Behav Ecol Sociobiol (1993) 33:159–167

Behavioral Ecology and Sociobiology

Immigration pattern and success in red squirrels

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Received December 12, 1992 / Accepted May 21, 1993

Summary. We studied the characteristics of immigrants and the effects of immigration on reproductive activity and spacing behaviour in red squirrels living in high-quality woodlands. Male immigration peaked in spring, female immigration in autumn. There was no sex bias in dispersal distance of local recruits or in the proportion of male/female immigrants, but more subadults than adults immigrated on the study plots. Hence, hypotheses explaining sex-biased dispersal were irrelevant in explaining immigration patterns in our study populations. Immigrant females were not in breeding condition, nor had they produced a litter prior to immigration. Hence breeding dispersal did not occur. Red squirrels are promiscuous, and females defend intrasexual territories while males have overlapping home ranges with a dominance hierarchy (Wauters et al. 1990; Wauters and Dhondt 1992). Site fidelity is very important to reproductive success and most parents still have a high residual reproductive value after having produced a litter. Under such circumstances, the resident fitness hypothesis (RFH; Anderson 1989) predicts that parents can benefit by forcing emigration of offspring if the latter are likely to find nearby vacancies. The settlement pattern of successful immigrants, which had a higher probability of becoming established when they had high body mass and when they were settling in plots with reduced intrasexual competition, agreed with the RFH and with the proximate dispersal mechanism suggested by Gliwicz (1992), that dispersal tendency in both sexes depends on the degree of intrasexual competition under local conditions. The fact that close inbreeding was never observed could indicate that random immigration of both sexes, within the social environment of a partly territorial, relatively long-lived species, has evolved not only to reduce competition for resources between parents and offspring but also as an inbreeding avoidance mechanism.

Key words: Immigration – Intrasexual competition – Spacing behaviour – Red squirrel

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Introduction

Dispersal, as defined for small mammals, is a one-way movement of individuals away from their home ranges (Stenseth and Lidicker 1992). After weaning, a small mammal has the choice of staying in its mother's home range (philopatry) or leaving to find a new place to live (dispersal). To understand the evolution of dispersal behaviour, two main questions have to be answered: who disperses and why do some members of a population disperse (Stenseth and Lidicker 1992)?

In most species, dispersal tendencies differ between juveniles and adults, between males and females or between different phenotypes (Myers and Krebs 1971; Gaines and McClenaghan 1980; Lidicker 1985). Natal dispersal (between the birth site and a potential breeding site, Greenwood 1980), is strongly male-biased in the majority of small mammals (Lidicker 1975; Holekamp 1984a; Wiggett and Boag 1989; Cockburn 1992), although in some microtines (Boonstra et al. 1987) and ground squirrels (Murie 1973) no sex bias was observed. Natal dispersal generally involves juveniles and subadults. However, in social species where dispersal is retarded non-reproductive adults can also show natal dispersal (e.g. marmots, Armitage and Johns 1982; Arnold 1990). Breeding dispersal, on the other hand, involves adults that have reproduced and move to other breeding sites (Greenwood 1980). In small mammals, both male (Krebs et al. 1976; Sherman 1977; Hoogland 1982) and female-biased breeding dispersal (Stenseth 1978; Jannett 1980; Harris and Murie 1984) occurs. In the latter, mothers abandon their breeding home range or nest site to their philopatric daughters (Cockburn 1992) and/or sons (Boutin et al. 1993).

To explain the function of dispersal in evolutionary terms, it has been argued that dispersal behaviour has evolved in order to avoid close inbreeding or achieve optimal outbreeding (Greenwood 1980; Schwartz and Armitage 1980; Bateson 1983; Holekamp 1984b; Cockburn et al. 1985; Holekamp and Sherman 1989; Stenseth and Lidicker 1992), as a consequence of female choice

(Hoogland 1982), to maximize mating opportunities in males (Dobson 1982), or to minimize intraspecific competition for environmental resources (Slade and Balph 1974; Greenwood 1980; Pfeifer 1982; Moore and Ali 1984).

All these hypotheses are intended to explain sex-biased dispersal in mammals. As to the question of which sex should disperse, the female choice hypothesis states that male dispersal is a consequence of philopatric females avoiding mating with related males or of females preferring strange males (Hoogland 1982). The mate competition hypothesis predicts that in polygynous mating systems males should disperse and females should not, but in monogamous mating systems, similar numbers of males and females should disperse (Dobson 1982), while according to Greenwood (1980) the sex that competes for resources for reproduction (in small mammals the females) should be philopatric, while the sex competing for mates (in the majority of mammals the males) should disperse, regardless of the mating system. All these hypotheses implying, on average, a gain in fitness to individuals that emigrate, were classified by Anderson (1989) under the 'emigrant fitness hypothesis'. As an alternative he proposed the resident fitness hypothesis (RFH), which rests on the propositions that dispersal arises from an interaction between dominants (parents) and subordinates (offspring) and that the behaviour evolved on the basis of parental benefit. Hence, parental manipulation (allocating offspring to philopatry or dispersal) might play a role in the evolution of dispersal systems (Hamilton and May 1978; Anderson 1989; Wolff 1992).

Our objective in this study was to determine who immigrates, and to test the various hypotheses on the ultimate causes of dispersal by examining sex bias in immigrants, the distances over which locally recruited juvenile males and females (*sensu* Wauters et al. 1993) moved, the reproductive activity of residents and immigrants and the factors affecting immigration success in a relatively long-lived rodent that reproduces for several years, the red squirrel (*Sciurus vulgaris*). Squirrels were studied in two study plots in continuous high-quality woodlands.

Materials and methods

The study species. Red squirrels are relatively long-lived, medium-sized rodents that show reproductive activity for up to 5 years (Wauters and Dhondt 1989). Hence, many females with offspring still have a high residual reproductive value. Dominant adults always remain in the same home range (Wauters and Dhondt 1992). The squirrels' social behaviour differs between habitats and between the sexes (Wauters and Dhondt 1992). Males have large, strongly overlapping home ranges and a marked dominance hierarchy, while dominant reproductive females defend exclusive core-areas against other dominant females (intrasexual territoriality). Subordinate females live as floaters or settle along the edges of dominant females' home ranges (Wauters and Dhondt 1992). As habitat quality can be measured at the level of the individual home range (Wauters and Dhondt 1989, 1992), the red squirrel is an ideal species for investigation of the relationship between habitat quality, space use and immigration.

Immigrants were animals that appeared on our study areas and were born elsewhere, hence a subset of all dispersers. Residents were: (i) adults that had established a permanent home range on the study areas, and (ii) locally born subadults that remained on the study areas.

Study areas. We used two study sites each of 30 ha. One was in the 'Merodese Bossen' at Herenthout (province of Antwerpen, N. Belgium), a mainly coniferous woodland of 212 ha, dominated by Scots pine (*Pinus sylvestris*) and Crosican pine (*P. nigra*). The south side of the study area is bordered by meadows and by a road and these were never crossed by resident squirrels. The west side is bordered by farmland and less suitable patches of wood. Along the north and east sides suitable habitat continues. The second study area lies in the 'Peerdsbos' at Schoten (province of Antwerpen, N. Belgium) a mainly deciduous woodland of 150 ha. The study plot is dominated by mature oak (*Quercus robur*) and beech (*Fagus sylvatica*) with some chestnut (*Castanea sativa*). The study area is bordered by houses and a road on the north side and by meadows and a motorway along the south and south-west sides, that were never crossed by residents. On the east side the forest continues.

Trapping and handling squirrels. Trapping was carried out at least for 4 days every 2 months from October 1984 to May 1992. During dispersal periods traps were set for more than 4 days, until no more new squirrels were trapped for at least 3 consecutive days. This to make sure that no immigrants were missed. A detailed description of the trapping procedure is given elsewhere (Wauters and Dhondt 1990). Data on local recruits were gathered as described by Wauters et al. (1993).

Every squirrel was individually marked, using small pieces of coloured wires inserted through the ear, or numbered metal ear-tags (type 1003 S National Band and Tag Co., USA). It was weighed to the nearest 5 g using a Pesola spring-balance and the length of the right hind foot (without the claw) was measured (to 0.5 mm). Its sex and age were determined. Subadult males are between 4 and 10 months old, with abdominal testes and a small scrotum. Subadult females are between 4 and 12 months old and have a very small vulva, while the nipples are still invisible. Adults are over 12 months. The reproductive status was also recorded. For males testes position (1 = abdominal, 2 = semi-scrotal, 3 = scrotal) and testes size (ranging from 1, very small, to 5, very large) were scored. Females were scored as anoestrous (1) or oestrous and post-oestrous (2).

Habitat quality. The abundance of high-energy food (tree seeds) was used as a measure of habitat quality. Food abundance was calculated in each small woodplot of different tree composition by counting fallen seeds (including the remains of food-items consumed before they had fallen) on three 1-m^2 plots placed on a randomly chosen line (Wauters and Dhondt 1989). For immigrants caught only once, food abundance in the woodplot where it was trapped represented habitat quality. For immigrants that settled, the percentage of overlap of a squirrel's home range with different woodplots was estimated, to calculate food abundance within its range.

Data analyses. All continuous variables used (body mass, foot length, and habitat quality) were normally distributed. Hence parametric statistics were calculated with STATGRAPHICS and GLIM.

We used logistic models to test the effects of various factors on: (i) immigration success (an immigrant that 'settled' in the study area, i.e. survived at least one winter, was scored 1; if it disappeared again it was scored 0); and (ii) on the future reproductive investment of the settled immigrant [an immigrated female which at least once produced weaned offspring was scored 1; if it never produced offspring it was scored 0; an immigrated male that became dominant, i.e. a rank I or rank II male (rank I males won all interactions with other males over their whole home range, rank II males won interactions with other males only in a part of their home range; Wauters and Dhondt 1989) was scored 1; if it remained subordinate (losing all interactions with other males) it was scored 0].

The logistic regression converts binary data into probability values by fitting a logistic curve through the available points (Clutton-Brock et al. 1987; Wauters and Dhondt 1989). The logistic model is described by:

$$P\ (Y_i=1)=\exp G\ (x_i)/1+\exp G(x_i)$$

and

$$G(x_i)=(A+B_1x_{i1}+B_2x_{i2}+\ldots+B_{17}x_{i17})$$

and where $A, B_1, B_2, \ldots, B_{17}$ = constants; x_{i1} = area (1 = coniferous, 2 = deciduous) x_{i2} = body mass (g); x_{i3} = foot length (mm); x_{i4} = habitat quality; x_{i5} = age (1 = subadult, 2 = adult); x_{i6} = sex (1 = males, 2 = females); x_{i7} = year; x_{i8} = disappear, same sex; x_{i9} = disappear, other sex; x_{i10} = year·habitat quality interaction; x_{i11} = sex·habitat quality interaction; x_{i12} = sex·body mass interaction; x_{i13} = sex·foot length interaction; x_{i14} = sex·age interaction; x_{i15} = sex·area interaction; x_{i16} = area·year interaction; x_{i17} = area·habitat quality interaction.

Variable x_{i4}, habitat quality, was the estimated food abundance within the woodplot that an immigrant entered or within the home range where it settled (10^3 kJ·ha^{-1}). Variable x_{i8}, disappear own sex, was scored 1 when no resident of the same sex disappeared, just before or during the main immigration period (March–May or August–October), from the woodplot that an immigrant entered; it was scored 2 when at least one resident of the same sex disappeared. Variable x_{i9}, disappear other sex, was scored similarly based on the disappearance of residents of the other sex from the immigrant. Woodplots, between 1.5 and 3.5 ha in the coniferous area and between 3.2 and 6.0 ha in the deciduous area, were of similar size to a squirrel's home range (mean home range size: coniferous area 2.73–4.45 ha, deciduous area: 4.45–6.39 ha, Wauters and Dhondt 1992). The parameters of the logistic model were estimated by maximum likelihood, which provides a convenient index of goodness-of-fit of a model including a particular set of parameters. We used a stepwise backward procedure to select a final model containing only significant parameters.

Results

Characteristics of immigrants

The immigration pattern was consistent over the whole study period of 7 years. There were two main immigration periods: the spring immigration peaked from April to early May, the autumn immigration from the end of August to mid-October (Fig. 1). Immigrants first caught between March and early June were considered spring immigrants, those first caught between August and December were considered autumn immigrants. A log-linear model testing the effects of age and sex on the timing of immigration showed a sex bias in immigration peak (factor sex: $G_{(1)}=28.58$, $P<0.0001$); most males immigrated in spring while the majority of females immigrated in autumn (Fig. 1). This corresponded with interactions with male aggressors being more frequent in spring (24 of 34, 71%) and those with female aggressors (30 of 48, 63%) more frequent in late summer-autumn ($\chi^2_{(1)}=8.72$, $P=0.003$).

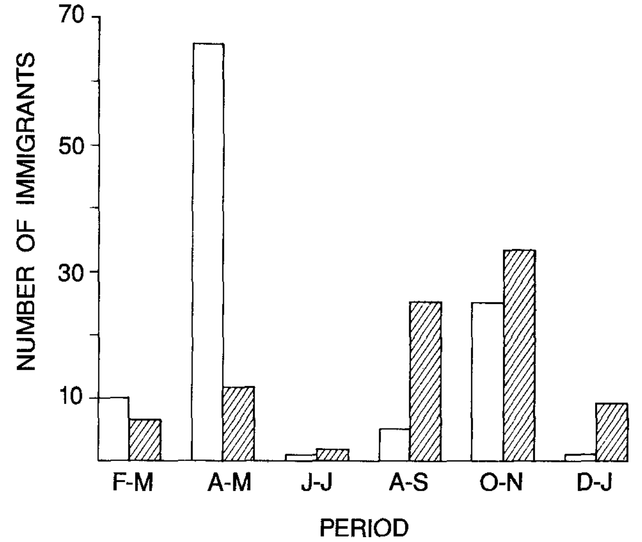

Fig. 1. The number of immigrants of each sex per 2-month period (first period is February–March): males □, females ▨

In order to test for sex and age biases among dispersers, we investigated movement patterns of local recruits and the proportions of males/females and adults/subadults among immigrants. Data on the distance between the centre of the natal home range and the centre of a squirrel's home range after it settled (see Wauters and Dhondt 1992 for calculation of home range centre) of 21 local recruits (12 males, 9 females) in the coniferous and 22 (9 males, 13 females) in the deciduous habitat were used to test for differences in dispersal distance between sexes and areas. Dispersal distances of local recruits varied strongly, between a minimum of 60 m and a maximum of 730 m ($\bar{x}\pm$SD: 'coniferous' males 237 ± 39; coniferous females 251 ± 32; 'deciduous' males 274 ± 53; deciduous females 335 ± 55 m). Locally recruited males did not disperse over longer distances than females and there was no habitat effect (2-way ANOVA: factor sex $F_{(1,39)}=0.63$, ns, factor area $F_{(1,39)}=1.63$, ns, 2-factor interaction $F_{(1,39)}=0.23$, ns). Strict philopatry, squirrels settling on their mother's home range, was observed for two males and two females. Hence there was no sex-bias in philopatry ($\chi^2_{(1)}=0.002$, ns). The possibility for close inbreeding (mother-son, father-daughter, brother-sister) was present for only 3 of 43 local recruits. Two philopatric daughters produced offspring when their fathers were still alive and one philopatric son took part at mating-chases when his mother was still producing young. However actual matings between close relatives were never observed (our unpublished data).

In Table 1 the numbers and percentages of male and female, adult and subadult immigrants are compared with those of residents. We tested for a sex and/or age bias among immigrants with a hierarchical log-linear model with sex, age, area and type (immigrant versus resident) as factors. The 4-way and all 3-way interactions were not significant, nor were the area-type ($G_{(1)}=2.2$, ns) and the sex-type ($G_{(1)}=0.3$, ns) interactions. However, there was a significant age-type interaction ($G_{(1)}=28.2$, $P<0.0001$). Hence, red squirrels do not show sex-biased immigration, but most immigrants were subadults (64%), while amongst residents the proportion of subadults was much lower (30%).

Table 1. The number of adult and subadult, male and female immigrants compared with residents

	Immigrants			Residents		
	Adults	Subadults	Total	Adults	Subadults	Total
Males	39	69	108	30	12	42
Females	34	60	94	29	13	42
Both	72	130	202	59	25	84

The data for the residents were averaged over 4 samples: one in April–May, one in September–October, over 2 years, one with poor reproduction (1986), one with good reproduction (1988)

Table 2. Mean body mass and mean foot length ($\bar{x} \pm SD$, sample size $= n$): (A) for each sex (M = males, F = females), type (Imm = immigrants, Res = residents), and age-group (Ad = adults, Sub = subadults); (B) immigrants and residents subdivided according to age; (C) 3-way ANOVA testing for the effects of sex, type and age on body mass and foot length

		Coniferous area					Deciduous area				
		n	body mass		foot length		*n*	body mass		foot length	
			$\bar{x}$	*SD*	$\bar{x}$	*SD*		$\bar{x}$	*SD*	$\bar{x}$	*SD*
A.											
Sex	M	76	309	29	59.1	1.5	79	311	24	59.1	1.2
	F	69	314	30	59.1	1.1	75	317	24	59.0	1.1
Type	Imm	106	308	29	58.9	1.2	96	311	22	59.1	1.2
	Res	39	320	29	59.5	1.4	58	319	27	59.1	1.1
Age	Ad	54	336	22	59.8	1.2	79	323	22	59.3	1.2
	Sub	91	297	24	58.7	1.2	75	304	22	58.8	1.1
B.											
Ad	res	21	338	21	60.0	1.2	40	325	22	59.3	1.1
Sub	res	18	301	23	59.1	1.3	18	306	31	58.6	1.0
Ad	imm	33	335	22	59.7	1.2	39	321	20	59.2	1.3
Sub	imm	73	296	24	58.6	1.5	57	304	19	58.9	1.1
C.			3-way ANOVA (*df* = 1, 138)					3-way ANOVA (*df* = 1, 147)			
Factor sex:			$F = 1.40$ NS		$F = 0.07$ NS			$F = 3.46$ NS		$F = 0.56$ NS	
Factor type:			$F = 0.49$ NS		$F = 1.50$ NS			$F = 0.26$ NS		$F = 0.22$ NS	
Factor age:			$F = 87.09$ **		$F = 25.34$ **			$F = 25.15$ **		$F = 4.38$ *	

Significance levels: * $P < 0.05$, ** $P < 0.001$, NS not significant

None of the 2-factor interactions is significant

Table 3. Number and percentage of sexually active adult males (scrotal testes) and females (oestrous or post oestrous) according to status (resident/immigrant)

	Residents	Immigrants
Males	121/131 92%	30/39 77%
Females	118/127 93%	15/34 44%

Sexual activity is scored per year and numbers of squirrels are summed over all years (1985–1991)

To test if immigrants were of poorer condition (smaller foot length, lower body mass) than residents, correcting for age effects and sex effects, a 3-way ANOVA with sex, type (immigrant/resident) and age as factors was calculated (Table 2). The type effect was not significant when corrected for differences in age composition between residents and immigrants in either of the two areas (Table 2B). Only age had a significant effect, both on body mass and on foot length (Table 2C), indicating that immigrants are not smaller and do not weigh less than residents of the same age-group.

The effects of immigration

One effect of being an immigrant might be a decrease in sexual activity. Male red squirrels are able to fertilize females when they have scrotal testes (Wauters et al. 1990). When testes are abdominal or semi-scrotal males are sexually inactive. Among adult immigrant males fewer animals had scrotal testes than among resident males (Table 3, $\chi^2_{(1)} = 7.22$, $P < 0.01$). Adult females can

Table 4. Two-way ANOVA on food abundance within a squirrel's home range with type (resident versus immigrant) and age (adult versus subadult) as factors, per habitat and per year

Year	Factor	Coniferous habitat			Deciduous habitat		
		df	*F*	*P*	*df*	*F*	*P*
1985	Type	1, 39	2.33	N.S.	1, 25	0.75	N.S.
	Age		0.08	N.S.		0.68	N.S.
1986	Type	1, 31	0.43	N.S.	1, 19	2.54	N.S.
	Age		6.19	0.03		0.44	N.S.
1987	Type	1, 33	0.56	N.S.	1, 26	0.02	N.S.
	Age		2.11	N.S.		1.30	N.S.
1988	Type	1, 32	0.07	N.S.	1, 32	1.08	N.S.
	Age		0.20	N.S.		1.64	N.S.
1989	Type	1, 31	0.02	N.S.	1, 31	2.48	N.S.
	Age		0.08	N.S.		0.20	N.S.
1990	Type	1, 43	0.92	N.S.	1, 37	3.08	N.S.
	Age		0.40	N.S.		0.86	N.S.

N.S. $P > 0.05$, not significant

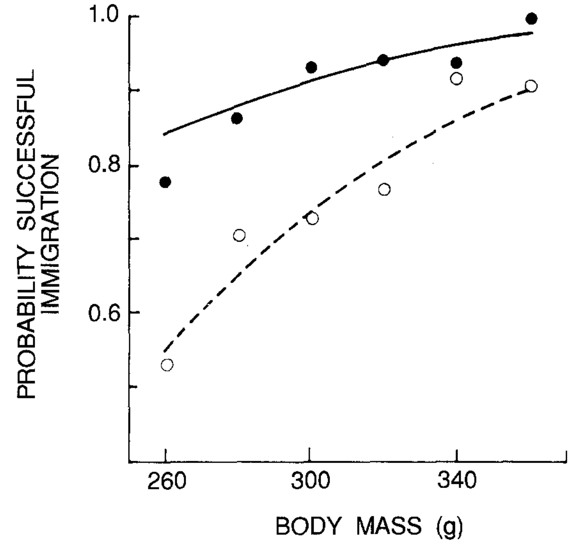

Fig. 2. Mean immigration success for 20-g weight intervals for squirrels immigrating in plots with (●) and without (○) disappearance of squirrels of the same sex. *Logistic curves*, representing the probability of being recruited as a function of body mass, were fitted for 'disappearance same sex' (——) and 'no disappearance same sex' (– – –) (see Methods for factor definitions)

Table 5. Logistic regression model predicting the probability of successful immigration in red squirrels ($n = 202$)

Full model	Model χ^2	*df*	*P*
	57.28	27	0.001
Selected parameters	$\Delta\chi^2$	Δdf	*P*
Body mass	10.1	1	0.005
Disappear same sex	26.0	1	0.0005

Selected model: $G(x_i) = -6.4\ (\pm 2.1) + 0.020\ (\pm 0.007)$ body mass $+1.46\ (\pm 0.32)$ disappear same sex

All parameters are tested with a stepwise backward procedure calculating the change in χ^2 ($\Delta\chi^2$ with Δdf) when a parameter is excluded from the model

be scored as sexually active when they are found in oestrus or post-oestrus (Wauters and Dhondt 1989). Significantly more resident females were sexually active than immigrants (Table 3, $\chi^2_{(1)} = 44.45$, $P < 0.0001$).

If immigrants are subordinate to local recruits we would expect them to be capable of settling only in poor-quality woodplots where few or no residents are present. A 2-way ANOVA was calculated comparing the food abundance of home ranges of residents with that of immigrants. We added age as a second factor to test for age effects on home range quality. Because of between-year differences in food abundance, data from each year were analysed separately (Table 4). No significant differences were found in the deciduous habitat. In the coniferous habitat adults were found in better home ranges than subadults in 1986 only. In all other years no significant effects of age or of immigrant versus resident were found (Table 4).

Not all immigrants succeeded in establishing a home range on the study area. In the coniferous habitat 35 of 54 (65%) male, and 35 of 52 (67%) female, immigrants settled on the study area. In the deciduous woodland similar proportions of successful male (35 of 54, 65%) and female (26 of 42, 61%) immigrants were observed.

The effects of cohort (year), area, age, sex, phenotypic characteristics, food and social organisation on an immigrant's probability of settling on our study areas were tested with a logistic regression model (for full model, see Methods). There was no significant effect of area, age or sex, nor of any interactions including one of these factors (Table 5), indicating that there was no sex or age bias in immigration success and that the factors affecting immigration success are similar in both coniferous and deciduous habitats. In the final model only body mass and the disappearance of a squirrel of the same sex as the immigrant significantly affected immigration success (Table 5, Fig. 2). The disappearance of residents of the opposite sex did not have a significant effect. Hence immigrants had a high probability of establishing residency when in good condition (high body mass) and when immigrating into woodlots where home ranges had become vacant because of mortality of residents of the same sex.

We also measured an immigrant's long-term success, by looking at future successful reproduction in females, or at obtaining a high dominance rank in males. High-ranked males are the ones most likely to mate and hence produce offspring (Wauters and Dhondt 1989; Wauters et al. 1990). The 1991 immigrants were excluded since we cannot yet determine their long-term success. In the coniferous woodland 24 (51%) male immigrants obtained a high dominance rank and 22 (51%) female immigrants produced offspring on the study area. In the deciduous woodland 19 male immigrants (48%) obtained a high dominance rank and 12 (36%) female immigrants produced offspring on the study area. In a logistic regression model we tested the same factors as for

Table 6. Logistic regression model predicting the probability of long-term immigration success in red squirrels ($n=163$)

Full model	χ^2	*df*	*P*
	57.09	25	0.001
Selected parameters	$\Delta\chi^2$	Δdf	*P*
Year · hab. qual. and habitat qual.	8.76	2	0.025
Year	10.10	5	0.1 > P > 0.05
Body mass	19.67	1	0.001

Selected model: $G(x_i) = -11.1\ (\pm 2.6) + 0.034\ (\pm 0.008)$ body mass $+ 0.00065\ (\pm 0.0004)$ habitat quality $- 0.00017\ (\pm 0.0008)$ year · habitat quality $- 1.1\ (\pm 0.8)$ year 2 $+ 1.1\ (\pm 0.6)$ year 3 $+ 0.28\ (\pm 0.59)$ year 4 $+ 0.27\ (\pm 0.76)$ year 5 $+ 1.33\ (\pm 0.66)$ year 6

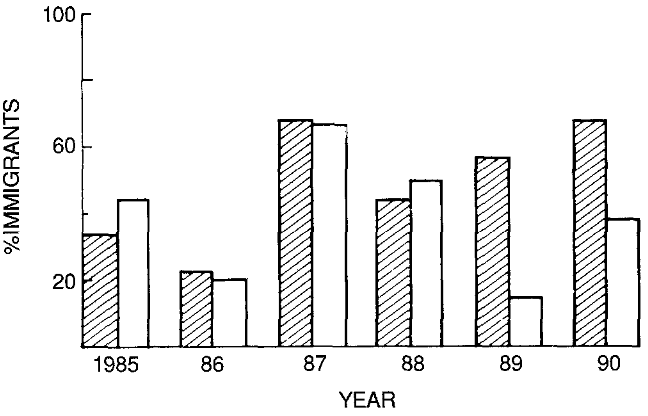

Fig. 3. The percentage of immigrants successful in the long term according to habitat (coniferous ▨, deciduous □) and year

short term immigration success (Table 6). The combined effect of the year · habitat quality interaction and habitat quality was statistically significant ($\chi^2_{(1)} = 8.76$, $P = 0.012$), indicating that the effect of habitat quality within a woodplot where the immigrant settled on long-term immigration success differed between years, being important only in years with many immigrants. In years with few immigrants (1986 in both areas, 1989 in the deciduous area; see also Fig. 3) both the proportion and the total number of immigrants successful in the long-term was so low that variation in habitat quality did not affect the probability of producing offspring or becoming dominant. Long-term immigration success varied between years, with only 30% of immigrants of the 1985 and 1986 cohorts becoming dominant and/or producing young against 69% in 1987 and 68% in 1990 in the coniferous habitat (Fig. 3). In the deciduous habitat we found a high proportion of successful immigrants in 1987 and 1988 and a low proportion in 1986 and 1989 (Fig. 3). Finally immigrants of high body mass were more likely to produce young (females) or become dominant (males) than lighter immigrants (Table 6).

Discussion

Combining data on immigration in two natural, unmanipulated populations, with all residents and all locally weaned juveniles marked prior to dispersal (Wauters and Dhondt 1990; Wauters et al. 1993), with the distances over which local recruits moved before settling, allowed us to test whether, as in the majority of mammal species (Greenwood 1980; Gaines and McClenaghan 1980), immigration onto a study grid and emigration from the natal site were sex biased. Since both study areas are only part of larger woodlands, we can not distinguish between intra- and interpopulation movements, but our data on local recruitment and recent telemetry data of dispersing juveniles (unpublished data) suggest that both occur.

Who immigrates?

Brandt (1992) argues that immigrants are likely to be less agressive and perhaps smaller or of lower body mass than residents because of the costs of dispersing. They might have been stressed energetically and physiologically or have experienced a series of defeats from resident animals. In grey squirrels genetic behavioural and colour morph differences appeared to be linked to local recruitment or dispersal (Pasitschniak-Arts and Bendell 1990). Local recruits were on average more aggressive than dispersers and more pepper morphs were recruited than black and grey morphs. There were no differences in body mass or size between recruits and dispersers.

In our red squirrels neither subadult nor adult immigrants are smaller or lighter than residents of the same age. Hence, body mass of locally recruited young in autumn or spring, i.e. 4–7 months after weaning, is not significantly higher than that of subadult immigrants, although heavy juveniles were more likely to be locally recruited (setting close to their birth place, within the study area) than lighter offspring (Wauters et al. 1993). This suggests that young with a low weaning mass do not show up as immigrants after disappearing from the natal range. Although immigrants were of similar size and body mass to residents, they did show behavioural differences. Fewer immigrants, both adult males and females, were in breeding condition than residents. The lower sexual activity of immigrants is probably caused by their lower social rank; they are always subordinate to residents (our unpublished data). In red squirrels dominance rank, which increases with age, affects mating behaviour in males (Wauters et al. 1990) and the probability of entering oestrus in females (Wauters and Dhondt 1989). Hence older, resident animals of high dominance rank are more likely to reproduce than low-ranked immigrants.

Between 60% (deciduous woodland) and 69% (coniferous woodland) of our immigrants were subadults that emigrated from their birth-place soon after weaning (natal dispersal). Other immigrants were adults which might initiate dispersal for proximate and/or ultimate reasons different from those affecting subadults.

None of the female immigrants, either in spring or in autumn, were in post-breeding condition (just finished lactating and still with enlarged nipples) indicating that in our red squirrel populations breeding dispersal of females did not occur. This is in contrast with pine squirrels, *Tamiasciurus hudsonicus*, and some microtines where adult females sometimes leave their home range or nest site, increasing the probabilitity of their female (and/or male in pine squirrels) offspring surviving until sexual maturity and subsequently breeding on the natal range (Stenseth 1978; Jannett 1980; Cockburn 1992; Boutin et al. 1993). In the ground squirrel, *Spermophilus columbianus*, adult females, in a low density population, also sometimes abandoned their nest sites to daughters (Harris and Murie 1984). However, in other ground and tree squirrel species, females that have obtained a breeding territory show very strong site fidelity (Thompson 1978; Armitage and Johns 1982; Murie and Harris 1984; Holekamp and Sherman 1989), as is the case in red squirrels (Wauters and Dhondt 1989, 1992). In the two cases of female philopatry we observed, the mother remained on her home range and the daughter settled on a part of the mother's home range.

The majority of adult male immigrants entered our study areas between late March and early May, just before the spring mating season (Wauters et al. 1990). Hence, adult male immigration might be a type of breeding dispersal in which sexually active males disperse in order to increase mating possibilities or home range quality, as found in some ground squirrels (Michener and Michener 1977; Sherman 1977; Hoogland 1982) and microtines (Myers and Krebs 1971). However, several observations run counter to the idea of breeding dispersal in male red squirrels. First, high-ranked males, those most likely to father offspring, normally occupy the same home range throughout their life (Wauters et al. 1990; Wauters and Dhondt 1992). Second, among adult males, fewer immigrants than residents were sexually active and probably had not shown sexually activity during the winter mating season. Third, new immigrants had a low social rank and were rarely observed playing an active part in a mating chase (Wauters et al. 1990) suggesting that these adults did not immigrate primarily to increase mating opportunities in the short term.

We conclude that in red squirrels in high-density stable populations only natal dispersal occurs, and that reproducing adults, due to the importance of being territorial in females or of a high dominance rank in males, do not undertake breeding dispersal. This, however, does not exclude the possibility that both adult and subadult males try to establish residency in plots where intrasexual competition for food and/or mates is reduced, in order to increase their future reproductive success.

Why become an immigrant?

Data on immigration in tree squirrels are very scarce. In grey squirrels, *Sciurus carolinensis*, more males than females immigrated to study plots and long-distance movements were male biased (Mosby 1969; Thompson 1978). In our red squirrel populations, however, males and females moved over similar distances from birthplace to potential breeding place and nearly equal proportions of males and females were found among immigrants. In both sexes philopatry was rare and most surviving male and female offspring dispersed away from the natal site, showing wide individual variation in dispersal distance. Hence, the hypotheses explaining sex-biased dispersal are irrelevant for explaining the immigration pattern in red squirrels.

Natal dispersal of both males and females has also been reported in *Microtus pennsylvanicus, M. ochrogaster* (Myers and Krebs 1971), *M. townsendii* (Krebs et al. 1976) and *Clethrionomys glareolus* (Kozakiewicz 1976; Gliwicz 1992). In the ground squirrel *Spermophilus franklinii* (Murie 1973) and the social Alpine marmot, *Marmota marmota* (Arnold 1990), males and females show similar dispersal behaviour. In the latter, dispersal is postponed until the second or third year of life when subordinate group members will leave the natal group in order to find a vacant breeding territory (Arnold 1990).

Anderson (1989), in his RFH, states that 'the probability that parents can benefit by forcing emigration of offspring may vary with the probability of nearby vacancies'. If young red squirrels were allowed to stay on the natal range, they would have to compete with the parents, often for several years, for food resources, a territory (females) or for a high rank in the dominance hierarchy (males). If, however, parents behaved in such a way as to make their offspring leave the natal site, the latter can find 'vacant' areas (areas of low local density in spring or late summer) where they will have to compete with fewer, and unrelated, conspecifics.

For red squirrels, food resources, energy-rich tree seeds, are in most years a limited resource (Wauters and Dhondt 1990; Wauters et al. 1992). Breeding females need patches of high food abundance from which they exclude other females (intrasexual territoriality) in order to be successful in producing offspring (Wauters & Dhondt 1992). Since they reproduce for several years, their residual reproductive value will in most cases be high and philopatric daughters would be competing for resources with their mother. Hence, avoidance of competition for food and space between close kin seems to have selected against female philopatry. In the absence of female philopatry, dispersal could still be sex-biased when males disperse over larger distances, as predicted by Greenwood (1980). Our data, however, showed no sex-bias in distance moved from the natal site or in the proportion of immigrants.

The proximate mechanism of natal dispersal proposed by Gliwicz (1992), based on observations in some populations of *Clethrionomys glareolus*, where females, although the territorial sex, predominated among dispersers, might help us to explain the absence of sex-biased immigration. Gliwicz (1992) suggested that the sex-ratio of dispersers, and hence dispersal tendency in both sexes, depends on the degree of intrasexual competition under local conditions (Gliwicz 1992). If this hypothesis holds, we predict that in red squirrels young should disperse away from their birth-place and that an immigrant will be more likely to establish residency in a woodplot where a vacancy is created by the disappearance of a resident of the immigrant's sex. If intrasexual competition is the major factor allowing settlement of immigrants, a decrease in local density due to mortality of squirrels of the opposite sex will not affect immigration success.

All our data support this hypothesis. First, heavier immigrants were more likely to establish residency than animals of lower body mass, and body mass is a good correlate of competitive ability of red squirrels at different ages (Wauters and Dhondt 1989, 1992; Wauters et al. 1993). Second, the probability of successful immigration increased for squirrels settling in woodplots where intrasexual competition was reduced through mortality of residents of the same sex. Intersexual competition seemed to have little effect, since reduced local densities caused by disappearance of squirrels of the other sex did not affect immigration success. This supports our idea (Wauters and Dhondt 1992) that behaviour and social organisation in male and female red squirrels are shaped by different ultimate causes, with intrasexual competition more important than intersexual competition. Third, both immigration peaks coincided with periods when food abundance or density, and consequently spacing behaviour, changed drastically. The spring immigration occured when tree seed crops become depleted and squirrels shifted their diet towards less energy-rich food-items which are temporarily abundant (Wauters et al. 1992), and when squirrels numbers are at their annual minimum (Wauters and Dhondt 1990). The autumn immigration coincided with the availability of the new seed-crop and occured after the main period (late spring–midsummer) of adult mortality (Wauters and Dhondt 1990). The seasonal differences in male and female immigration were related to seasonal variation in aggressive behaviour, males being more engaged in interactions in spring and females in autumn. Males increase their home ranges in spring (Wauters and Dhondt 1992), resulting in more frequent male-male interactions which may force subordinate males to disperse in search for areas with low male densities. Breeding females use small core-areas around the nest from March to mid-May and from July to mid-September (Wauters and Dhondt 1992). After the breeding season, adult females start to forage more intensively over the whole home range, resulting in more frequent interactions with floaters. As a result, more subordinate females will be searching for a place to immigrate in autumn.

Our data support the RFH of Anderson (1989), in the sense that it is advantageous for dominant residents (parents) to force their offspring to emigrate away from the natal site (no strict philopatry) in order to avoid competition for resources, social status and to avoid close inbreeding. As a proximate mechanism, intrasexual competition for resources explains the immigration pattern of both male and female red squirrels living in continuous high quality habitats. An immigrating female seems to settle in the nearest vacant home range where a good seed-crop is available (Wauters and Dhondt 1992), defending an intrasexual territory, while an immigrating male settles in an area where local male density, and hence intrasexual competition for mates and food, recently decreased.

Acknowledgements. We are grateful to P. Casale for field assistance and to L. Bijnens for help with the statistical analyses. Stan Boutin and an anonymous referee gave useful comments on an earlier version of the manuscript. We thank the families Stoelen and Bittebier, Merodese Bossen, and Baron Van Havre and the city of Antwerp, Peerdsbos, for permission to use their estates as study areas. L.W. was supported by a grant (840068) from the IWONL Brussels. The study was further supported by grant 2.0076.87 of the FKFO and by grant STEP-C-0040 from the EC to A.D.

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