factor immigrant age class or instead of it. In the former case, the three continuous variables were standardized within each age class to avoid colinearity among variables. In the latter case, the three continuous variables were not standardized to keep the differences in traits between the two age classes. Models were compared by their AIC$_c$ values (Akaike Information Criterion corrected for small sample size). The models for which the difference in AIC$_c$ with the best model was ≥ 2 were considered to provide the best fit to the data.

Residents

The social organization of founder females during the immigration period was investigated using trapping locations. For each session and each population, we calculated the average distance between their activity centres, as well as the ratio of traps used by more than one female to the total number of traps visited by all these females. Variation in the former was analysed with a linear mixed model (LMM) and variation in the latter with a binomial GLMM. All founders but one were breeding, and all field-born females but one remained sexually immature during the experiment. For each group of resident females, treatment effects on mortality and dispersal rates between two trapping

sessions were analysed with binomial GLMMs ($N = 120$ for each group, i.e. founder and field-born females). Finally, recruitment and growth rate of the resident populations during the immigration period were analysed ($N = 120$). Recruitment was estimated by the number of newly weaned juveniles captured in each plot and each trapping session and was analysed with a Poisson GLMM. Population growth rate between two capture sessions was calculated as $\ln(N_{t+1}/N_t)$ with N_t being the population size at capture session t. Repeated measures through time for all plots were analysed with an LMM. Population size and density of adult females at time t were included in these two analyses to control for density dependence.

Results

IMMIGRANT FEMALES

Out of the 120 immigrant females, 49 died (22 out of 60 adults and 27 out of 60 juveniles) between release and the next trapping session. Survival probability during this period was affected by the interaction between immigrant age class and the density of adult females in the plot, but not by food distribution or the other variables (Table 1). Survival of adult immigrants decreased with adult female density, whereas survival of juveniles had an opposite relationship to adult female density. When comparing models with the four different intrinsic factors (Table S1), the two best models included, in addition to the interactive effect of adult female density and immigrant age class, a negative effect of the standardized mass at release on survival probability (GLMM: estimate = −0·49 ± 0·23). The second best model (ΔAIC$_c$ = 0·6) included a positive effect of the standardized PC1 score (GLMM: estimate = 0·31 ± 0·23). The third best model, in which age class was

Table 1. Survival and dispersal probabilities between release and the next trapping session (10 days) in relation to age class of immigrants (group of reference: adult females), food distribution (group of reference: clumped food), adult male and female densities and session of release

Response	Factors	Estimate ± SE	Statistics	P
Survival	Intercept	1·42 ± 0·73	$Z = 1·94$	0·052
	Adult female density	−0·25 ± 0·19	$Z = −1·31$	0·190
	Immigrant age class	Juvenile: −2·15 ± 0·96	$Z = −2·23$	0·026
	Adult female density × Immigrant age class	Density:Juvenile: 0·57 ± 0·27	$Z = 2·11$	0·035
	Adult male density	0·16 ± 0·17	$LR = 0·85$	0·356
	Session of release	0·08 ± 0·14	$LR = 0·32$	0·573
	Food distribution	Dispersed: 0·21 ± 0·45	$LR = 0·21$	0·644
	Food distribution × Immigrant age class	Dispersed:Juvenile: −0·46 ± 0·91	$LR = 0·25$	0·615
	Plot identity	$\sigma^2 = 0·126$		
Dispersal	Intercept	4·58 ± 1·90	$Z = 2·41$	0·016
	Session of release	−1·85 ± 0·47	$Z = −3·95$	<.0001
	Adult male density	−1·52 ± 0·50	$Z = −3·01$	0·003
	Adult female density	2·29 ± 0·56	$Z = 4·08$	<.0001
	Immigrant age class	Juvenile: 8·35 ± 3·04	$Z = 2·75$	0·006
	Adult female density × Immigrant age class	Density:Juvenile: −1·56 ± 0·74	$Z = −2·12$	0·034
	Food distribution	Dispersed: −2·16 ± 1·42	$LR = 2·49$	0·114
	Food distribution × Immigrant age class	Dispersed:Juvenile: 2·24 ± 2·81	$LR = 0·68$	0·410
	Plot identity	$\sigma^2 = 3·948$		

$N = 120$ females for survival analysis; $N = 71$ females for dispersal analysis. *LR*, likelihood ratio.

replaced by PC1 score, had a similar AIC$_c$ (AIC$_c$ = 147·0; ΔAIC$_c$ = 1·7) than the best model with age class only (AIC$_c$ = 147·1). According to this model, immigrants with low PC1 scores survived better at high densities of adult females, while immigrants with high PC1 scores performed better at low densities.

Forty out of the 71 surviving immigrants dispersed from their release plot (18 out of 38 adults and 22 out of 33 juveniles). Dispersal was affected by the interaction between immigrant age class and the density of adult females in the plot (Table 1). Adult immigrants had a higher propensity of dispersing when adult female density increased, while an opposite relationship to adult female density was observed for juvenile immigrants. In addition, dispersal probability decreased with the density of adult males and through the season, but was not affected by food distribution (Table 1). When comparing models with the four different intrinsic factors (Table S2), the inclusion of mass at release, PC1 or PC2 scores into the model described in Table 1 did not improve the AIC$_c$ score. The second best model, replacing the age class by mass at release, had a slightly worst fit (ΔAIC$_c$ = 1·8). In addition, juvenile immigrants tended to settle in a dispersed food treatment plot more often than did adults (likelihood ratio test: LR = 3·49, d.f. = 1, P = 0·062).

Twenty-five out of 71 surviving immigrants bred successfully (16 out of 38 adults and nine out of 33 juveniles). Breeding probability decreased through the season (GLMM: estimate = −1·03 ± 0·24; LR = 32·3, d.f. = 1, P < 0·0001), but it was not affected by food distribution and immigrant age class or by the other tested factors (all P > 0·09). However, when comparing models with the four different intrinsic variables (Table S3), the two best models included a positive effect of PC2 score on breeding probability (GLMM: estimate = 0·84 ± 0·39). The second best model also included a negative effect of PC1 score (GLMM: estimate = −0·51 ± 0·35).

RESIDENT FEMALES AND POPULATION GROWTH

The proportion of traps shared among founder females was not affected by food distribution (LR = 0·08, d.f. = 1, P = 0·778), and contrary to the pre-immigration period, average distance between activity centres of females was shorter in the dispersed food treatment than in the clumped treatment (LMM: contrast = −3·28 ± 1·53, t_{15} = −2·14, P = 0·049; Fig. 1).

Seventeen out of 58 founder females and 57 out of 214 field-born females died during the immigration period. The mortality rate of founder resident females was affected by an interaction between food distribution and immigrant age class (LR test: LR = 6·38, d.f. = 1, P = 0·012; other factors: P > 0·083). In the clumped food plots, founder females died at a higher rate when immigrants were adults than juveniles, while in the dispersed food plots, an opposite relationship was observed (Fig. 2). Immigrant age class affected mortality of field-born females, which died more

frequently when juvenile immigrants were introduced (LR = 4·51, d.f. = 1, P = 0·034; Fig. 2; other factors: P > 0·251).

Eight founder females and 32 field-born females dispersed out of their plot. Dispersal probability of founder resident females was not affected by food distribution (LR = 3·11, d.f. = 1, P = 0·079), immigrant age class (LR = 1·66, d.f. = 1, P = 0·198) or the other variables (P > 0·093). Dispersal probability of field-born resident females decreased through time (GLMM: estimate = −0·48 ± 0·15; LR = 10·30, d.f. = 1, P = 0·001) but was not affected the other factors (P > 0·396). Mortality and dispersal probabilities differed between the different categories of females: founder residents had the lowest rates, followed by field-born residents, adult immigrants and juvenile immigrants (Table 2; overall effect of the category of females on mortality, LR = 17·9, d.f. = 3, P = 0·0005; on dispersal, LR = 55·4, d.f. = 3, P < 0·001).

The number of weaned offspring per plot, corrected for a positive effect of adult female density (GLMM: estimate = 0·39 ± 0·05, Z = 7·47, P < 0·001), time (0·34 ± 0·06, Z = 5·61, P < 0·001) and a negative effect of population size (−0·07 ± 0·01, Z = −5·68, P < 0·001), was not significantly affected by food distribution and immigration age class (all P > 0·180). However, the growth rate of populations, corrected for a positive effect of adult female density (LMM: estimate = 0·08 ± 0·03, t_{96} = 2·89, P = 0·005), time (0·06 ± 0·03, t_{96} = 1·79, P = 0·076) and a negative effect of population size (−0·03 ± 0·01, t_{96} = −4·69, P < 0·001), was affected by the interaction between food distribution and immigrant age class (LR = 4·70, d.f. = 1, P = 0·030; Fig. 3). At the end of the experiment, a post hoc test indicated that population size was higher in plots experiencing dispersed food and adult immigrant than in plots with dispersed food and
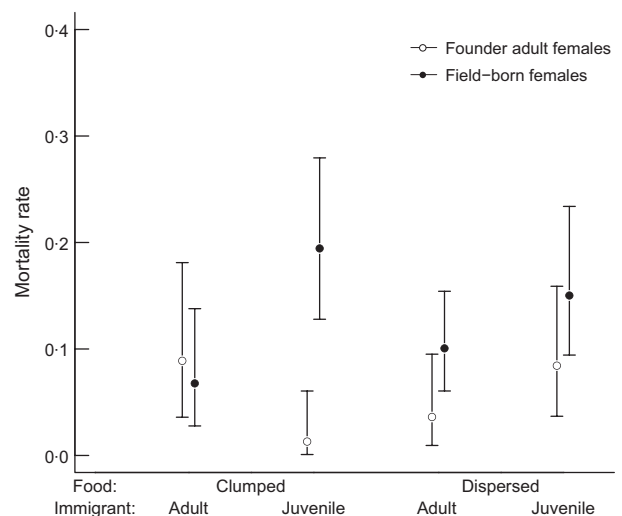

Fig. 2. Mean (± 95% highest posterior density intervals) mortality rate between two trapping sessions for resident founder females and field-born females. Food treatment was a clumped or a dispersed distribution of food and immigration treatment consisted in the introduction of adult or juvenile female immigrants.

Table 2. Probabilities of dying or dispersing between two trapping sessions for four categories of females: founder residents, field-born residents (group of reference), adult immigrants and juvenile immigrants. These probabilities were analysed with binomial generalized linear mixed models (GLMM)

| Response	Groups of individuals	Estimate ± SE	Statistics	P
Mortality	Intercept	-1.71 ± 0.16	$Z = -10.7$	< 0.0001
	Contrast (founder residents)	-0.28 ± 0.30	$Z = -0.94$	0.348
	Contrast (adult immigrants)	0.71 ± 0.24	$Z = 2.89$	0.004
	Contrast (juvenile immigrants)	0.72 ± 0.26	$Z = 2.75$	0.006
	Plot identity	$\sigma^2 = 0.078$		
Dispersal	Intercept	-2.36 ± 0.19	$Z = -12.6$	< 0.0001
	Contrast (founder residents)	-1.37 ± 0.40	$Z = -3.42$	0.001
	Contrast (adult immigrants)	0.64 ± 0.29	$Z = 2.19$	0.028
	Contrast (juvenile immigrants)	1.27 ± 0.28	$Z = 4.48$	<0.0001
	Plot identity	$\sigma^2 = 0.145$		
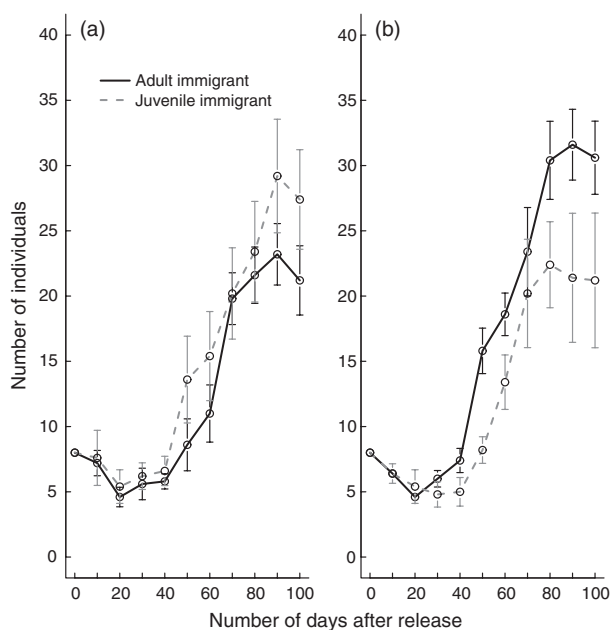
Fig. 3. Population trajectories (mean population size ± SE) in clumped food treatment (a) and dispersed food treatment (b) for plots experiencing regular immigration of adult females or regular immigration of juvenile females. The minimum number of alive individuals was calculated inside each plot and averaged across replicates (5 replicates per food distribution and immigrant age class combination).

juvenile immigrant ($P = 0.026$), and slightly higher than in plots with clumped food and adult immigrant ($P = 0.057$).

Discussion

Recent reviews have indicated that both intrinsic and extrinsic factors can influence the settlement success of immigrants (Clobert *et al.* 2009; Cote *et al.* 2010) and have suggested that immigrants' traits are likely to have significant effects on resident populations (Bowler & Benton 2005). Here, we experimentally tested for the first time how the spatial distribution of food within plots and

the age class of immigrants affect the success and the demographic impact of immigration. Adult female bank voles differed from juveniles in body mass and aggressiveness towards unfamiliar females (PC2 score), but sociability (PC1 score) was only weakly and non-significantly related to age class. Our results demonstrated a strong competition between immigrants and residents, notably among individuals of the same age class. They also pointed out that different individual traits were involved at different stages of the immigration process and that demographic consequences of immigration were context dependent.

IMMIGRATION PROCESS

On average, female immigrants survived less and dispersed more than resident females. These differences between residents and immigrants might be explained by the aggressiveness of resident females towards unfamiliar same-sex individuals (Ishibashi, Saitoh & Kawata 1998; Ylönen & Horne 2002), which increases wounding and lethal injuries (in small mammals, see Lin, Hayes & Solomon 2004; Smith & Batzli 2006; Riotte-Lambert, Rémy & Andreassen 2012) and raises the probability of movement for immigrants (Brandt 1992). Note, however, that our estimates of the costs of immigration might be biased because we likely released females that would not disperse in natural conditions. For example, Gundersen, Andreassen and Ims (2002) introduced root voles (*Microtus oeconomus*) into small populations and found that individuals that had previously successfully dispersed survived better than residents forced to immigrate.

While a lower percentage of adult female immigrants bred compared to adult female residents (42% vs. 98%), surviving juvenile immigrants were much more likely to breed than field-born resident females (27% vs. 0·5%). This fitness advantage of juvenile immigrants over field-born residents might contribute to explain the prevalence of natal dispersal over breeding dispersal in bank voles (Le Galliard *et al.* 2012). More generally in mammals, juveniles are more prone to disperse than adults, as they gain higher

benefits from this strategy through settling in a more suitable area (e.g. lower resource competition), avoiding reproductive suppression by relatives and/or avoiding inbreeding (Lambin, Aars & Piertney 2001; Bowler & Benton 2005; Stockley & Bro-Jørgensen 2011).

We found some evidence of intraclass competition between immigrants and residents, affecting survival and dispersal of individuals, as observed in other studies (Andreassen & Ims 2001). Such competition is expected when individuals can assess the dominance status and fighting ability of their opponents before a contest ever takes place, and fights occur preferentially among individuals of the same dominance status (Maynard Smith & Harper 1988). In our study, the mortality and dispersal of adult immigrants increased with increasing density of adult females in the release plot. Moreover, founder resident females survived less when immigrants were adults than juveniles in the clumped food treatment, and field-born resident females had higher mortality rates when immigrants were juveniles than adults in both food distribution treatments. In addition, the settlement of immigrant females in the release plot was influenced by the number of adult males. This indicates that immigrant females also cued on the number of potential mates to decide where to settle (Danchin, Heg & Doligez 2001) and that low availability of mates could trigger subsequent dispersal of females as a strategy to search for mates (Kokko & Rankin 2006; Kokko & Wong 2007; Perez-Gonzalez & Carranza 2009; Le Galliard et al. 2012).

EXTRINSIC AND INTRINSIC DETERMINANTS OF IMMIGRATION SUCCESS

Contrary to our predictions, the spatial distribution of food had little effect on the settlement success of immigrant females relative to intrinsic factors and the density of resident females. In a similar way, no significant difference in immigration rates and success was observed between two populations of female red squirrels occupying habitats contrasted for their food distribution and differing in their social organization (Wauters & Dhondt 1993; Wauters et al. 2004). We observed only marginal effects of food distribution on the settlement behaviour of immigrants. Juvenile female immigrants tended to settle preferentially in the dispersed food treatment, most likely because clumped food imposed higher foraging costs on young, subordinate immigrants through frequent aggressive encounters with residents at the food hopper (Goldberg, Grant & Lefebvre 2001).

In sharp contrast, significant effects of intrinsic factors on immigration success were uncovered. Probabilities of survival and dispersal of immigrant females were influenced by adult female density in opposite ways for adult and juvenile immigrants. Body mass at release, standardized within each age class, was negatively correlated with the survival probability of immigrants shortly after release. This result is inconsistent with the accepted opinion that larger or heavier individuals should have a higher probability of successful immigration (Wauters & Dhondt 1993; Bowler & Benton 2005). We can suggest that immigrant females of higher body mass were subjected to more aggression from the resident females, as they represented more threatening competitors (Back et al. 2002). In addition, the behavioural dimension associated with variation in amicable-approaching behaviours (PC1, a sociability axis) had an influence on survival, with more social immigrants within each age class having a higher probability to survive than less social ones. An alternative model suggested a density-dependent effect of PC1 score on survival, with less social immigrants surviving better at high densities of adult females, while more social immigrants performed better at low densities. These results indicate that sociability towards unrelated adults is involved in settlement success and that more studies are needed to investigate the role of individual behaviours on the dispersal response to density (Cote & Clobert 2007).

Finally, conditional on survival after settlement, breeding probability of immigrants decreased with their PC1 score (sociability) and increased with their PC2 score (a measure of their aggressiveness). Thus, the asocial and aggressive behaviours of an immigrant predict its effective immigration better than age class or body mass at release. This effect is likely due to a relationship between asocial and aggressive behaviours and the ability to take over resident females' territories and/or repel intruders and protect pups against infanticide (Koskela, Mappes & Ylönen 1997; Ylönen & Horne 2002).

EFFECTS OF IMMIGRATION ON RESIDENT POPULATIONS

Quite surprisingly, the introduction of immigrants reversed the relationship between the food distribution and the social organization of resident females. Prior to the introduction of immigrants, founder females were more aggregated in the clumped treatment than in the dispersed treatment as predicted by home range theory (Maher & Lott 2000) and demonstrated in an earlier study (Rémy et al. 2013). Yet, founder females reacted to immigration by segregating in space within the clumped food treatment while they aggregated within the dispersed food treatment. We can speculate that it became costly for females from the clumped food treatment to maintain a territory located close to the food hopper as soon as unfamiliar immigrants were introduced, because clumping increases aggression rates and the risk of infanticide by immigrants (Lambin & Krebs 1993; Ylönen, Koskela & Mappes 1997; Andreassen & Gundersen 2006). In the dispersed food treatment, introduction of immigrants may have decreased the territory size of resident females and reduced the distance between those females (Brandt 1992). More detailed measurements of female home ranges before and after the immigration period should have been done to validate this suggestion.

Populations grew substantially during the summer season and reached high densities at the end of the experiment (Ylönen, Kojola & Viitala 1988). Thus, high immigration rates of unfamiliar females did not cause population collapse, such as found by Andreassen & Gundersen (2006) when they simulated root vole male turnover (emigration of resident males followed by immigration). Immigration of females may have less severe consequences than immigration of males, as negative impact on resident females might be compensated by the subsequent reproduction of immigrant females (Clinchy 1997; Lin, Hayes & Solomon 2004). Despite that, differences in growth trajectories between treatment groups were seen during the breeding season. Contrary to our previous study (Rémy *et al.* 2013), we did not observe a consistently higher population growth in plots with clumped food. In the dispersed food treatment, populations grew faster and reached a higher density at the end of the experiment when adult immigrants rather than juveniles were introduced, while an opposite trend was observed in the clumped food treatment. This interactive effect of age class of immigrants and food distribution on population growth paralleled the differential mortality of resident founders in response to our treatments. As adult females importantly contribute to population growth through the production of recruits, a higher mortality of founder females in one treatment group might have reduced population growth or at least delayed it if immigrant females took over the territory of residents (López-Sepulcre, Kokko & Norris 2010).

Conclusion

As suggested by Clobert *et al.* (2009) in a recent review about condition-dependent dispersal, our data indicate that intrinsic factors have density-dependent effects on immigration success. Our findings also emphasize the importance of both spatial distribution of resources and immigration patterns in population dynamics of small rodents (Andreassen *et al.* 2013). In a broader context, our results are relevant to conservation actions, such as the reinforcement of declining populations through the introduction of small groups of individuals. They showed that the success of such actions would be dependent on the ecological and social conditions of resident populations as well as on the individual characteristics of released animals (e.g. Bremner-Harrison, Prodohl & Elwood 2004).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Model statistics for the effects of adult female density and individual characteristics of immigrants on survival probability.

Table S2. Model statistics for the effects of adult male density, session at release, adult female density and individual characteristics of immigrants on dispersal probability.

Table S3. Model statistics for the effects of session of settlement and individual characteristics of immigrants on breeding probability.