

Master of Science Thesis

**Competition for space as a mechanism for density- and
frequency-dependent selection on bank vole (*Myodes
glareolus*) females**

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LINDBLOM, H.: Tilakilpailu frekvenssistä ja tiheydestä riippuvan valinnan mekanismina metsämyyränaarailla (*Myodes glareolus*)

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TIIVISTELMÄ

Evoluutiobiologeja ovat pitkään askarruttaneet mekanismit, jotka ylläpitävät geneettistä vaihtelua yksilön kelpoisuuteen vaikuttavissa ominaisuuksissa. Yksi mahdollinen selitys on frekvenssistä ja tiheydestä riippuva valinta. Varsinkin negatiivinen frekvenssistä riippuva valinta voi lisätä harvinaisten ominaisuuksien osuutta populaatiossa. Tämän pro gradu -työn tarkoituksena on tutkia mahdollisia ekologisia- ja käyttäytymismekanismeja, jotka selvittäisivät tiheydestä ja frekvenssistä riippuvan valinnan merkitystä metsämyyränaaraiden (*Myodes glareolus*) lisääntymismenestyksessä. Metsämyyränaaraat ovat lisääntymisaikanaan territoriaalisia, mutta niillä on toistensa kanssa osittain päällekkäiset liikkuma-alat. Oma territorio on edellytys naaraiden lisääntymiselle ja siksi territoriaalisuutta voidaan pitää osana lisääntymispanostusta. Naarailla tavataan kahta lisääntymistaktiikkaa: alhaisen lisääntymispanostuksen naaraat tuottavat pieniä poikueita, joissa poikasen koko on suuri, kun taas korkean lisääntymispanostuksen naaraat tuottavat suurempia poikueita, joissa poikasten koko on pieni. Eri lisääntymistaktiikoiden lisääntymismenestystä tutkittiin kokeessa, missä manipuloimme kahta eri tekijää: taktiikoiden osuutta populaatiossa sekä populaatiotiheyttä. Metsämyyränaaraat jaettiin 13 ulkotarhaan (á 0.2 ha) joko alhaiseen (4 naarasta / tarha) tai korkeaan tiheyteen (8 naarasta / tarha) siten, että lisääntymistaktiikat olivat populaatiossa vuorollaan joko harvinaisia tai yleisiä. Tilankäyttöä tutkittiin kaksi viikkoa kestävässä pyyntijaksossa, jolloin naaraat imettivät ja odottivat seuraavaa poikuetta. Tulosten mukaan alhaisen lisääntymispanostuksen naaraat menestyivät paremmin matalissa tiheyksissä (vain tiheydestä riippuvaa valintaa). Sen sijaan korkean lisääntymispanostuksen naaraat menestyivät parhaiten korkeissa tiheyksissä edustaessaan harvinaista lisääntymistaktiikkaa (sekä negatiivista frekvenssistä riippuvaa valintaa että tiheydestä riippuvaa valintaa). Tulokset viittaavat lisäksi siihen, että tiheydestä riippuva valinta alhaisen lisääntymispanostuksen naarailla saattaa selittyä niiden tilankäytöllä. Sen sijaan suuren lisääntymispanostuksen naarailla negatiivinen frekvenssistä riippuva lisääntymismenestys ei ollut yhteydessä niiden menestykseen tilakilpailussa.

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ABSTRACT

Evolutionary biologists have long been troubled by the mechanisms that cause genetic variation in fitness related traits. One possible explanation is found in frequency- and density-dependent selection. Especially negative frequency-dependent selection can increase the amount of rare phenotypes in the population. The aim of this thesis is to explore possible ecological and behavioural mechanism, which could explain density- and frequency-dependent selection on the reproductive success of bank vole (*Myodes glareolus*) females. During their breeding season bank vole females are strictly territorial but they have partly overlapping home-ranges. Territory is a prerequisite for breeding and thus it can be considered as a part of reproductive effort. Bank vole females have two genetically determined reproduction effort (RE) tactics: low RE type produces small litters with large offspring and high RE type large litters with small offspring. Breeding success of different reproductive tactics was investigated in an experiment, where we manipulated two separate factors: frequencies of different reproductive tactics in the population and the population density. Females were divided into 13 outdoor enclosures (sized 0.2 ha), either to low density (4 females / enclosure) or high density (8 females / enclosure) so that each of the two reproductive tactics were one at the time either rare or common in the population. Spacing behaviour was monitored during a two week long trapping period, when females were lactating and gravid. According to the results, low RE females had higher breeding success in low densities (only density-dependent selection), but high RE females succeeded best while in high density as rare breeding tactic (both negative frequency-dependent and density-dependent selection). Furthermore, present results indicate that density-dependent selection among low RE females might be explained by their spacing behaviour. Instead, the negative frequency-dependent breeding success among high RE females was not connected with their success in the space competition.

Contents

1. INTRODUCTION	5
1.1. Frequency- and density-dependent selection	5
1.2. Life-history tactics	6
1.3. Spacing behaviour of bank vole females	6
2. METHODS	6
2.1. Study species	6
2.2. Study procedures	7
2.3. Experimental design	8
2.4. Spacing behavior	8
3. RESULTS	9
4. DISCUSSION	10
ACKNOWLEDGMENTS	16
LITERATURE	17

1. INTRODUCTION

Evolutionary studies have traditionally focused on the question of what maintains phenotypic and genetic variation in populations (Price & Schluter 1991, Roff 2002). According to Fisher's (1930) fundamental theorem, variation in natural populations should decrease as a result of selection. Yet many fitness related traits contain considerable amounts of genetic variation (Mappes & Koskela 2004, Sinervo et al. 2000). One possible explanation is offered by negative frequency- and density-dependent selection (Sinervo et al. 1996).

Negative frequency-dependent selection can favour rare genotypes and thus promote genetic variation. Negative frequency-dependent selection is central also e.g. in rare-type mating advantage (Gross 1985, Sinervo & Lively 1996), parasite-host coevolution (Dybdahl & Lively 1998), polymorphism (e.g. Roff 1998) and speciation (Doebeli & Dieckmann 2000). Density-dependent selection seems to promote cyclic changes in frequencies of genotypes (Sinervo & Lively 1996, Sinervo et al. 2000). Only few studies have handled negative frequency- and density-dependent selection together (lizards: Sinervo et al. 2000, Comendant et al. 2003, bank voles: Savolainen 2004, Mappes et al. 2008), and even fewer have examined spacing behaviour as a mechanism of these selection types.

The study species in this Master's thesis is the bank vole (*Myodes glareolus*). In addition to using over-lapping home-ranges, each bank vole female competes for exclusive breeding territory which is a prerequisite for breeding (Bujalska 1985). Spacing behaviour of vole females is known to be affected by female's reproductive cycle (Koskela et al. 1997), population density (Koskela et al. 1999, Mappes et al. 2008), food availability (Koskela et al. 1998), predation risk (*Microtus agrestis* and *M. rossiaemeridionalis* Norrdahl & Korpimäki 1998) and relatedness (Sera & Gaines 1994: *Microtus ochrogaster*; Lambin & Krebs 1993: *Microtus townsendii*). Overtaking and maintaining an own territory is energetically costly (Gosling et al. 2000: *Mus musculus*) and thus breeding vole females are forced to allocate energy between nursing and defending territory.

1.1. Frequency- and density-dependent selection

Frequency-dependent selection occurs when fitness of a strategy depends on the relative amount of representatives of other strategies in population and it was first described by Fisher (1930). In positive frequency-dependence, fitness of an individual increases when the relative amount of individuals representing the same strategy in the population increases. The opposite takes place in negative frequency-dependence; individual's fitness is enhanced when it represents a rare strategy. Such examples have been reported in natural populations e.g. in male guppies (*Poecilia reticulata*) (Olendorf et al. 2006) and side-blotched lizards (*Uta stansburiana*) (Sinervo & Lively 1996). Negative frequency-dependent selection is one of the strongest candidates for the mechanism behind existence of genetic polymorphism.

Intensity of density-dependent selection varies with the population fluctuation, so that when the population size is highest also the density-dependent selection is strongest. It can lead to chaos dynamics, where population size varies frequently and sharply because it increases the number of individuals. These kinds of chaos dynamics are typical to North-European bank vole populations (Hansson & Henttonen 1985). Negative density-

dependence may also stabilise the population size by increasing the mortality and decreasing the number of born individuals.

1.2. Life-history tactics

Female bank voles represent two different kind of breeding tactics. High reproduction effort (RE) females produce big litters with small offspring, and low RE females small litters with large offspring. RE type is genetically determined (Mappes & Koskela 2004). Size at birth seems to predict the age of maturation and size of the first litter (Mappes & Koskela 2004) and thus the life-time breeding success of females (Prevot-Julliard et al. 1999). Nevertheless, producing large offspring is costly to the mother, and the size of a pup is a trade-off between the quality and number of offspring. Allocating larger amount of energy to reproduction reduces the amount of energy left for mother's own growth and survival.

1.3. Spacing behaviour of bank vole females

Female bank voles are strongly territorial during their breeding season, and an own territory is a prerequisite for breeding (Bujalska 1985). Territory is an exclusive breeding area within a larger home range and it is vigorously defended against other adults. Size of the territory has been shown to be connected with the reproductive success among stranger females (Mappes et al. 1995). Defensive aggression and scent marking are at highest during lactation period when new born pups are most vulnerable (Rozenfeld & Denoël 1993, Koskela et al. 1997, Koskela et al. 2000). Koskela et al. (1997) showed that female's home range size decreased according to their reproductive state. Home range sizes were largest during non-pregnancy and grew smaller towards parturition and lactation period. However, during lactation territory size is at its largest. Jonsson et al. (2002) conducted an experiment that showed the sensitivity of home-range size to available food resources. Same study showed that territory size was not affected by food resources. These results indicate that home range is used for foraging food and territory is an exclusive breeding area which females defend in order to deter infanticide. Occupancy of a territory can be considered to be part of reproductive effort.

The origin of territoriality in *Myodes* (rodents formerly known as *Clethrionomys*) has been a source for diverse discussion during the past decades (e.g. Bujalska 1991, Ostfeld 1990, Ims 1987, Wolff 1993). According to the food defence theory, female bank voles adjust their space use in relation to available food resources (Ostfeld 1985, Ostfeld 1990, Ims 1987). Pup-defence theory contradicts the food-defence theory and explains female territoriality as a response to infanticide, which is a mechanism of nest/territory competition (Wolff 1993, Wolff & Peterson 1998, in *Microtus pennsylvanicus* Fortier & Tamarin 1998).

In this masters' thesis the main hypothesis is that spacing behaviour works as a mechanism mediating different kind of selection types. Spacing behaviour of lactating female bank voles was monitored in large outdoor enclosures, where the density of population and frequency of different breeding tactics were manipulated.

2. METHODS

2.1. Study species

The study species, bank vole (*Myodes glareolus*) is a small rodent species common in Northern Europe (Stenseth 1985). The main habitats are forests and fields and the diet

consists of forbs, shoots, seeds, berries and fungi (Hansson 1985). Females produce 2-10 offspring (usually 4-8) in a litter during breeding season which lasts from March to September in Central Finland. During one season female can give birth to 4 litters (Koivula et al. 2003). Pregnancy lasts for 19-20 days and pups are weaned at the age of three weeks (Mappes et al. 1995). The density of breeding females is limited through their territoriality (Bujalska 1985) and in high densities the maturation of young females is suppressed by social interaction among females (Kruczek & Marchlewska-Koj 1986). The patterns and amplitude of density variation show considerable geographical variability, and both stable and cyclic populations are found (Hansson & Henttonen 1985). Bank vole is the most common mammal in Finland and it has been used extensively in research because it breeds easily in captivity, is not sensitive for handling and its trappability is good.

2.2. Study procedures

Experimental animals originated from artificial selection lines at the University of Jyväskylä. Founder animals for the selection lines were caught in Central Finland (62°37'N, 26°20'E).

In the truncation selection experiment, two lines were selected according to litter size of females (for details see Schroderus et al. 2008). The selection experiment was based on between family selection procedure (Falconer & Mackay 1996), which prevents the possibility of inbreeding. Animals were kept in standard mouse cages (43 x 26 x 15 cm) where food pellets and water were continuously available. Wood shavings and hay were used as bedding. The animals were maintained on 16 L : 8 D photoperiod.

The study started by mating a fraction of the females ($n = 91$) obtained from the selection experiment with randomly chosen males of the same line. The difference between the two groups was further increased by choosing only the females with lowest RE ($n = 39$) and highest RE ($n = 33$) for the present experiment (see the formula for RE below). All females were of the same age and in a similar reproductive state. Characteristics of these mothers and their offspring and statistical tests are presented in the Table 1.

Table 1. Characteristics (mean \pm SE) of two female tactics (low or high reproductive effort, RE). Random assignment to the different manipulation groups (frequency and density) is tested by three-way ANOVA. All possible two and three-way interactions were non-significant ($P > 0.11$). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

	Low RE ($n = 39$)	High RE ($n = 33$)	Source of variance ($F_{1,64}$)		
			RE tactic	Frequency	Density
Reproductive effort	0.61 \pm 0.02	0.88 \pm 0.02	59.56 ***	0.11 ^{ns}	1.91 ^{ns}
Litter size	3.82 \pm 0.14	6.15 \pm 0.18	76.36 ***	0.10 ^{ns}	3.52 ^{ns}
Mean body mass of offspring (g)	1.97 \pm 0.03	1.84 \pm 0.02	10.60 **	0.02 ^{ns}	2.07 ^{ns}
Mean head width of offspring (mm)	8.28 \pm 0.05	8.09 \pm 0.04	6.81 *	0.00 ^{ns}	0.07 ^{ns}
Post-partum body mass of mother (g)	22.4 \pm 0.4	24.6 \pm 0.4	6.87 *	0.01 ^{ns}	0.27 ^{ns}
Post-partum head width of mother (g)	13.8 \pm 0.07	13.8 \pm 0.06	0.07 ^{ns}	1.34 ^{ns}	0.10 ^{ns}

Females were paired with a randomly chosen male representing the same breeding tactic as female by keeping them in the same cage for a week after which they were separated. As the time of parturition approached, the cages with pregnant females were inspected twice a

day to determine the time of parturition and to enable post-partum mating. As soon as a litter was discovered, mothers were removed for measuring and then transferred to a smaller mating cage with a new male representing the same breeding tactic as the female. Pairs were monitored to make sure that copulation took place, and after that females were returned to their litter. All the new-born pups were weighted with electronic scales (to closest mg) and measured for their head width under a stereo microscope. The head width of mothers after parturition was measured with digital calliper to closest mm and body mass with electronic scales also to closest mg. Reproductive effort of mothers was determined by using the formula described by Millar (1977) and by Ebenhard (1990). $RE = L \times M / M_m$, where L is the litter size, M the weight of offspring at the time of birth and M_m the weight of mother after giving birth.

2.3. Experimental design

The 72 females gave birth in the laboratory in early July, and after that the females with their new-born individually marked pups were released to 13 large outdoor enclosures (each 0.2 ha). Each enclosure is surrounded by galvanised metal sheet app. 1 m high and buried 0.5 m deep into the ground in order to prevent study animals from escaping. The fences did not protect voles effectively from predators, such as red fox (*Vulpes vulpes*) and birds of prey. Each enclosure had a set of 20 Ugglan multiple-capture live traps, distributed in a 4 x 5 array with 10 meters between them. Traps were placed inside protective aluminium chimneys and baited with sunflower seeds, wheat and potatoes. Otherwise voles were dependant on naturally occurring food resources.

None of the mothers abandoned their pups during the releasing process. Four males were introduced to each enclosure to keep females in reproductive condition. These males might mate with the females, but we were not able to measure the success of the possible subsequent breeding events.

In the enclosures, both the densities (4 or 8 females / 0.2 ha) and frequencies (1:3 [4 enclosures]; 3:1 [4], 2:6 [2], 6:2 [3]) of different reproductive tactics (low or high RE) were manipulated (see the design in Table 2). The choice of 4 and 8 females per enclosure to low and high experimental densities respectively, was based on our earlier studies showing that 4-6 females can gain a territory and breed simultaneously in the same enclosure (Oksanen et al. 2003).

Table 2. The design of the experiment. Number of females per enclosure, number of enclosures (in parenthesis) and total number of females in each treatment.

	Low density	Low density total	High density	High density total	Overall total
Rare low RE + Common high RE	1 + 3 (4)	4 + 12	2 + 6 (2)	4 + 12	
Rare high RE + Common low RE	1 + 3 (4)	4 + 12	2 + 6 (3)	6 + 18	
Total (low Re + high RE)		16 + 16 = 32		22 + 18 = 40	32 + 40 = 72

2.4. Spacing behavior

Spacing behaviour was monitored during a two-week long trapping period in July: when spacing behaviour monitoring period started, the pups were about one week old. During this time, when females were nursing their pups, each enclosure was trapped 11-16 times. In the beginning of the trapping period all the traps were checked three times a day: in the

mornings, afternoons, and late evenings. Later on, due to unusually hot weather, the amount of trappings was reduced to mornings and late evenings only, which caused the variation in trapping times. After each capture females were released back to enclosure immediately after they had been identified and trap location recorded.

The size of a home range was determined by using minimum convex polygon method (Koskela et al. 1997). The activity centre was calculated as the arithmetic mean point of each individual's capture coordinates (Hayne 1949). Nearest neighbour distance was calculated from distances between the activity centres of neighbouring females. The size of territory was estimated to be the difference between home range area and the home range overlap. Trappability was calculated by dividing number of time the individual was caught by number of trappings. Mean trappability for all test animals was 82%, and it was not affected by RE type ($p = .264$), frequency ($p = .472$) nor density ($p = .567$). Relative fitness was defined as a number of weanlings / mean number of weanlings in the population. Proportion of weaned offspring was defined as the number of weanlings of a single female in relation to all offspring of the same generation.

3. RESULTS

Breeding success of bank vole females was measured by using three different variables: 1) the number of weaned offspring, 2) proportion of weaned offspring and 3) relative fitness of females. These variables were dependent on effort type, frequency and density (three-way interactions: $F_{1,64} = 7.16$, $p = .009$; $F_{1,64} = 7.82$, $p = .007$; $F_{1,64} = 7.16$, $p = .009$, respectively). When different RE types were analysed separately, results showed that low RE type females were most successful in their reproduction when they were in low densities (Figure 1a). Whether they represented rare or common breeding tactic did not have a significant difference. However, high RE females were most successful when they were rare breeding tactic in high densities (Figure 1b, Table 3).

Indicators of the spacing behaviour were the size of territory, home-range, overlapping areas of home-ranges of adjacent females and nearest neighbour distance. Density was the most important factor explaining the sizes of territories ($F_{1,54} = 30.38$, $p = .000$) and home ranges ($F_{1,54} = 10.44$, $p = .002$). In high density enclosures voles had smaller home ranges and territories than in low density enclosures (Figures 2a,b). RE line or frequency of different tactics did not explain home-range, territory sizes and over-lap area nor the distance to the nearest neighbour (see table 4).

As low RE type was more sensitive to density-dependent selection, and high RE type responded to both the frequency- and density-dependent selection, the RE types were further analysed separately. In these analyses it was particularly studied whether different selection mechanisms were related to the spacing behaviour in different RE types (Table 5). In enclosure of high population density, low RE females weaned more pups when their distance from nearest neighbour increased, but in low densities the number of weaned offspring did not correlate significantly with the distance to nearest neighbour (Figure 3a). Results from number of weaned offspring in relation to territory size were similar; low RE type weaned more offspring in high density when their territory size grew bigger, but such effect was not observed in low density (Figure 4a). Size of the home range or over-lapping area did not explain the number of weaned offspring and these spacing traits did not significantly interact with the different selection mechanisms (Table 5).

4. DISCUSSION

Results here show that different breeding tactics are prone to different types of selection: low RE females to density-dependent and high RE females to frequency-dependent selection (see results also by Savolainen 2004, Mappes et al. 2008). Savolainen (2004) and Mappes et al. (2008) suggested that this could result from low RE females being poorer defenders of their territory, and this could be due to their lighter weight: they were approximately 2 g (8-9 % of total weight) lighter compared to the high RE females. This explanation contradicts slightly with Koskela et al. (2000) results. In their experiment it was found that female body weight did not correlate with the defence activity, but the litter size did correlate positively with defence activity. This is supported by our results for low RE females. The proportion of weaned offspring of low RE females was dependable on density (see Table 3). And high population density was the most important explainer for territory sizes; with an increasing density the sizes of territories were smaller (Figure 2b). Figures 3 and 4 show how low RE females' breeding success improved if they could keep large territory exclusively to themselves. This phenomenon was only found in high densities where competition between females is harsher. In low density the territory size did not affect the weaning success of low RE females (Figure 4a).

Besides the size of territory, density was the single factor explaining home range and nearest neighbour distance for both breeding tactics. Among high RE females, breeding success was not related with any measurements of spacing behaviour (Table 5). And so, for example the negative frequency-dependence could not be explained by the more efficient occupation of territories among high RE females. Still they were the most successful breeding strategy when most of other females in the population were low RE females, and population density was high. It is hard to imagine what it is in these conditions that favours high RE females. Low RE females proved to be successful defenders of their territory also in high density, so the success of high RE females cannot be explained by their more effective defence. They are also allocating larger deal of their energy to breeding, so they could not afford very energy consuming defence strategy.

Results of this thesis are not in accordance with similar research conducted previously by Sinervo et al. (2000). They acquired clear results supporting r- and K-selection, of frequency- and density-dependent selection for females representing different breeding tactics in the population of side-blotched lizard (*Uta stansburiana*). Females producing large, high quality offspring had better breeding success when they were in high population density and females producing small offspring succeeded in low densities. Differences in our results could be explained by different external factors. Bank voles are exposed to severe seasonal changes, which result in a yearly population crashes. In addition to yearly fluctuations caused by seasonality, bank vole populations fluctuate with a frequency of 3-5 years. In Central Finland population densities fluctuate between 1 or 2 individuals per hectare to as many as 100 individuals per hectare (Hansson & Henttonen 1985). Population fluctuations of this magnitude create very different selection pressures with time.

Results of this study could be interpreted so that low RE females reserve their resources to survival and high quality offspring. Thus they would be most likely to survive the seasonal decline in population density created by winter and be first to breed when the breeding season begins in the spring. Their proportion in the population would stay relatively high for a while, before the high RE females offspring increase in number. At this point, when population density is rather low, there is no severe intraspecific

competition and even the “lower quality” pups would do fine. As high RE tactic produces more efficiently, their proportion of the population would increase toward the end of the breeding season and this will increase competition for available resources. However, high RE females would be beaten by the higher quality individuals of low RE strategy in the winter survival. Similar change in population structure would take place in vole cycles occurring every 3-5 years.

These thoughts are mere speculations and there is no empirical data showing that this kind of cycles in breeding strategies would occur in natural populations of bank voles. It would be very interesting to define breeding strategies of captured wild females at different phases of yearly population fluctuation and on different phases of vole cycles. Another issue that requires an explanation is how high RE females managed to achieve their best reproductive success when they were the rare breeding strategy in high population density. Negative frequency dependence seems to be in action, but the mechanism was not found in spacing behaviour.

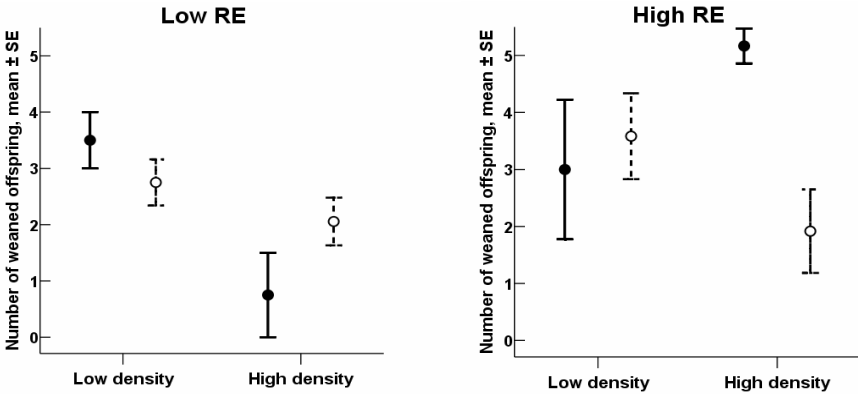


Figure 1. Number of weaned offspring in different densities for a) low RE and b) high RE types. Closed circles and solid lines are rare; open circles and dashed lines common type.

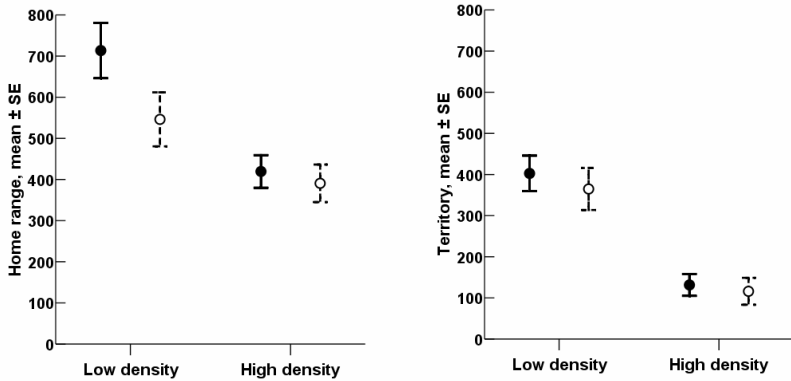


Figure 2. a) Size of home ranges and b) territories (m²) in low and high densities for different RE tactics. Closed circles and solid lines low RE; open circles and dashed lines high RE tactics.

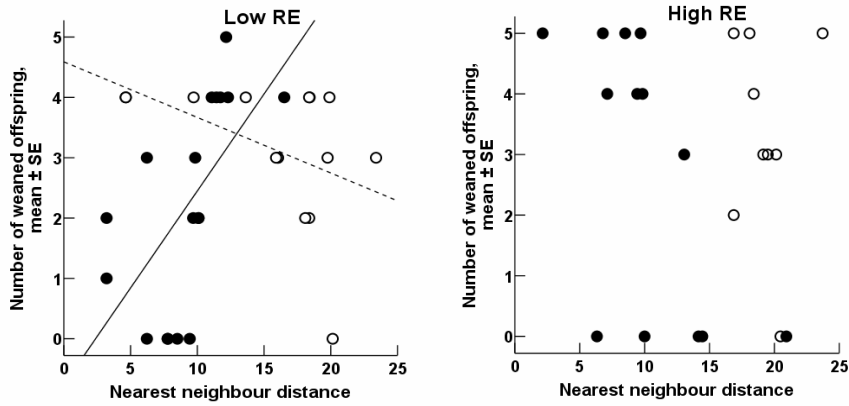


Figure 3. Number of weaned offspring in relation to nearest neighbour distance (m) in different densities for a) low RE and b) high RE females. Closed circles and solid lines high density; open circles and dashed lines low density. Lines shown in the picture a) are from regression analysis.

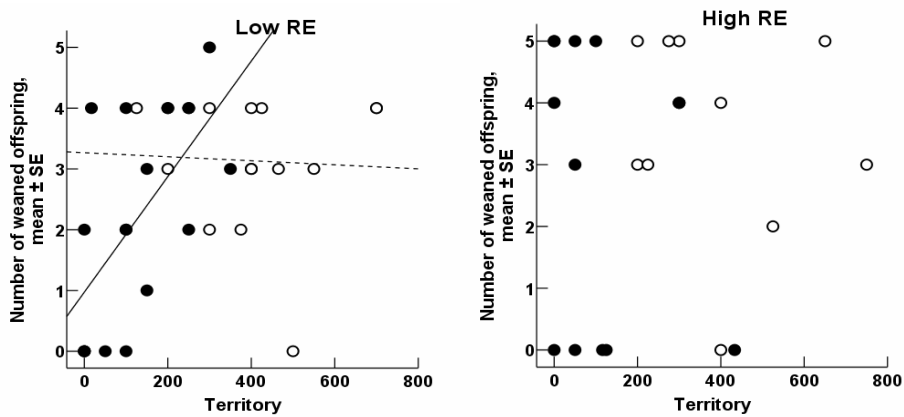


Figure 4. Number of weaned offspring in relation to territory size (m^2) shown separately for a) low RE and b) high RE females. Closed circles and solid lines high density; open circles and dashed lines low density. Lines shown in the picture a) are from regression analysis.

Table 3. Effects of frequency and density on breeding success; measured as number of weanlings, proportion of weaned offspring and relative fitness of females. The effect of enclosure was included in the model as a random factor.

Low RE line	Number of weaned offspring				Proportion of weaned offspring				Relative fitness of females			
Source	df	MS	F	p	df	MS	F	p	df	MS	F	p
Frequency	1	.48	.19	.667	1	.00	.01	.935	1	.07	.19	.667
Density	1	18.57	7.26	.011	1	4.20	11.04	.002	1	2.51	7.26	.011
F *D	1	6.61	2.59	.117	1	.809	2.13	.154	1	.89	2.59	.117
Error	34	2.56			34	.38			34	.35		

High RE line	Number of weaned offspring				Proportion of weaned offspring				Relative fitness of females			
Source	df	MS	F	p	df	MS	F	p	df	MS	F	p
Frequency	1	12.19	2.19	.149	1	1.30	4.35	.046	1	1.65	2.19	.149
Density	1	.43	.08	.783	1	.00	.01	.930	1	.06	.08	.783
F *D	1	25.19	4.53	.042	1	2.04	6.79	.014	1	3.41	4.53	.042
Error	30	5.56			30	.30			30	.75		

Table 4. Effects of breeding line, frequency and density and their interaction on spacing behaviour. The effect of enclosure was included in the model as a random factor.

	Home Range				Territory				Over-lap				Nearest neighbour distance			
	df	MS	F	p	df	MS	F	p	df	MS	F	p	df	MS	F	p
Line	1	118065.56	2.48	.122	1	2562.40	.11	.742	1	85841.14	2.16	.147	1	.17	.87	.355
Frequency	1	1002.60	.02	.885	1	6100.03	.26	.611	1	2156.56	.05	.817	1	.02	.11	.745
Density	1	498287.27	10.44	.002	1	709541.23	30.38	.000	1	18618.07	.47	.496	1	5.75	28.66	.000
L * F	1	7083.40	.15	.702	1	1403.10	.06	.807	1	14791.64	.37	.544	1	.13	.66	.420
L * D	1	32187.58	.68	.415	1	898.52	.04	.845	1	22330.43	.56	.456	1	.10	.50	.485
F * D	1	1426.30	.03	.863	1	1561.90	.07	.797	1	3.08	.00	.993	1	.01	.03	.865
L * F * D	1	8808.77	.19	.669	1	1860.84	.08	.779	1	2572.28	.07	.800	1	.00	.00	.966
Error	54	47708.46			54	23358.36			54	39670.16			54	.20		

Table 5. Effects of frequency, density and spacing behaviour (territory size, home range overlap size, home range size and nearest neighbour distance) on breeding success of different breeding tactics. The effect of enclosure was included in the models as a random factor.

Number of weaned offspring								
Low RE					High RE			
Source	df	MS	F	p	df	MS	F	p
Frequency	1	.59	.33	.574	1	6.20	1.22	.280
Density	1	9.41	5.17	.031	1	2.28	.45	.509
Territory	1	10.90	5.99	.021	1	2.79	.55	.465
F * D	1	.01	.01	.942	1	4.90	.97	.336
F * T	1	.82	.45	.508	1	.89	.18	.679
D * T	1	13.14	7.22	.012	1	.04	.01	.933
Error	26	1.82			22	5.05		
Frequency	1	1.13	.50	.487	1	16.73	3.83	.063
Density	1	.16	.07	.794	1	.45	.13	.751
Overlap	1	.53	.24	.632	1	1.66	.38	.544
F * D	1	1.31	.57	.455	1	20.43	4.68	.042
F * O	1	1.48	.65	.427	1	7.56	1.73	.202
D * O	1	3.97	1.75	.198	1	.11	.03	.876
Error	26	2.27			22	4.37		
Frequency	1	1.08	.43	.519	1	19.77	4.36	.049
Density	1	2.33	.92	.347	1	.24	.05	.822
Homerange90	1	.21	.08	.778	1	.38	.08	.775
F * D	1	.64	.25	.620	1	3.59	.79	.383
F * HR90	1	.98	.39	.540	1	11.97	2.64	.118
D * HR90	1	.15	.06	.807	1	.89	.20	.662
Error	26	2.53			22	4.54		
Frequency	1	.32	.19	.666	1	.33	.08	.785
Density	1	25.81	15.43	.001	1	.06	.01	.906
Dismin	1	3.84	2.30	.142	1	4.96	1.15	.296
F * D	1	.68	.40	.531	1	2.33	.54	.471
F * Dismin	1	.24	.14	.709	1	.02	.01	.944
D * Dismin	1	22.51	13.46	.001	1	3.39	.78	.386
Error	26	1.67			22	4.33		

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