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Survival and lifetime reproductive success in dispersing and resident red squirrels

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Abstract. Dispersal in red squirrels (*Sciurus vulgaris*) is not sex-biased and strict philopatry is rare. The immigration pattern suggests that nearly all animals have to disperse away from the natal site and that dispersal in this species is the outcome of local (intrasexual) competition. If this interpretation is correct, we predict that dispersers and residents, of both sexes, should have equal survival rates and lifetime reproductive success. Body mass, longevity, reproductive success and dominance rank of 34 resident offspring (settling within 400 m of the natal range) and 70 immigrants (dispersers) were compared. Immigrants did not weigh less than residents as adults, nor did they have a higher mortality during the pre-settling period. Survival rate, lifetime reproductive success (females) and the proportion of males obtaining a high dominance rank were similar for residents and dispersers, and no sex effect was found on either of the parameters studied. These results are consistent with the hypothesis that local competition determines whether an individual disperses further away or settles close to its birthplace.

Key words: Dispersers – Residents – Lifetime reproductive success – Survival – Red squirrel

Introduction

After weaning, mammals settle on their natal home ranges (philopatry) or leave in order to find a new place to live (natal dispersal). Dispersal is often sex-biased; more males disperse than females, or males disperse over longer distances. This bias is reversed in other taxa, such as birds (Greenwood 1980).

Many hypotheses on dispersal patterns concentrate on costs and benefits of dispersal and philopatry (Bengtsson 1978; Stenseth and Lidicker 1992). Potential benefits of dispersal are heterosis and the avoidance of close inbreeding (Greenwood 1980; Cockburn et al. 1985; Packer 1985; Stenseth and Lidicker 1992), escaping high levels of intraspecific competition for resources and mates (Greenwood 1980; Dobson 1982; Brandt 1992), or finding suitable habitats (Lidicker 1975; Shields 1983; Johnson and Gaines 1990). Potential benefits of philopatry are local adaptation through inheritance of favourable gene combinations (Shields 1983; Lynch 1991), and increased familiarity with the physical and social environment which may result in an increased ability to defend resources or escape predators (Shields 1983) and/or in decreased levels of agonistic behaviour initiated by adult residents (Brandt 1992).

Comparisons of dispersers and residents in several taxa have tended to show that philopatry is advantageous. Dispersers were found to survive less well in carnivores (Harris and Trewhella 1988; Woollard and Harris 1990; Harrison 1992), deer (Hölzenbein and Marchinton 1992), rodents (Leuze 1980; Garrett and Franklin 1988) and some birds (Fleischer 1983; Eden 1987; Strickland 1991), although other studies on both mammals and birds found no difference (Storm et al. 1976; Dhondt 1979; Keppie 1979; Hines 1986). Effects on reproduction have less often been found (Newton and Marquiss 1983; Krohne and Burgin 1987; Pärt 1991).

An alternative approach does not consider dispersal and philopatry as adaptive choices by individuals, but focuses on the proximate causes. For instance, several authors view dispersal as the outcome of local competition (Waser 1985; Anderson 1989; Gliwicz 1992). Our study of immigration patterns in the red squirrel (*Sciurus vulgaris*) suggests that dispersal in this species is the result of intrasexual competition for food resources (males and females) and for mates (males) (Wauters and Dhondt 1992, 1993). There is no sex bias in dispersal, strict philopatry is rare, and immigrant success is strongly affected by local density of residents of the same sex. If our interpretation, that juvenile squirrels disperse randomly until they find a suitable home range, is correct, we predict that dispersers and residents should not differ in survival rates and lifetime reproductive success, and that this is true for

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both sexes. We tested this prediction by comparing data on competitive ability, survival, dominance rank and reproductive success of locally born offspring settling close to their birth-place (residents) and immigrants born elsewhere (dispersers), in two red squirrel populations.

Materials and methods

Red squirrels were studied between October 1984 and October 1992 in two study sites (a coniferous and a deciduous site) of 30 ha each, which were part of larger woodlands at Herenthout (about 300 ha) and Schoten (about 600 ha), province of Antwerpen, N. Belgium. Both study sites were on the edge of the forest and surrounded by unsuitable habitat on the west and south sides (coniferous site) or on the north, west and south sides (deciduous site) (Wauters and Dhondt 1993). Both woodlands were high-quality habitats with adult densities ranging from 0.8 to 1.3/ha.

Trapping was carried out for at least 4 days every 2 months from October 1984 to October 1992. During dispersal periods or when weaned juveniles were observed, trapping was continued until no more unmarked squirrels were seen. All squirrels were individually marked and their body mass was measured, at each recapture, to the nearest 5 g, using a Pesola spring balance.

Since strict philopatry, settling on the natal home range (the home range of the mother), hardly occurred (Wauters and Dhondt 1993), we defined "residents" as those young that established residency in a home range of which the centre was less than 400 m away from the center of their natal range. Since this is less than twice the diameter of the natal home range (200 m, Wauters and Dhondt 1992), a resident's home range overlapped with a home range adjacent to the natal range. "Dispersers" were squirrels that were not born on the study site and established a home range more than 400 m away from a potential birth-place (i.e. >400 m from those edges of the study sites that bordered the rest of the forest).

Data were gathered on 34 residents and 70 immigrants (representing dispersers) that settled on a home range on the study sites and that could be monitored from 12 months old until they disappeared. Since radiotracking showed that established adults hardly ever abandon their home ranges (Wauters and Dhondt 1992), they were considered dead when no longer caught. Hence, to calculate longevity and lifetime reproductive success, only animals that died before January 1992 were used. For 73 squirrels, 47 residents and 26 immigrants, we could monitor survival over the period between the start of dispersal movements (at 4 months old) and the squirrels reaching sexual maturity (at 12 months old). Survival over this pre-settling period was monitored using radio telemetry ($n = 21$), recaptures and finding remains of dead animals.

As a measure of condition and competitive ability we used body mass during the first winter as adult (c. 18 months old) which correlated well with survival and dominance position (Wauters and Dhondt 1989). A squirrel's lifespan was estimated using the last trapping session (or observation) the squirrel was recaptured (Wauters and Dhondt 1989). Female reproductive success was estimated by locating nests of lactating females and marking young in or around the nest (between 3 and 8 weeks old) and subsequently counting the number of weaned young observed around the nest. The total number of young weaned (10 weeks old) over a female's lifespan was used as measurement of lifetime reproductive success (LRS) (Wauters and Dhondt 1989; Wauters et al. 1993). Dominance rank of males was assessed by observing male-male interactions: males winning all their interactions and those winning in a part of their home range only were ranked as dominant males, others were ranked as subordinates (Wauters and Dhondt 1989). Dominant males were considered as potential fathers, subordinate males were assumed not to be reproducing (Wauters et al. 1990).

When data were normally distributed, parametric statistics were calculated with the SAS procedure GLM (SAS Institute 1990); otherwise non-parametric statistics were used.

Results

Survival in the pre-settling period

Mortality rates of male (4 of 13, 31%) and female (5 of 13, 38%) dispersers were not significantly different from those of male (8 of 23, 35%) and female (11 of 24, 46%) residents (log-linear model: factor status $G_{(1)} = 0.24$, ns). No sex-effect was found on mortality during the pre-settling period (factor sex: $G_{(1)} = 0.75$, ns).

Body mass of residents and immigrants

A squirrel's body mass is a good indicator of its condition and is correlated with the food abundance in its home range (Wauters and Dhondt 1989). We compared body mass at 18 months old of residents and immigrants of both sexes, with a two-way ANOVA (Table 1). Females were slightly heavier than males whether resident or immigrant (sex effect $F_{(1,\ 100)} = 4.51$, $P = 0.036$, sex by status interaction $F_{(1,\ 100)} = 2.64$, ns), but no difference in body mass was found between residents and dispersers (status effect $F_{(1,\ 100)} = 1.04$, ns).

Lifetime reproductive success and longevity

Of the 22 resident females 15 (68%) produced offspring that survived at least until weaning, against 20 of the 33 immigrant females (61%). The proportion of successful females did not differ between residents and immigrants ($\chi^2_{(1)} = 0.33$, ns). The distribution of lifetime reproductive

Table 1. Mean body mass (g) of locally recruited residents and immigrants according to sex

	Residents			Immigrants		
	n	Mean	SD	*n*	Mean	SD
Males	12	320.0	17.5	37	331.2	17.3
Females	22	335.9	22.6	33	333.3	20.8
Total	34	330.3	22.2	70	332.2	14.5

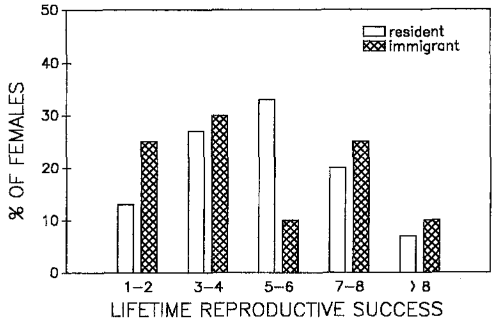

Fig. 1. Variation in lifetime reproductive success (total number of young weaned over a female's lifespan) in resident and immigrant females

Table 2. Longevity (in monts) of locally recruited residents and immigrants, according to sex

	Residents					Immigrants				
	n	Mean	SD	Median	(range)	*n*	Mean	SD	Median	(range)
Males	12	32.8	11.0	31	(15–55)	37	39.7	16.3	35	(20–83)
Females	22	38.5	18.0	30	(18–77)	33	40.4	17.9	32	(17–80)
Total	34	36.5	15.7	31	(15–77)	70	40.0	12.6	35	(17–83)

success did not differ significantly for resident and immigrant mothers that produced at least one young (Fig. 1, two-sample Kolmogorov-Smirnov test, $P > 0.9$), nor was there a difference in the mean number of young produced (mean ±SD: residents 5.33 ± 2.48, immigrants 4.70 ± 2.68, one-way ANOVA, $F_{(1,\,33)} = 0.503$, ns). Male LRS could not be measured directly, but we compared the proportion of resident and immigrant males that attained a high dominance rank. Similar proportions of residents (8 of 12, 67%) and immigrants (29 of 37, 78%) became dominant males ($\chi^2_{(1)} = 0.67$, ns).

There was no difference in longevity between males and females (Kruskal-Wallis $H_{(1)} = 0.012$, ns). Combining data from both sexes, longevity did not differ significantly between residents and immigrants (Table 2, Kruskal-Wallis $H_{(1)} = 1.025$, ns).

Dispersal distances, which were known for 14 young that settled as adults and could be monitored until their death, were not significantly correlated with longevity ($r = 0.13$, ns) or with LRS of females ($r = 0.22$, $n = 8$, ns).

Discussion

When using immigrants to represent dispersers, in a comparison with resident animals, the following conditions have to be met: both groups have originated in similar habitats (presumably, similar population characteristics); no differential mortality occurred between weaning and first capture; and all immigrants were caught before disappearing again from the study sites. Our study fulfilled most of these these conditions. First, our study sites were representative plots within larger forests, surrounded by smaller but similar woodlands. Assuming that most emigrants travel between 500 and 1700 m (unpublished data), nearly all immigrants must have been born in those forests, or in the nearby woodlands. Second, by limiting our analyses to squirrels first caught around the age at which dispersal starts (4–5 months old, unpublished data), we obtained comparable data on early survival of residents and immigrants. However, we could not measure the actual cost associated with dispersal movements and some mortality might already have occurred among dispersers before they were tagged. These costs can only be measured accurately by radio-tagging juveniles before they start dispersing and by monitoring their survival over the entire dispersal-period (Larsen and Boutin 1994). Finally, since immigration is concentrated in time, immigrants are very trappable, and trapping sessions were prolonged until no more unmarked squirrels were caught or observed, the possibility of systematically overlooking dispersers could be excluded.

In male collared flycatchers (*Ficedula albicollis*) and gray jays (*Perisoreus canadensis*), birds that dispersed less far or stayed in the natal territory survived better than those dispersing (Pärt 1991; Strickland 1991). Philopatric magpies (*Pica pica*) survived better the first winter than dispersers, but no differential survival between residents and dispersers from fledging to breeding was found (Eden 1987). In great tits (*Parus major*) some studies have found differences in survival rate between residents and dispersers depending on age and sex (Clobert et al. 1988), while others have not (Dhondt 1979). In the same species, reproductive parameters, including laying date, clutch size and the number of fledglings, also differed according to dispersal distance, and females dispersing more than the median distance were more likely to raise offspring that subsequently bred in the wood (Greenwood et al. 1979). In blue grouse (*Dendragapus obscurus*) neither survival nor reproductive rate differed between long- and short-distance dispersers (Hines 1986). In sparrowhawks (*Accipiter nisus*) and collared flycatchers differences in reproductive performance between short and long distance dispersers were only significant in one sex (Newton and Marquiss 1983, Pärt 1991). These data on birds show that the potential costs or benefits of dispersal differ according to age and sex, which may explain differences in dispersal behaviour between sexes and age-classes (Clobert et al. 1988).

In some mammals where mortality was studied over the dispersal period or during the first year of life, dispersers survived less well than non-dispersers (Garrett and Franklin 1988; Woollard and Harris 1990). In red foxes (*Vulpes vulpes*) and black-tailed prairie dogs (*Cynomys ludovicianus*) the higher mortality among dispersers might be due to them being subordinate to philopatric offspring and/or in poorer condition (Garrett and Franklin 1988; Woollard and Harris 1990). In water voles (*Arvicola terrestris*) increased mortality among dispersers was partly explained by a higher predation risk when traversing marginal habitats. Also in American red squirrels (*Tamiasciurus hudsonicus*) the risk of predation, mainly by goshawks (*Accipiter gentilis*), significantly increased when juveniles started to disperse and travelled off their natal territories (Larsen and Boutin 1994). Larsen and Boutin (1994) found that nearly 50% of their radiotagged juveniles that acquired territories remained philopatric (settled on or immediately adjacent to their mother's territory) and that the furthest settlement distance was only about three territories away. However, offspring that dispersed further before settling were more likely to obtain large, high quality territories and had a higher winter survival, suggesting that the costs of moving off the natal territory may be balanced by the advantages of locating a superior territory (Larsen and Boutin 1994).

In our red squirrel populations immigrants did not weigh less than residents, nor did they settle in areas with lower food resources, indicating that they were not in poorer condition, nor subordinate to residents (Wauters and Dhondt 1993). In both study sites, specialized predators, goshawk or pine marten (*Martes martes*), were absent and most dispersers did not have to traverse unsuitable habitats (unpublished data). Thus, the costs of dispersing through high-quality, continuous woodlands seem low, resulting in similar mortality rates among resident and dispersing red squirrels. Differences in habitat structure and in the abundance of predators are likely to affect the costs of movements off the natal range. In small (25–55 ha) fragmented woodlands, local recruitment was higher and immigration rate lower than in large woodlands, indicating that more juveniles settled close to their birthplace when the proportion of unsuitable habitat surrounding the natal home range increased (Wauters et al. 1994).

Finally, we found that similar proportions of immigrant and resident males achieved a high dominance rank and were likely to father offspring (Wauters et al. 1990), and that lifetime reproductive success did not differ between resident and immigrant females. No sex effects were found on the relationships between status (resident/disperser) and longevity or reproduction.

Hence, our data agree with predictions based on the red squirrel's dispersal pattern (Wauters and Dhondt 1993) and are consistent with the hypothesis (Waser 1985; Gliwicz 1992) that competition for resources, depending on local conditions, such as local food abundance, the sex and dominance rank of neighbouring squirrels, and habitat structure, determines whether an individual disperses further away or settles close to its birthplace.

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