Z. Säugetierkunde 55 (1990) 161–175 © 1990 Verlag Paul Parey, Hamburg und Berlin ISSN 0044-3468

### Red squirrel (*Sciurus vulgaris* Linnaeus, 1758) population dynamics in different habitats

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Receipt of Ms. 7. 12. 1988 Acceptance of Ms. 20. 6. 1989

#### Abstract

Between October 1984 and January 1988 the dynamics of two red squirrel (*Sciurus vulgaris* Linnaeus, 1758) populations in a coniferous and a deciduous woodland was studied. Squirrels were livetrapped and individually marked. Density fluctuated annually, with variation in food abundance and winter temperature. Annual survival was positively correlated with food abundance, and higher for adults than for subadults. The proportion of females entering oestrus and of oestrous females breeding successfully were density dependent. The number of young weaned per successful female was positively correlated with food abundance. Variation in the timing of immigration between males and females was related to differences in social behaviour. The emigration-rate in both populations increased at high density and decreased when density was low. Hence, density regulating processes seemed to be at work through density dependent reproduction and emigration.

#### Introduction

Many species of Holarctic tree squirrels have been, or still are, important game animals. They were hunted for their fur, for food or sport, and for wood management purposes. Biologists have made use of data on fur returns and of shot squirrels to study different aspects of their population ecology: reproductive activity and litter size (OGNEV 1940; BROWN and YEAGER 1945; SMITH 1968; DEGN 1973; TITTENSOR 1977; RUSCH and REEDER 1978), sex-ratios (SHORTEN 1954; UHLIG 1957; LAMPIO 1967; KEMP and KEITH 1970; FARENTINOS 1972; NIXON et al. 1975), and the effect of variation in food abundance on density fluctuations (MIKHEEVA 1973; LYUBETSKAJA 1976; KEMP and KEITH 1970; NIXON et al. 1975).

The counting of dreys has been used to estimate squirrel density in grey *Sciurus* carolinensis (DON 1985) and in red squirrels (*Sciurus vulgaris* Linnaeus, 1758) (WAUTERS and DHONDT 1988).

Where these studies provide information on population structure and density at a specific time, and give crude indices of year to year changes in numbers, they are unsuitable for discovering short-term density fluctuations or for examining the importance of different population processes.

Detailed studies, using live-trapping, on unexploited populations of pine squirrels *Tamiasciurus hudsonicus* (KEMP and KEITH 1970; RUSCH and REEDER 1978; HALVORSON and ENGEMAN 1983), tassel-eared *Sciurus aberti* (FARENTINOS 1972), grey (THOMPSON 1978; KENWARD 1985; GURNELL 1987), fox *Sciurus niger* (HANSEN and NIXON 1985) and red squirrels (TITTENSOR 1977; TONKIN 1983; WAUTERS and DHONDT 1985, 1986; HOLM 1987), describe density changes over several years and investigate the effects of reproduction, survival and dispersal. Most of these studies have been relatively short-termed: in only two cases populations have been followed in detail for more than ten years now (HALVORSON and ENGEMAN 1983; GURNELL 1983, 1987).

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We have been studying a red squirrel population in a coniferous habitat from August 1983 onwards and a second population in a mainly deciduous habitat from October 1984 onwards. In this paper we use data until January 1988, and we (i) describe and compare density fluctuations in both populations, (ii) describe the sex-ratio and age structure of both populations, and (iii) examine the different population processes: survival, reproduction and dispersal.

#### Study areas

We used two study sites of 40.5 ha each. One in the "Merodese Bossen" at Herenthout (Province of Antwerpen, N. Belgium) is mainly coniferous woodland of 212 ha dominated by Scots pine, *Pinus sylvestris*, and Corsican pine, *Pinus nigra*, with some larch, *Larix decidua*, and a few plots with mature oak, *Quercus robur*, and beech, *Fagus sylvatica*. The south-side of the study-area is bordered by meadows and by a road, that were never crossed by resident squirrels. The west-side is bordered by squirrels. Along the north and east-side suitable squirrel habitat continues.

The second study area lies in the Peerdsbos at Schoten (Province of Antwerpen, N. Belgium) a mixed mature wood of 150 ha dominated by oak, beech and birch, *Betula* sp., with some chestnut, *Castanea sativa*, and maple, *Acer pseudoplatanus*. A few plots are planted with Scots or Corsican pine and some spruce, *Picea abies*. The study area is bordered by houses and a road on the north-side and by meadows and a motorway along the south and west-side, that were never crossed by residents. On the east-side the forest continues.

#### Material and methods

#### Trapping squirrels

The coniferous population was first sampled in August 1983. During the first year trapping was carried out at any possible occasion, and trapping-intensity and trapping success varied over the year (WAUTERS and DHONDT 1986). From October 1984 onwards both populations were sampled very intensively. Two types of traps were used. Wooden box traps ( $60 \times 17 \times 17$  cm) placed on the ground or on small tables at about 1 m height, and "British squirrel-traps" (J. HOLM pers. comm.) that were hung up against the trunk of the tree at about 1 m height. Traps were baited with a handful of sunflower seeds, three hazelnuts and three peanuts. In the coniferous woodland traps were placed on a 75 m grid (about 1.5 traps/ha) while in the deciduous woodland they were randomly distributed at a density of 1.2 traps/ha. In both study-areas trapping sessions of four days pre-baiting followed by four days of trapping were performed every five weeks. This allowed us to tag all resident squirrels in both study-areas and to have a high percentage of recaptures in each session. Moreover squirrels entering the population through reproduction or immigration were also easily captured and marked. Hence, density was known at each moment. We examined two characteristics of trappability: 1) Trapping success (Ts), which was calculated using the following formula: Ts = (number of captures) number of trap-days; x 100 %, with 30 traps set for four days equals 120 trap-days; and 2) the proportion of animals present on the study area that were recaptured in a trapping session.

Squirrels that were only trapped in edge-traps along those sides of the study-areas where suitable habitat continued (north and east-side in the coniferous, east-side in the deciduous woodland) were not regarded as belonging to the resident population. Hence they were not used in density-estimations.

Data on home range use (WAUTERS and DHONDT 1985; unpublished data) of radio-tagged animals also helped in determining which squirrels were residents in the study-area, and which only visited it occasionally.

#### Handling squirrels

Every squirrel was individually marked using small pieces of coloured wires inserted through the ear. At each recapture the squirrel was weighed, and its body measurements were taken (WAUTERS and DHONDT 1989a). Information about the age, sex and reproductive status of the squirrel was also recorded. Subadults are between four and ten months old, males having abdominal testes and a small scrotum; females having a small unperforated vulva. Adults are over ten months.

#### Estimating survival, reproduction and dispersal

Between October 1984 and October 1987 local survival was estimated from one trapping session to the next using the following formula: survival-rate from time t-1 to time t =[(number of tagged squirrels present at t-1 and at t) / (number of tagged squirrels present at time t-1)]  $\times$  100 %.

From January 1985 till October 1987 data were available for all reproductive periods. The number of females in oestrus, the percentage of oestrous females lactating and successfully lactating were estimated while examining the reproductive status of recaptured females. Not all juveniles were marked. However, trapping of weaned juveniles, marking of juveniles in the nest, and observations of lactating females and their young allowed estimates of the number of young per successful reproducing female (WATERS and DHONDT 1989b). That most juveniles were marked before, or soon after weaning, allowed us to distinguish them from immigrants.

Reliable data on dispersal of mammals are often hard to get, since it is not always possible to distinguish between emigration and mortality. However most immigrating squirrels could be trapped rather easily. When many new squirrels appeared in a trapping-sample, the number of days traps were set was increased, till no more unmarked immigrants were captured. In most trapping sessions however immigrants were captured during the first two days and there was no need to trap for more than four days.

#### Environmental factors

Mean monthly temperatures are derived from the nearest station of the Koninklijk Metereologisch Instituut at Geel (15 km to Herenthout).

Food abundance was estimated using counts of fallen seeds on one square meter plots (WAUTERS and DHONDT 1988).

#### Analysing data

Since analyses of both reproduction and dispersal involve several parameters that contribute to total gains or losses in the population, and are affected by different environmental factors, the data were transformed logarithmically. This allowed us to add up values of each parameter and hence calculate the total gains or losses from one generation to the next for both reproduction and dispersal. The method is analogues to a k-factor analysis (DEMPSTER 1975) with the difference that our analysis was performed separately for reproduction and dispersal, as the different parameters contributing to reproduction and dispersal were not completely separated in time. Table 1 describes the sequence of parameters included in the analyses.

In order to combine the data set from the coniferous area (4 years) and the deciduous area (3 years), we normalised our data (in a set of normalised data,  $x_i$ ,  $\overline{x} = 0$  and  $s_x = 1$ ), when the effect of environmental factors and when density dependence was investigated.

#### Results

#### Trappability

In both study-areas trapping success differed significantly between three periods (November–February, April–July, August–October), based on seasonal differences in the availability of tree seeds as primary food-resource (WAUTERS and DHONDT 1987), (Kruskal-Wallis analysis of variance: coniferous area H = 13.26; d.f. = 2; P < 0.01; deciduous area H = 10.70; d.f. = 2; P < 0.01). When in April–July tree seeds are no longer available to squirrels, the highest trapping success was reached. It was lowest in winter, when high energy food is most abundant. Squirrels thus became more trap-addicted when natural food was rare, and more trap-shy when natural food was abundant.

The proportion of resident squirrels recaptured in a trapping session varied less being usually over 75%. The proportion of squirrels recaptured differed significantly between the three periods described above (Kruskal-Wallis analysis of variance: coniferous area H = 9.00; d.f. = 2; P < 0.02; deciduous area H = 9.89; d.f. = 2; P < 0.01). It was highest in the April–July period, when food is less abundant.

#### Density fluctuations

Squirrel numbers fluctuated over the year and between years (fig. 1). Also the abundance of tree seeds fluctuated between years (table 2). The seed-crop in year t was significantly correlated to October-density the next year (t+1), (r = 0.743; n = 8; P < 0.05) (fig. 2). In both habitats the October-density of 1986 was lower than expected based on the size of the

## Table 1. The different parameters involved in calculating the total gains or losses from one generation to the next for both reproduction and dispersal, using logarithmics

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$N_0$ = potential n° young in spring litter (= n° adult females present in January × 3.2 embryos/ female)
$k_1 = $ losses due to females not entering oestrus
$N_1$ = potential n° young produced by oestrus females in spring
$k_2 = $ losses due to breeding-failure of oestrus females
$N_2$ = potential n° young produced by successfully breeding females
$k_3 = $ losses due to nestling mortality
$N_3 = actual n^\circ$ young weaned in May
$k_4$ = female mortality and/or emigration from first to second breeding season (difference
between log $N_0$ and log $N_4$
female)
$k_5 = $ losses due to females not entering oestrus
$N_5$ = potential n° young produced by oestrus females in summer
$k_6 = losses$ due to breeding-failure of oestrus females
$N_6$ = potential n° young produced by successfully breeding females
$k_7 = $ losses due to nestling mortality
$N_7$ = actual n° young weaned in September
Dispersal
$k_0$ = gains due to winter-spring immigration
$N_0$ = actual n° immigrants in winter-spring
$k_1$ = further population increase due to spring reproduction
$N_1 = n^\circ$ immigrants and weaned juveniles in spring
$k_2 = $ losses due to summer emigration
$N_2 = n^\circ$ immigrants and spring juveniles still present in October
$k_3 = gains due to autumn immigration$
$N_3$ = actual n° immigrants entering the population in autumn
$k_4$ = further population increase due to summer reproduction
$N_4 = n^{\circ}$ immigrants and weaned juveniles in autumn
k <sub>5</sub> = losses due to autumn-winter emigration
$N_5 = n^2$ immigrants and juveniles recruited in winter population

seed-crop the previous winter. The 1985–86 winter was the coldest of the four winters (mean max. temperature over the November–February period:  $3.4 \,^{\circ}$ C, against  $6.1 \,^{\circ}$ C in 1983–84,  $4.9 \,^{\circ}$ C in 1984–85 and  $4.4 \,^{\circ}$ C in 1986–87). Furthermore squirrel numbers tended to increase after a year with low density, and to decrease after a year with high density. However, in a multiple linear regression model the partial effects of food abundance (p = 0.013) and of winter temperature (P = 0.049) were statistically significant, while that of density the previous year (P = 0.255) was not. Variation in food abundance (partial r = 0.943) and in winter temperature (partial r = 0.920), together explained 96.6 % of the variation in squirrel-density between years.

#### Sex-ratio

Over the three years juveniles were captured and marked in the nest or soon after weaning, 58 young (28 males, 30 females) were tagged in the coniferous and 46 (23 males, 23 females) in the deciduous habitat. In both habitats sex-ratios of juveniles did not differ from an even sex-ratio.

Changes in the sex-ratio of the whole population (adults, subadults and juveniles) with time (fig. 1), did not occur randomly (Runs-test; coniferous area: r = 3; N = 34; P < 0.001; deciduous area: r = 2; N = 34; P < 0.001).

In the coniferous woodland more males than females were present from October 1984 until August 1985 (fig. 1). In September the number of females increased suddenly, due to

large numbers of females immigrating. From September 1985 until March 1987, females outnumbered males (fig. 1). In the spring of 1987 a slightly male biased immigration resulted in an even sex-ratio. The ratio of males over females stayed approximately 1:1 for the rest of the year (fig. 1). No apparent relation existed between sex-ratio and density. In



Fig. 1. Variation in squirrel numbers and in sex-ratio (males : females) between October 1984 and January 1988 in both habitats (coniferous = C, deciduous = D). Dotted area is the April-September period (spring and summer)





Year (t)	Seed-crop in winter t t+1 (10 <sup>3</sup> Kcal/ha)	N and (N/ha) in October year t	Survival (%) year t t+1 (adult surv.)	Number of immigrants and juveniles (recruited imm. + juv)					
Coniferous woodland									
1983	152.5	43 (1.04)	54 % (76 %)	_					
1984	184.9	55 (1.36)	53 % (62 %)	_					
1985	135.0	57 (1.41)	44 % (53 %)	49 (21)					
1986	112.0	41 (1.01)	46 % (50 %)	25 (10)					
1987	-	46 (1.14)	- '	39 (17)					
Deciduous woodland									
1983	189.1	-		_					
1984	742.6	35 (0.86)	47 % (65 %)	_					
1985	1051.5	40 (0.99)	52 % (61 %)	30 (18)					
1986	1607.5	34 (0.84)	53 % (61 %)	23 (13)					
1987	-	47 (1.16)	_	44 (20)					

Table 2. Changes in food abundance, squirrel numbers, annual survival and annual recruitment of immigrants and juveniles, between October 1983 and October 1987

the deciduous woodland more males than females were present from October 1984 until January 1987 (fig. 1). In February 1987 a lot of females immigrated into our study area and the sex-ratio became 1:1 (fig. 1). From February 1987 until January 1988, the sex-ratio



*Fig. 3.* Age structure of the squirrel population in both habitats in October of 1985, 1986 and 1987. Coniferous area  $\square$ , deciduous area  $\square$ . In the deciduous area no difference could be made between 2 year old and older squirrels in 1985, between 3 year old and older in 1986 and between 4 year old and older in 1987

varied between 0.85 and 1.05, hence close to a 1:1 ratio (fig. 1). In the deciduous woodland males outnumbered females when densities were low to moderate (October 1984, 1985, 1986). The sex-ratio was 1:1 when density was high (October 1987).

#### Age-structure

The age-structure showed the same trend in both populations (fig. 3). The total number of three year old and older squirrels stayed rather constant over the years. In the coniferous woodland it varied from 11 in 1985 and 1986 to 13 in 1987, while in the deciduous woodland 10 squirrels were older than two in each year.

In all years and in both habitats the majority of the squirrels (71 %–81 %) were less than three years old, with yearlings and two year old squirrels as dominant age-categories (fig. 3). The percentage of subadults and yearlings was positively correlated with squirrel density (normalised data: r = 0.864; n = 6; P < 0.05). Thus when the proportion of immature squirrels in the population had increased, density was high, and when it had decreased density was low.

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Table 3. Differences in local survival in both habitats according to age and season and differences
in annual survival according to sex, from October 1984 to October 1987
Three-way G-statistics were used

Season	C Adults	Coniferous area Subadults	G(age)	Adults	Deciduous area Subadults	G(age)	
W 84–85 S 85	26/34 (76 %) 23/26 (88 %)	8/21 (38 %) 6/8 (75 %)	7.632 P<.05	17/20 (85 %) 13/17 (76 %)	8/15 (53 %) 3/8 (38 %)	7.772 P<.05	
G(season) =	= 3.017 N.S.			G(season) = 0.957  N.S.			
W 85–86 S 86	31/38 (82 %) 21/31 (68 %)	6/20 (30 %) 5/6 (83 %)	7.973 P<.02	22/28 (79 %) 17/22 (77 %)	7/12 (58 %) 4/7 (57 %)	1.765 N.S.	
G(season) =	= 0.046 N.S.			G(season) = 0.	056 N.S.		
W 86–87 S 87	27/35 (77 %) 18/27 (67 %)	3/6 (50 %) 2/3 (67 %)	0.946 N.S.	24/25 (96 %) 16/24 (67 %)	3/9 (33 %) 2/3 (67 %)	11.17 P < .01	
G(season) = 0.248  N.S. $G(season) = 4.334  N.S.$							
		Coniferou	Deciduous area				
		Males	Females	Ma	Females		
$84-85 \qquad 16/31 (52 \%) \qquad 13/24 (54 \%) \qquad 8/19 (42 \%) \qquad 8/16 (50 \%)$ G (see) = 0.147 N S and G(area) = 0.103 N S							
85-86	11/2	27 (41 %)	15/31 (48 %	) 11/22 (	(50 %) 10	0/18 (56 %)	
G(sex) = 1.2 86-87 G(sex) = 0.0	257 N.S. and G 9/1 001 N.S. and G	(area) = 1.577 18 (50 %) (area) = 0.261	N.S. 11/23 (48 % N.S.	) 9/18 (	(50 %)	9/16 (56 %)	
S = April-Sept.; W = OctMarch.							

#### Local survival

Data on local survival according to half-year periods (autumn-winter period from October to March, spring-summer period from April to September), habitat type, age group and sex are summarised in table 3. Over the three years local survival was studied (October 1984–October 1987), no significant difference was found between years or areas (3-way Gtest: factor year G = 0.019; d.f. = 4; N.S.; factor area G = 0.292; d.f. = 3; N.S.; 3-factor interaction G = 1.328; d.f. = 2; N.S.). LAMPIO (1967) suggested that due to changes in ranging behaviour and mobility, survival of male red squirrels differed from female survival. A 3-way G-test (factors sex, area, and survival) showed no differences in local survival according to sex or habitat type (table 3). In red squirrels body weight changes according to variation in food abundance and weather conditions (WAUTERS and DHONDT 1989a). Moreover a squirrels' chance of survival was correlated with its body weight (WAUTERS and DHONDT 1989b), so that older heavier squirrels survived better than younger squirrels of lower body weight. Therefore we tested for differences in local survival according to season and age using a 3-way G-test. Since no differences in survival were found between males and females, data on both sexes were combined. Separate analyses were made for each year survival was studied and for both areas. Seasonal differences in survival were statistically not significant (table 3), but differences between age-groups were significant in 1984–85 and 1985–86 in the coniferous and in 1984–85 and 1986-87 in the deciduous woodland (table 3). In all cases adults survived better than subadults.

The effect of winter-cold on survival was tested by correlating the mean monthly max. temperatures during the wintermonths (November–February) with monthly survival, combining the data of both habitats (fig. 4). Monthly survival during winter decreased significantly with temperature (r = 0.784; n = 18; P < 0.001).



*Fig. 4.* Linear correlation of mean monthly maximum winter temperature with monthly survival (from November to February) over the three years of study, in both habitats. Coniferous area  $\circ$ , deciduous area  $\bullet$ 

Although changes between years in half-year survival-rate were small and statistically not significant, a positive correlation existed between food abundance in year t and annual survival (year t to t+1) (r = 0.760; n = 7; P < 0.05). No density dependent effect on survival was found.

Survival from year t to t+1 was not significantly correlated with density at year t+1 (r = 0.668; n = 7; 0.1 > P > 0.05), although a tendency existed of higher densities after a year with a high survival-rate.

#### Reproduction

In order to invest in reproduction females must have a high body weight (WAUTERS and DHONDT 1989b). The percentage of females that came into oestrus varied between years (table 4) and between reproductive seasons (spring or summer reproduction).

The measurement of reproductive rate that can be compared between years is the number of juveniles weaned per adult female, which is the product of the proportion of adult females in oestrus, with the proportion of oestrus females that reproduced successfully and with the number of young weaned per successful female. The importance of each of these parameters was analysed as described in the methods and as shown in table 1.

Since the abundance of tree seeds and winter temperature both affect body weight in red squirrels (WAUTERS and DHONDT 1989a), and a minimum body weight is required to enter oestrus (WAUTERS and DHONDT 1989b), the effect of winter temperature and food abundance on  $k_1$  and of food abundance on  $k_5$  was tested. No significant relations were found however. The number of squirrels present at the start of the breeding season might also have an effect on the number of females entering oestrus. When density is high, intraspecific competition for food becomes more intense and many of the yearling females will decrease in weight and hence will not be able to enter oestrus. Normalised density at the onset of pre-oestrus (December or April) was positively correlated to  $k_1$  or  $k_5$  (r = 0.698; n = 12; P < 0.02).

Once a female is in oestrus and has mated she can still fail in raising young. Losses of young caused by breeding-failure ( $k_2$  and  $k_6$ ) added most strongly to total reproductive losses (K) and was positively correlated with it (r = 0.964; n = 6; P < 0.01), (fig. 5).

Year	n	Oestrus (%)		(%)	Total	Successful			Mean n°	Mean n°
		0×	1×	$2 \times$		$1 \times$	2×	Total	young or	young/m
Coniferous area										
1985	15	1	4	10	14(94)	1	6	13 (93)	2.00	1.73
1986	20	4	5	11	16 (80)	3	1	5 (31)	1.80	0.45
1987	17	0	5	12	17 (100)	6	3	12 (71)	1.75	1.24
Deciduous area										
1985	10	1	4	5	9 (90)	5	0	5(56)	1.80	0.90
1986	15	2	3	10	13 (87)	6	0	6 (46)	1.83	0.73
1987	17	1	5	11	16 (94)	8	2	12 (75)	2.17	1.53

Table 4. Annual reproduction in both habitats from 1985 to 1987

Adult females divided into three categories: not in oestrus  $(0\times)$ ; one breeding season in oestrus  $(1\times)$ ; both breeding seasons in oestrus  $(2\times)$ . Adult females = AF; successfully reproducing females = SF

Breeding-failure can have two reasons: 1. an oestrus female does not have a sufficiently high body weight to cope with the increasing energy-costs of pregnancy, and the embryos are lost; 2. an oestrus females gives birth to a litter, but is not able to raise her young due to a strong drop in body weight while lactating, or due to nest-disturbance or nest-predation (WAUTERS and DHONDT 1989b). Since food abundance affects body weight and a high body weight is necessary to reproduce successfully (WAUTERS and DHONDT 1989b), the size of the seed-crop might influence breedingsuccess. Moreover successful breeding was only observed in dominant (rank I) females in the coniferous woodland, while in the deciduous woodland also a few lower ranked females (rank II) succeeded in raising young when food was very abundant. Related to their dominance position these rank-I females inhabit



Fig. 5. The different k-values for reproduction as explained in Table 1, according to year and habitat

home ranges with intrasexual exclusive core-areas. Within these core-areas nests can be effectively defended, and interference from other squirrels minimalised (unpubl. data). When female density increases however, more subordinate females enter the population, and a lower proportion of females is able to establish a core-area than at low density. Hence the proportion of females successfully breeding is likely to fluctuate according to female-density. Therefore a multiple linear regression analysis of food abundance and female density at the onset of breeding on  $k_2$  and  $k_6$  was performed, for each habitat separately. In the coniferous area breeding-failure was strongly correlated with female density (partial r = 0.959; n = 6; P < 0.01), but not with food abundance (partial r =

-0.445; N.S.). In the deciduous habitat no relation was found.

Finally losses of young occur through mortality of sucklings between birth and weaning in litters of successfully breeding females  $(k_3 + k_7, fig. 5)$ . Since a female's body weight must be sufficiently high while lactating, and body weight depends on food-availability (WAUTERS and DHONDT 1989b), the size of the seed-crop is likely to influence suckling mortality. Food abundance the previous winter was negatively correlated to  $k_3 + k_7$  (r = -0.884; n = 6; P < 0.02). In addition the mean number of young weaned per successful female was higher following a winter with a large seed crop, than after a winter with a smaller seed-crop (r = 0.976; n = 6; P < 0.001).

#### Dispersal

Only a small proportion of squirrels that are born in a woodlot take up residence in the vicinity of their birth-place. Most juveniles disperse when about three months old (unpublished data). Adult squirrels, once they have established a home range, normally remain resident for the rest of their lives (Gur-NELL 1987; WAUTERS and DHONDT 1985). Hence dispersal does not take place the whole year round, but peaks in April-June and October-November, with some winter dispersal round January-February (fig. 6). A three-way analysis of variance was calculated to test the effects of area, sex and season on the number of immigrants. None of the three factors examined had a significant effect on the number of immigrants. The two-factor interaction between sex and season however was statistically significant (F = 29.81; d.f. = 1, 17; P < 0.001), while the others were not (2factor interactions: area and sex F = 2.217; d.f. = 1, 17; N.S.; area and season F = 0.55; d.f. = 1, 17; N.S.). This suggested that there were differences in immigration rate between males and fe- Fig. 7. The different k-values for dispersal as explained males according to the time of the year, in Table 1, according to year and habitat



Fig. 6. Autumn-winter (A-W) and spring (S) immigration for males (M) and females (F) in both habitats between 1984 and 1987. Immigrants that did not settle in the study-area , and recruited immigrants



that were similar for both habitats. We therefore calculated a one-way ANOVA testing the effect of season on the number of immigrants, for each sex separately. Both in males (F = 8.721; d.f. = 1, 10; P < 0.02) and in females (F = 21.788; d.f. = 1, 10; P = 0.001), the number of squirrels immigrating differed according to the time of the year (fig. 6).

The number of squirrels that immigrated into the study areas differed between years. Table 1 shows how immigration and emigration rate were analysed. Total annual immigration rate  $(k_0 + k_3)$  showed the same pattern in both habitats (fig. 7). Since winter temperature fluctuates similarly in both habitats, and differences in winter temperature cause differential winter-survival of juveniles and subadults (which will immigrate in late winter or in the following spring), and because spring reproduction varies between years (spring-born juveniles immigrate next autumn), the effect of winter temperature on immigration rate the following year was tested. A positive correlation (r = 0.931; n = 6; P < 0.01) suggested that more squirrels immigrate after a relatively warm winter than after a cold winter.

Since both increased density and lower food abundance are likely to increase intraspecific competition, which on its turn might affect dispersal, a multiple linear regression analysis of density (spring and autumn) and food abundance on emigration rate in springsummer ( $k_2$ ) and in autumn-winter ( $k_5$ ) was performed. Spring density was positively correlated with  $k_2$  (partial r = 0.888; n = 6; P < 0.02), and autumn density with  $k_5$  (partial r = 0.879; n = 6; P < 0.02). No correlations were found with food abundance. Thus emigration rate was higher at high density and decreased when squirrel numbers were low.

#### Discussion

#### Changes in numbers

Due to the fact that most squirrel studies have been relatively short-termed, evidence of density regulation, or the lack of it, is very scarce.

In our populations changes in density between years were not similar in both studyareas. Density fluctuations were positively correlated with food abundance and winter temperature, both factors explained together 96 % of the annual variation in density. Since these factors are density independent, they are not able to regulate red squirrel numbers. However the annual changes in density, from 1.01/ha to 1.41/ha, or 39 % in coniferous woodland, and from 0.84/ha to 1.16/ha, or 38% in deciduous woodland, were small compared with the annual changes in food abundance (65 % in the coniferous, up to 750 % in the deciduous area, table 2). Thus, density fluctuations appear to be dampened. When density of the previous year was added to the regression model, its partial correlation coefficient (r = -0.630) was statistically not significant and it did not explain any additional variation in population density. It must be mentioned however that in the coniferous habitat no extreme shortate or abundance of food has been observed over the four year study-period, while in the deciduous habitat, as mentioned above, density varied little, despite extreme changes in the seed-crop of deciduous trees. TONKIN (1983) found similarly small changes in red squirrel numbers (0.5 to 0.8/ha) accompagnied by stronger changes in the acorn and hazelnut-crop in a British deciduous woodland.

If red squirrel populations are regulated to some extent, it is important to know where during the annual population-cycle density-regulating factors act, and on which processes (survival, reproduction, dispersal).

#### Survival

Local survival was not related to density in our two populations. On the other hand mean monthly temperature in the winter-months (November–February) was strongly correlated with monthly survival. The effect of temperature on survival, especially during periods of

stressing weather conditions, has also been demonstrated for other squirrel-species. In fox (NIXON and MCCLAIN 1969) and pine squirrels (RUSCH and REEDER 1978) winter temperature was positively correlated with survival. In tassel-eared squirrels living in mountaneous areas with long periods of snow cover, the length of the period with a snow-depth of > 10 cm is strongly correlated with annual mortality (STEPHENSON and BROWN 1980; BROWN 1982). The size of the seed-crop positively influenced local survival in our study-areas. TONKIN (1983) also found a higher survival in a year following a good seed-crop and a poor survival when deciduous trees produced a small crop. Food abundance positively influenced survival also in pine squirrels (KEMP and KEITH 1970; RUSCH and REEDER 1978; HALVORSON and ENGEMAN 1983), tassel-eared squirrels (KEITH 1965) and grey squirrels (NIXON et al. 1975; GURNELL 1987).

Although differences in survival between males and females are observed in pine (RUSCH and REEDER 1978) as well as in red squirrels (LAMPIO 1967), we found no such differences in our study-areas. In pine squirrels males survived better than females, while in Scandinavian red squirrels the opposite was suggested based on sex-ratio data of shot animals. In both studies differential predation-pressure is used to explain these differences. The fact that important predators as marten, *Martes martes*, and goshawk, *Accipiter gentilis*, are absent in our study-areas, while others as fox, *Vulpes vulpes*, stoat, *Mustela erminea*, and buzzard, *Buteo buteo*, are rare, might be responsible for the equal survival-rates of both sexes, despite behavioural differences and differences in mobility (WAUTERS and DHONDT 1985, 1986). Year round survival of adult red squirrels (mean 61%) was higher than that of subadults (mean 27%). This is also the case in other squirrel-species, especially in winter (BARKALOW et al. 1970; KEMP and KEITH 1970; NIXON et al. 1975; THOMPSON 1978; STEPHENSON and BROWN 1980; HALVORSON and ENGEMAN 1983; TONKIN 1983).

#### Reproduction

Reproductive rate, expressed as the number of young weaned per adult female, was investigated using transformed data (table 1). A first k-value referring to losses of young caused by infertility of adult females (not entering oestrus) was density dependent. While most of the females entered oestrus at lower densities, fewer females were in a good condition (> 300 g, WAUTERS and DHONDT 1989b) when density was high.

A significant effect of female density on breeding success was found in the coniferous woodland. As discussed above this was related to the social organisation of the population (ranging behaviour and dominance position) which differed according to habitat type. Since the k-values ( $k_2$  and  $k_6$ ) referring to losses of young due to breeding-failure were large and strongly correlated with total K, female density has a strong effect on the rate of reproductive increase in the squirrel population. Hence density fluctuations caused by reproduction are at least dampened due to density dependent effects.

The number of young weaned varied according to food abundance, with more young produced per successful female after a year with a heavy seed-crop. In pine squirrels, where mean litter size varied from 2.8 to 4.7, the date of onset of breeding was significantly correlated with mean yearly litter size over four years (RUSCH and REEDER 1978). Onset of breeding on its term was influenced by the length of the period of snow-cover and by the size of the seed-crop.

#### Dispersal

In general the majority of dispersing squirrels are subadults and juveniles in search for an area to settle (MOSBY 1969; THOMPSON 1978). In our red squirrel populations the total number of dispersing squirrels was not related to food-supply, nor was it density dependent. In contrast the proportion of immigrants and juveniles that settled ranged from 35 % in the coniferous and 43 % in the deciduous woodland when squirrel numbers were

high, up to 50% and 64% respectively at low density, and was strongly density dependent. TONKIN (1983) found only 33 % to 38 % of immigrants becoming residents in her study-area. Similar data are found in grey and fox squirrels, where juveniles and subadults are thought to be sensitive to changes in density, due to their low position in the social hierarchy (NIXON et al. 1975). When densities are high mortality and dispersal increase in these low ranked individuals. THOMPSON (1978) stated that in grey squirrels the dispersal of surplus young animals, caused by intraspecific agonistic behaviour of residents during autumn (when seeds are harvested and cached), is a major factor in the determination of winter density. The results of his study agree with the general idea of pre-saturation dispersal (LIDICKER 1962). Also in territorial pine squirrels a similar mechanism is found. In autumn resident adults reaffirm their year-round territories in suitable habitat, while juveniles disperse and try to establish transient territories in less suitable (deciduous) habitat or become floaters with no territory (KEMP and KEITH 1970; RUSCH and REEDER 1978). Since they need a large midden of cached food (cones, nuts) to survive winter (SMITH 1968), only pine squirrels that established a territory in suitable habitat will have a high survival, while many dispersing young animals will die.

Furthermore sex-ratios of immigrants were male biased in late spring and female biased in autumn-winter in both our study-areas. We suggest that these differences in immigration-rate and timing between the sexes are related to seasonal changes in the intensity of intraspecific competition that are triggered by changes in the food-supply and in home range use. The situation presented here is typical for the coniferous habitat, but might be applied to the deciduous habitat also if some minor changes are made. From September onwards, throughout winter adult females do no longer defend their young, which have become independent, and concentrate their activity in small areas of their home range where seed abundance is high. Dispersing females now have the chance to immigrate into suitable habitat between the core-areas of the adult females' ranges. There however intraspecific competition with other immigrants and with juveniles is high, and many of them, as well as many juveniles, are forced to emigrate. Only the more dominant, with the highest body weight (WAUTERS and DHONDT 1989b) are able to establish permanent home ranges. From March onwards until September adult females become very aggressive towards other squirrels, especially other females, while defending nesting-sites and possibly also patches of good foop-supplies scattered throughout their home range. No further immigration is possible at this time. In males, which use their home ranges more homogeneously and which show stronger overlap of ranges, competition for food is more intense as long as tree seeds are available (July to April). Therefore only few immigrants will enter the population during this period. In May and June however squirrels feed on food-resources that are overabundant, but only for a short time (WAUTERS and DHONDT 1987), and two or three squirrels sharing the same oak searching for flowers and insects are not a rare sight. Moreover in May adult males are occupied in several mating-chases and hence do not have the time to interact with immigrating subadults. Therefore immigrationrate of males is highest in the May-June period, while in July, when the new cone-crop is harvested (WAUTERS and DHONDT 1987), some will be forced to emigrate and others will establish residency.

We conclude that although red squirrel numbers clearly fluctuate in relation to changes in food-supply and weather conditions, these fluctuations are dampened by density dependent processes. Both in reproduction (% of adult females entering oestrus and number of females successfully breeding) but especially in dispersal (recruitment rate of immigrants and juveniles) regulating processes are at work, triggered by the intensity of intraspecific competition, which increases at high density and decreases at low density. More data, however, over a longer time period, on the relationship between social behaviour, spatial organisation, food-supply and population processes are needed to confirm our conclusions about density regulation in red squirrel populations.

#### Acknowledgements

We thank Mr. STOELEN, Mr. ONZEA, Merodese Bossen, and Baron VAN HAVRE and the city of Antwerp, Peerdsbos, for permission to use their estates as study-areas; ERIK MATTHYSEN and NICO MICHIELS for their comments on earlier drafts of this manuscript. LUC WAUTERS was supported by a grant (nº 840068) from the Institute for the development of Scientific Research in Industry and Agriculture, I.W.O.N.L., at Brussels. The study was further supported by grant nº 2.0076.87 of the F.K.F.O. to André Dhondt.

#### Zusammenfassung

#### Populationsdynamik von Eichhörnchen (Sciurus vulgaris Linnaeus, 1758) in verschiedenen Habitaten

Von Oktober 1984 bis Januar 1988 untersuchten wir die Populationsdynamik von Eichhörnchen (Sciurus vulgaris) in einem Nadel- und einem Mischwald. Dazu wurden die Hörnchen regelmäßig lebend gefangen und individuell farbig markiert. Ihre Dichte schwankte im Jahreslauf und wurde vom Nahrungsangebot und der Winterkälte beeinflußt. Die jährliche Überlebensrate war positiv mit dem Nahrungsangebot korreliert und bei Adulten höher als bei Jungtieren. Der Anteil von Weibchen, die in Östrus kamen und von solchen, die Junge aufzogen, war dichteabhängig. Die Zahl der in einem Wurf aufgezogenen Jungen war ebenfalls positiv mit der verfügbaren Nahrungsmenge verknüpft. Männchen und Weibchen wanderten in unterschiedlichen Jahreszeiten zu, was mit Unterschieden im Sozialverhalten erklärt werden konnte. Die Emigrationsrate war in beiden Populationen bei höherer Dichte größer als bei geringerer. Die Dichte wurde also offenbar über die Fortpflanzungs- und die Abwanderungsrate gesteuert.

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Zeitschrift/Journal: <u>Mammalian Biology (früher Zeitschrift für</u> <u>Säugetierkunde)</u>

Jahr/Year: 1990

Band/Volume: 55

Autor(en)/Author(s): Dhondt André A., Wauters Luc

Artikel/Article: <u>Red squirrel (Sciurus vulgaris Linnaeus, 1758) population</u> <u>dynamics in different habitatsCÿ<sup>3</sup>Aÿ 161-175</u>