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UNIVERSITY OF JYVÄSKYLÄ

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Für meine Eltern,
die mir Neugierde, Freude, Mut und Sisu mitgegeben haben.

Die Neugierde solch eine Arbeit zu beginnen,
die Freude daran mit Tieren, Zahlen und Wörtern zu arbeiten,
den Mut dafür ans heisse oder kalte Ende der Welt zu fahren,
und genug Sisu, bis zu diesem Büchlein durchzuhalten.

ABSTRACT

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Diss.

Populations of small mammals can fluctuate in size responding to social and environmental variation, such as density-dependence, density of competitors, predation, seasonality, and/or food availability. Little is known about how the variation of population size can be mediated through individual behaviour, and how changes in individual life history, in turn, can respond to population size. In this thesis, life history variables of bank vole females (*Clethrionomys glareolus*, an arvicoline rodent) were investigated in experiments manipulating density of competitors and con-specifics in large outdoor enclosures. Voles were bred in the laboratory and released in experimental populations of known age structure and reproductive history in order to study life history traits at different ages. In four experiments, half of the enclosures were manipulated by adding voles of a competitor species, the field vole *Microtus agrestis* and the other half served as controls. In one experiment enclosures were manipulated by food addition. In all experiments, density of con-specifics was closely monitored, and seasonal change in the environment was used as a co-variate when interpreting the results.

Presence of field vole competitors decreased predominantly the survival of bank vole females, whereas the breeding rate or the maturation of young females was not altered. Different cohorts of females were differently affected, with year born breeding females more susceptible to the effects of field vole competition than over-wintered breeding females. No survival decrease was found in young, immature females and in adults over the non-breeding season. Based on these results, it may be an advantageous strategy for year born females, when field vole competitors are abundant, to delay maturation, because once matured, her future survival chances could be decreased. High density of con-specifics decreased the reproduction of individuals by delaying maturation in spring or by decreasing the rate of breeders in summer. Survival was not affected by con-specifics. The results suggest that population interaction with a different vole species influences not the same life history traits than density-dependence of con-specifics does, and thus may alter the dynamics of population size fluctuations in different ways.

Key words: *Clethrionomys glareolus*; density-dependence; fitness constraints; interspecific competition; life history; maturation; reproduction; seasonality; supplemental feeding; survival.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals. I have personally performed most of the work in paper I, II, III and V. For paper IV, I performed the data analysis and the writing of the article plus large parts of the field work.

I   Eccard, J. A. and Ylönen, H. 2001. Initiation of breeding after winter in bank voles: effects of food and population density. Canadian Journal of Zoology 79: 1743-1753.

II   Eccard, J. A. and Ylönen, H. 2002. Direct interference or indirect exploitation? Experimental evidence of fitness costs of interspecific competition in voles. Manuscript (submitted).

III   Eccard, J. A. and Ylönen, H. 2002. Who carries the costs of interspecific competition in an age structured bank vole population? Manuscript (submitted).

IV   Eccard, J. A., Klemme, I., Horne, T., and Ylönen, H. 2002. Effects of competition and season on the maturation of young bank vole females. Evolutionary Ecology, in press.

V   Eccard, J. A. and Ylönen, H. 2002. Interspecific competition in small mammals: Performance of the subordinate species along a gradient of competitor densities. Manuscript.

PREFACE

When listening to me explaining plans for this thesis, my mother asked the haunting question "und wer will das wissen?" I did not have a great answer then. I have finished my doctoral thesis and I still wonder. Maybe the handful of small mammal scientists wants to know? Or the Academy who pays us? Maybe only me and my supervisor. Luckily I have come across a number of people in conferences, that seemed to be terribly interested. There is a legion of scientists out there in the web or in the real world that thinks that vole science is really important work. And I met a few other motivated enthusiasts when doing fieldwork. Is that motivation enough? There is of course my own motivation, **I** want to know, and I enjoy the process of finding out. It includes touching warm little animals, includes being outside more than ever in my city dwellers life, enjoying the splendid wonders of endless summer daylight and winter northern lights, or the pallid desert sky, the cold night air, and the eternity of stars in the South. It includes being creative, developing and trying to find a feasible solution for an experiment, communicating with colleagues and students, it includes mediation of ideas and findings in graphics, posters, and texts. All my creative energy over the last years has gone into science, and suddenly I am led to believe, its must be some kind of creative art. Who needs art?

I want to thank my supervisor Hannu Ylönen for all the support, the freedom he gave me during this thesis, both in the choice of topics within the thesis but also in my involvement in other research sidelines. I enjoyed our cooperation throughout this thesis, especially those last few months of close contact, intense writing; frequent exchange and co-workership have been very communicative, productive and pleasant. There may be a trade off between close guidance and freedom and I would again choose the latter if I had to choose a second time. Thank you Hannu!

I want to thank my dearest Thomas Müller for his loving care and support over the years. I have been very lucky that you dared to come with me to this end of the world, and without you I would have never went that far for such a long time. Thank you for your interest in my work and my writings, for your constructive critics and the discussions and also the practical help. Soon we will both start the probably most exciting project of our lives, lets rather call it a mission, and I am proud and happy that you are with me!

My thanks also to my department of Evolutionary Ecology, to its leaders Jonna Mappes, Veijo Kaitala, and Rauno Alatalo. The Evolutionary Ecology Graduate School of our department, Turku and Oulu University has been a place of inspiration for me, and so were Research Seminars and Round Tables in the institute. A big thank you also to Taina Horne, who has contributed a lot to my writing during the last year. Your help has been very tough on me in the beginning, but it has always meant improvement and learning for me. Thanks to Leena Lindström, Anna Dubiec and Emily Knott who have helped me improving the thesis itself, and to Hans-Ulrich Peter und Günther Köhler for overcoming meine Wortlosigkeit in the German summary (Chapter 6). Thanks and greetings to all my college graduate students and our staff for sharing the

1   INTRODUCTION

Life history of individuals is determined by evolutionary factors such as the phylogenetic history of the species, the environment in which it evolved, and also by the reaction to the current environmental condition. Both the genotype and the phenotype of an individual contribute to its fitness. Individuals vary in their phenotypic condition, thus vary in fitness and allow for natural selection (Darwin 1859) to take place between them. Principal life history traits are bound together by numerous trade-offs, such as those between the current reproduction and survival, between current and future reproduction, or between the number and size of offspring (Stearns 1992). Different ways to balance these trade-offs in a variety of dietary, physical and social circumstances have lead into a rich diversity of life history strategies (Bronson 1989).

Most small mammals are characterised by a short life span and multivoltine life history, i. e. they reproduce repeatedly. Typical life history trade-offs for small mammals include to trade-off the number of pups against the size of pups within a litter, or the age at first breeding for the future survival through a long non-breeding season. Age at first breeding is an important life history trait in a short lived small mammal, since it can influence individuals future breeding success, growth of the individual and its life span (Flowerdew 1987). In arvicoline small mammals of the northern hemisphere, females born early in the breeding season usually reproduce in the summer of their birth. Females born late in the breeding season can follow two different life history patterns: they either start reproducing as young females during the same season or not mature and delay the start of their reproduction into the next breeding season (Tkadlec & Zejda 1998a, Prévot-Julliard et al. 1999). This two principles of life history patterns can lead to a distinct bimodal distribution of age at first breeding within a population. It can also lead to a distinct bimodal distribution of the age of breeders in late summer, when breeders are either over-wintered and several months old, or born during the same season and only a few weeks old. Since old and young breeders may vary in their reproductive output, the proportion of young breeders can be of great importance for population growth and density fluctuations in arvicoline rodents (Boonstra 1994, Tkadlec & Zejda 1998b).

The demography of small mammals has long been of interest for ecologists, and there are countless studies on the variation in population size and structure observed between years, with season, with interaction with other species' populations, or with the food availability (see Stenseth 1999 for a review). However relatively little is known how social and environmental variation affects the individuals within the population. Life history traits and trade-offs can be varied in different social and environmental conditions and, in turn, affect population dynamics.

In my thesis I have investigated life history traits of the bank vole *Clethrionomys glareolus* (Schreber 1780), an arvicoline rodent, and their reaction to different physical and social environmental variation. I conducted experiments by manipulating competition, diet and density in the environment to reveal their effects on life history traits of the bank voles. The traits investigated were survival at different life stages, reproduction, offspring characteristics, and age at first reproduction in females but also behavioural traits like spacing behaviour were observed. Observations were interpreted also in the context of seasonality of the environment. In the following chapters I first will introduce the investigated species, and the methods and experimental set up used throughout the different experiments of the thesis. In the third chapter I will describe the major fitness constraints for bank voles that I have investigated, and will relate the results of my own experiments to this background. Conclusions are following in the last chapter.

2 METHODS

2.1 Study species

"Forty percent of mammals species are rodents. …The typical *mammal… probably would be a terrestrial rodent, that is heavily preyed on by other vertebrates. As a consequence, its life expectancy would be measured in months, and it would have undergone intense selection to maximize its reproductive potential. Our hypothetical rodent would mature quickly, and thereafter it would rapidly and repeatedly reproduce large litters of young unless prevented from doing so by adverse environmental conditions."*

(Bronson 1989)

Arvicoline (previously called microtine) rodents include the voles and the lemmings. These are small to medium sized rodents distributed over the Northern Hemisphere up into the arctic. They are mostly ground living, with short limbs, small eyes and ears and a short tail. Arvicolines are characterised by a high reproductive potential and multivoltine (many reproductive events) life history. Females have a postpartum oestrus and can conceive a new litter immediately after giving birth. Thus, females can suckle one litter while being pregnant with the next. Life span in most species depends on the age of first reproduction; however, most individuals can reproduce only during one reproductive season. Arvicoline rodents form an important part of the northern ecosystem and food chain, by preying themselves heavily on grasses, seeds and mosses, and by being preyed upon by birds and other mammals (Burt & Grossenheider 1976, Corbet & Ovenden 1980). Population density can fluctuate dramatically between years and within one season, and fluctuation patterns become more regular, extreme and longer in the higher latitudes (Hansson & Henttonen 1985).

The focal arvicoline study species is the bank vole (Rötelmaus, metsämyyrä), *Clethrionomys glareolus* (Table 1). Bank voles are forest inhabitants, distributed over large parts of Eurasia (Stenseth 1985). They are beautiful little creatures with a henna-reddish fur and are more mouse-like than vole-like in appearance. Female bank voles are exclusively territorial towards each other

during the breeding season (Kalela 1957). In some geographic regions bank voles over-winter socially with other males and females (Ylönen & Viitala 1985). The density of breeding females is limited through their territoriality and, in high density years, many young females have to delay their maturation due to a lack of available breeding territories (Bujalska 1985, Prévot-Julliard et al. 1999). Bank voles compete with other *Clethrionomys* species and the different species of this genus have a similar social system. Total numbers of breeding females of the genus is limited through the same mechanisms as those operating within *C. glareolus* (Viitala 1977, Löfgren 1995).

Bank voles interact with field voles (Erdmaus, peltomyyrä) *Microtus agrestis* in most parts of their range. Social system and diet of the two genera are very different (Table 1), Field voles are considered a grassland species (Myllymäki 1977) and bank voles a forest species, but their habitat overlap can be considerable in modern, fragmented landscapes.

TABLE 1   Characteristics of the study species, bank voles and field voles,
(letters in brackets refer to the references below)

Species	bank vole *Clethrionomys glareolus*	field vole *Microtus agrestis*
Habitat	forest, forest edges, successional stages of clearcuts *(a, d, n, i)*	meadows, mires, sucessional stages of clearcuts *(a, c, d, n, i)*
Diet	omnivore: seeds, lichens, forbs, insects *(b)*	herbivore: grasses, seeds, forbs *(c)*
Social system in breeding season	Breeding females territorial, Stable breeding density also a high population densities *(e, f, o, p)*	kin clusters of breeding females, high breeding densities *(k, l, m)*
non-breeding season	social over-wintering *(g)* in some geographic regions	??

a: Henttonen et al. 1977, *b:* Hansson 1985a, 1985b, *c:* Myllymäki 1977, *d:* Henttonen et al. 1987, *e:* Bujalska 1985, *f:* Kalela 1957, *g:* Ylönen & Viitala 1985, 1991, *i:* Henttonen & Hansson 1984, *k, l:* Pusenius & Viitala 1993a, 1993b, *m:* Pusenius et al. 1997, *n:* Hansson 1983, *o:* Prévot-Julliard et al 1999, *p:* Tkadlec & Zejda 1998a

In Scandinavia, populations of the two species fluctuate in synchrony, and in high densities their habitat overlap increases (Henttonen et al. 1977, 1987, Henttonen & Hansson 1984). Field voles are double to triple the size of bank voles, and dominance in arvicolines seems to be size related (Hanski & Henttonen 1996). Bank voles are regarded as the subordinate competitor and field voles the dominant competitor, and competition between them appears to be

asymmetric. There is plenty of evidence showing that the presence of field voles reduces bank vole abundance on a local scale, and that field voles can exclude bank voles from their preferred habitats (Hansson 1983, Löfgren 1995). However, little is known about mechanisms of competition between the two vole species, especially since their social systems are very different. A major part of this study (manuscripts II, III, IV and V) investigates species interaction and the effect of field vole presence on the bank vole's life history traits.

2.2   Experimental design

The experiments in this thesis were conducted largely in outdoor enclosures near Konnevesi Research Station, Central Finland (62°37′N, 26°20′E). Experimental populations of bank voles were bred in the laboratory from a lab stock of wild captured bank voles. Voles of the same age and reproductive history were brought to the enclosures as experimental populations. The demography of experimental populations varied according to the investigated life history trait. In some enclosures the environment was manipulated (food addition I, field vole addition II, III, IV, V), others served as controls. Performance of the individuals (survival, space use, pregnancies, maturation, and growth) was monitored over a defined experimental period in the enclosures by live trapping. To measure offspring characteristics and to observe the accurate date of birth of litters, pregnant females were taken to the laboratory to single cages shortly before they gave birth. A part of the food addition experiment (I) was conducted in the forests around Konnevesi station on unfenced forest plots. Here, the natural, free ranging bank vole population was monitored over one winter, and half of the plots where food supplemented while half served as controls.

In the experiments on the effect of competition with field voles (II, III, IV, V) the general design of all the enclosure experiments has been additive, monitoring a bank vole population with or without an additional field vole population. The additive design is used to detect the existence of competition and its effects on one of the competitors (Connell 1983). For this study it was the design of choice to know whether or not competition with field voles would affect a particular life history trait of bank voles.

An additive design, however, has the disadvantage that, if effects of competition are detected it is difficult to assign them to either interspecific competition or the general effect of increased densities, since total densities of individuals are higher in the competition treatments than in the controls (Connel 1983, Begon et al. 1996). To distinguish effects of interspecific and intraspecific competition, a substitutive experimental set up can be useful; in which total densities of individuals are kept constant and the proportion of one species to the other is varied (De Wit replacement series 1960, with plant seedlings, DeBenedictis 1974, with tadpoles). Such a set up, however, has its limitations when working with an organism which possesses a *social system*, even more so if the investigated species do not have the same social system. Territorial bank vole

females use the available space differently than kin-clustered field vole females (see Table 1 for references). In winter, the species may compete for food resources and an as a result, investigator may choose to keep the total vole biomass per enclosure constant, with field voles being bigger than bank voles. In territorial breeders, one may choose to keep space use constant, with bank voles having bigger territories, thus conversion factors may change. Furthermore, depending on the sex and cohort investigated and on the season in which the experiment is staged, decisions on which *density* to keep constant must be adjusted. To know the density under which to perform a substitutive experiment, one needs to know the densities in which competition occurs in the particular study system (Connell 1983) or, as in this study, for the investigated life history trait to be measurably affected. The additive experiments of this thesis can lay foundations for conducting substitutive experiments in the future, by separating those traits which are affected by competition from not-affected traits (II, III, IV) and by monitoring performance of individuals in different competitor densities (V).

Experiments on the effects of interspecific competition were conducted serially from 1998 to 2001. Data on different life history stages was partly collected simultaneously from the same enclosures but used in different manuscripts (late summer 1998). To ease understanding of the structure of data and material, I have added a table explaining the sequence of experiments and the use of data in the manuscripts included in this thesis (Table 3).

TABLE 2   Chronological sequence of field period of enclosure experiments on inter-specific vole competition in Konnevesi, Central Finland. Focal species: bank voles under the influence of field voles (unless otherwise stated)

Year	month	Parallel enclosures	Duration per replicate	Cohort investigated, LH variables	Manuscript
1998	6	8	3 weeks	Breeding females	II
	7	8	3 weeks		
	8	8	3 weeks	Breeding females (age structured), weanlings	II, III., IV
	9	8	3 weeks		
	10-5	8	7 months	Wintering, initiation of spring breeding	Unpubl.
1999	5	3	3 weeks	Breeding females, different competitor densities	V
	6	4	3 weeks		
	7	4	3 weeks		
	8	8	3 weeks	Field voles under influence of bank voles	Unpubl.
	10-5	8	7 months	Wintering, behavioural trials, initiation of spring breeding	Unpubl.
2000	6	4	3 weeks	S, R, in different competitor densities	V
	7	8,8,4	10 days	weanlings	IV
2001	7	4	3 weeks	Breeding females, different competitor densities	V
		(4)		(also intra-specific)	Unpubl.
				Behavioural trials	Unpubl.
				Physiological stress measures	Unpubl.

3 RESULTS AND DISCUSSION – FITNESS CONSTRAINTS IN BANK VOLES

3.1 Interspecific competition

Competition between species is a major factor shaping ecological communities (Connell 1983, Schoener 1983, Gurevitch et al. 1992). Research on competition in small mammals has been mainly focusing on the spatial distribution of populations and the competitive exclusion of one species by the other (Grant 1972, Connell 1983 for review, Hansson 1983, Morris et al. 2000). Interspecific competition can furthermore affect species abundance (Abramsky et al. 1979, Munger & Brown 1981, Löfgren 1995) or individual foraging behaviour (Kotler & Brown 1988, Abramski et al. 1990). Little research has been conducted on the effects of competition on life history traits of the individuals, highlighting the need for more connection between the fields of life history theory and community ecology (Stearns 1992). A major part of this thesis deals with the effects of competition by field voles on life history traits of bank voles (II, III, IV, and V).

The results of this thesis on competition effects are summarised in table 2. They show that the presence of field voles decreased survival as the major fitness variable of bank voles. The decrease was dependent on age, sex and breeding stage of the individual bank vole. The survival of breeding year born females was decreased when they were coexisting with field voles (III), while survival of bank vole males (V), immature females (IV), and over-wintered breeding females was not affected (II, III). However, when numbers of field voles were raised over a threshold, survival of all functional groups of bank voles decreased drastically (V). Winter survival over many months seemed not to be affected by coexistence with field voles in the enclosures (Iverson & Turner 1972, Eccard, unpublished data).

TABLE 3   Main life history traits investigated in this thesis (roman numerals) and other studies (letters, references below). Increase ↑ or decrease ↓ or no influence O of the selected trait under an increase of field vole numbers (left) or bank vole numbers (right). Symbols relate to the sources listed in the same order

Life history traits of C. glareolus females	Increase of Microtus numbers		Increase of Clethrionomys numbers	
Survival				
of breeding females	↓↓↓↓	II, III, V, a, b	oooo	I, c, f, p
overwintered	o	III		
year born	↓	III		
of immature females	o	IV	o	p
of adults over summer	↓↓↓	II, III, V	o	I
of adults over winter	o	r, t	o	I
Reproduction				
Pregnancy rate of breeding females	oo	II, III	↓	V, e, u
Maturation of weanling females	o	IV	↓↓↓	e, f, g
Pregnancy of weanling females	o	IV	↓↓↓	e, f, g
Offspring quality	ooo	II, III. IV	o	q
Space use and behaviour				
Size of breeding territory	↓↓↓	II, III, V	↓↓↓ but o	II, h, v but c
Home range of juveniles	o	IV	o	c
Winter home range size	↑	t	o	r
Avoidance behaviour summer	↑↑↑ but o	II, i, j, but g	o	r
Avoidance behaviour winter	oo	k, r	o	r
Initiation of spring breeding	o	r	delay	I
Maturation if juveniles	delay	IV	delay	e, f

*: weanling females are ca three-week-old immatures, shortly after being weaned and leaving their mother's nest

Sources: I, II, III, IV, V: manuscripts of this thesis, a: Hansson 1982, b: Hansson 1983, c: Bujalska & Grüm 1989, d: Henttonen & Hansson 1984, e: Bujalska 1985, f: Prévot-Julliard et al. 1999, g: Löfgren 1995, h: Ylönen 1990, i: Halle et al. 1999, j: Grant 1969, k: Iversen & Turner 1972, p: Yoccoz et al. 2001, q: Mappes et al. on density and breeding (unpublished), r: Köhler et al. 2000, t: Eccard et al. on winter demography (unpublished), u: Ims 1987, v: Viitala 1984

Territory size of breeding bank vole females decreased in the presence of field voles (II, III, IV) probably through behavioural interactions also described for the red vole *C. rutilus* in Finnish Lapland in peak densities of its dominant competitor the grey-sided vole *C. rufocanus* (Viitala 1984). We did not observe home range decrease of immature bank voles in the presence of field voles (IV), and also during winter when voles were not in breeding condition we recorded no differences in home range size. (unpublished). These observations suggest that behavioural interactions between field voles and immature or not breeding bank voles might differ from those with breeding bank voles females.

The combined results on survival and space use of bank voles suggest, that a certain life history strategy could be advantageous for bank voles in coexistence with field voles: a year born bank vole female should rather not breed during the summer of her birth. If she stayed immature, her late summer and autumn survival would not be affected by field voles and also her subsequent survival as an over-wintered females in next season will not be affected. If she matured in the summer of her birth, she may face higher mortality through interaction with field voles. However, in the experiment examining maturation of juvenile females (IV), females did not behave as suggested above: they did not delay their breeding into the next season in the presence of field voles. It is possible that the maturation experiment (IV) was not conducted at sufficiently high densities to evoke the predicted response, although field vole densities were higher than in those experiments in which a general, lower bank vole survival was found (II, III).

3.2   Density-dependence

Intrinsic regulation of population size is a density-dependent process, which alters birth and death rates. Population growth rate thus depends on density as a negative feedback loop on population numbers (Lack 1966, Flowerdew 1987). Changes in population growth rates (births and deaths) can also be described as changes of life history patterns in individuals of the population. However, not all individuals will react similarly to density changes, because each is trying to maximise its fitness. The strength of density-dependence shows seasonal variation (Yoccoz et al. 2001) probably because many life history processes take place only during some parts of the year, for example the maturation of immatures only during the breeding season, and not all processes are equally density-dependent.

Arvicoline populations can vary tremendously in their density. The main regulative process of high densities seems to be the suppression of maturation and breeding (Bronson 1989) through hierarchical or territorial behaviour (Flowerdew 1987). In bank voles, breeding of immature females is suppressed in high densities, probably through a lack of available breeding territories: young females in high density delay their breeding into the next season (Bujalska 1985, Tkadlec & Zejda 1998a, Prévot-Julliard et al.1999), thus altering their age at first breeding. This leads to an increased frequency of females in the population first breeding at older ages. It remains questionable whether a delay of breeding until old age is an optimal strategy for females in high density (Kaitala et al. 1997) or a constraint to their fitness (Kokko & Ranta 1996, Prévot-Julliard et al. 1999). Density-dependent effects in bank voles mainly affect reproduction of individuals. In Table 2 the influence of increasing bank vole density is summarised, derived from studies of this thesis (roman numerals) and other studies (letters, references below).

In the food addition experiment (I), a surprising suppression of the initiation of breeding after winter was found. Density of females was highly variable

on a local scale and a proportion of the over-wintered females was not able to breed due to high local densities. We had expected however, that densities after a winter would be sufficiently decreased through the natural, high winter mortality to allow all female winter survivors to occupy a territory and breed. This finding supports the notion that a delay of breeding until old age is a constraint rather than an optimal strategy, since females can also face density constraints in spring even if the total population density is usually lower in spring than in autumn. The survival probability over the winter of young females which had reproduced and young females which had not reproduced is an important comparison deciding the optimality of a strategy. Recent findings suggest that the difference between young reproduced and young not-reproduced females may not be as high as assumed in the optimality model (Prévot-Julliard et al. 1999). Summer born females may reproduce both in the summer of their birth and in the following breeding season (Viitala 1977), therefore it would be in any case better to attempt breeding in the summer of birth.

In an experiment on the strength of interspecific competition (V), we found interspecific competition interacting with intra-specific density-dependence. Since competition with field voles had reduced the numbers of bank voles, the survivor's chances of breeding actually increased. The result illustrates clearly that regulation of breeding numbers in bank voles is a purely density-dependent and thus, an intra-specific regulated process. Given the initial density of bank voles is above breeding density, not all females can occupy breeding territories. If initial territory owners die through the interference with field voles, non-breeding females can utilise the gap and start breeding regardless of the high numbers of life-threatening field voles around them. We had not been able to detect this pattern in the earlier experiments (II and III) because we had removed the bank vole males from the enclosures after a short period to allow fertilising the females. Bank voles' breeding rates were thus frozen to the level at the start of the experiment, before the forces of interspecific competition had altered the strength of the density-dependence.

Territory size of breeding bank voles was decreasing in higher bank vole density in late summer compared to lower density in early summer (II). In northern latitudes similar correlations were previously found between different density years (Ylönen et al. 1988, Henttonen, personal communication), however data from a island study (Bujalska & Grüm 1989), did not confirm this correlation in Central Europe possibly because nutritive of bank vole populations situation may differ from the boreal North and influence behaviour.

3.3 Seasonality

Most habitats experience some degree of seasonal variation in climate and diet. This is most pronounced in higher latitudes with extreme variation in day length and temperature, but also applies to tropics with strongly seasonal rainfall patterns. In our system, the bank vole in boreal forests, breeding season lasts five months, followed by a seven month long non-breeding season (Kai-

kusalo 1972). Winter and summer vary in day length, microhabitat (snow cover) and food supply, but day length seems to be sufficient to stop bank voles from breeding in the laboratory, even if temperatures and food supply are not restricted (own observation).

Season was not manipulated in the experiments of this thesis, because all experiments were conducted outdoors. All results, however, had to be interpreted in the context of the rather extreme northern seasonal environment. When not visiting the enclosures for a few days in Midsummer, one hardly recognised the place, since grasses grow decimetres in few days and a new colour of flowers may have emerged.

Plant biomass and seed availability of different plant species changes dramatically over the short boreal summer. In some of the summer experiments, results would be obscured when neglecting seasonal differences between the different runs (II, III, IV, and V). In the density experiment, for example, in which numbers of field voles were varied (V), survival numbers and breeding numbers per enclosure were increasing linearly with the progressing season. Size of a breeding territory in arvicoline females is food dependent and decreasing with increasing food availability (Ostfeld 1985); thus an increase in the numbers of breeders per enclosure indicates increasing food supplies. However, experiments were conducted only during early to mid summer. In late summer the effects of progressing season were reversed: less breeders and less survivors (III), ceasing maturation (IV) and an age dependent cessation of breeding (III).

Seasonal events seemed most obvious in the experiment on variations in the onset of breeding season (I), where populations were monitored over winter into spring. In this experiment however, the individuals response to seasonal cues was largely altered by the availability of supplemented food and by density-dependence (chapter 3.2 and 3.4).

3.4 Diet

Food availability may be an important factor limiting the length of the reproductive season (Bronson 1989). Food quality or quantity can vary with seasons or habitats and the food availability is reflected in many life history traits, such as offspring size or number, and body size or growth of adults (Flowerdew 1987, Boutin 1990), but also in behavioural traits, such as individual's home range size (Andrzejewski & Mazurkiewicz 1976, Ostfeld 1985). Food supplementation studies with arvicoline rodent populations have shown to prolong the breeding season or to induce winter breeding (Bujalska 1975, Andrzejewski & Mazurkiewicz 1976, Ylönen & Viitala 1985, Schweiger & Boutin 1995) but they may not alter density-dependent structure in the population growth rate or the social system (Yoccoz et al. 2001). Supplemental food studies over the winter in high latitudes are rare (Henttonen et al. 1987, Boutin 1995, Prévot-Julliard 1999, Yoccoz et al. 2001), for logistical reasons of working in low temperatures and supplying food to animals in the subnivean environment (under

the snow). To my knowledge there exist no earlier studies where food of *different quality* was supplied simultaneously to arvicoline populations, monitored parallel over wintertime.

In the food addition experiment (I), large quantities of sunflower seeds and barley were fed to enclosed populations and small quantities of spruce seeds, a natural winter food, was fed to free ranging bank vole populations. In enclosed populations, the breeding season started over a month earlier than that of free ranging populations although the population density in the enclosures was several fold higher. There were no differences in the average breeding date between populations receiving the two food qualities. In free ranging populations, no differences were found at the start of the breeding season caused by supplemental feeding of spruce seeds. Food quantity seemed to be more important than food quality, but there may have been also other differences besides supplemental food between enclosed and free ranging populations contributing to the observed differences in the onset of breeding. The novel findings of this experiment were concerning differences in the individual onset of breeding, related to local density variations *within* the food treatments (chapter 3.2).

4   CONCLUSIONS

"....seek simplicity and distrust it." (Whitehead in Birch 1979)

In this thesis I have investigated fitness and life history traits of the bank vole, an arvicoline rodent, under variation of interspecific competition, density of con-specifics, seasonality and food supplementation. Competition with an arvicoline competitor, the field vole, decreased the survival of bank voles as the main fitness component. Females of different age groups and maturity were, however, affected to different degrees by the presence of field voles. In coexistence with field voles, it may be advantageous for young individuals to stay immature and delay breeding to the next season, since young sexual mature females suffer lower survival in presence of field voles than young immatures. Once old and over-wintered, survival of sexual mature females is less affected by the presence of field voles than if they had matured at young age and smaller body size. During the breeding season, the species interact through direct interference competition, since dominance in arvicolines is related to body size. Year born bank voles are smaller than both over-wintered bank voles and all field voles, and the combined effects of intra- and interspecific aggression may lead to the observed reduced survival. Density-dependence affected directly the maturation of bank vole females, thus, age at first breeding can be significantly delayed in high densities of con-specifics, even after winter, when densities are generally low but may be high at some localities. Food addition in high quantities initiated an earlier onset of breeding after winter, however, laws of density-dependence and breeding suppression were working on females also in food treatments. Seasonality is an important physical factor to be taken into account, since many life history processes are expressed only during short periods of the year. Especially in northern latitudes seasonality is extreme, and outcomes of the same experiment may thus change within weeks. Changes in food availability may alter densities of individuals in populations, even if the density-dependent nature of those life history traits of individuals does not change.

Life history traits investigated at the individual level may help explain population density changes and the interaction between species within communities. Variation in life history traits, in turn, can be caused by density-

dependence and interaction with other species. While interspecific competition with a socially very different vole species affected mainly survival, the density-dependent competition with con-specifics affected mainly the reproductive traits of individual. However, individuals vary in their fitness and not all individuals react similarly to the same environmental conditions. Life history theory may offer an important tool to explain the mechanisms of density-dependence and link them to models and theories of population fluctuation. Also a community level approach to the fluctuation of arvicoline populations including several species may profit from including life history theory and a more individual-based approach.

YHTEENVETO

Kilpailun ja vuodenaikaisvaihtelun vaikutus metsämyyrän elinkiertopiirteisiin

Eliöiden populaatiotiheyttä säätelevät ympäristön vaihtelu ja populaation koosta ja rakenteesta riippuvat sosiaaliset tekijät. Ensinmainittuihin voidaan lukea saalistuspaine, vuodenaikaisesti vaihtelevat olosuhteet ja/tai ravinnon laatu ja saatavuus, sekä lajien välinen kilpailu. Viimemainittu sisältää populaation sisäiset tiheydestäriippuvat prosessit. Eläinyksilöiden elinkierto on muokkautunut lajin evoluution kautta, mutta se vaihtelee vallitsevien ympäristöolosuhteiden asettamien rajoitteiden mukaisesti. Monet elinkiertopiirteet ovat olosuhteisiin sopeutuneita kompromisseja, kuten esimerkiksi yksilön kasvun ja lisääntymisen alkamisajankohdan välinen suhde, nykyisen ja tulevan lisääntymisen suhde tai poikueen koon ja jälkeläisen laadun välinen mahdollinen ristiriita.

Myyräpopulaatioiden tiheydenvaihtelut ovat suuria ja myyrien lisääntymispotentiaali on suuri. Korkean populaatiotiheyden aikaan voi populaation sisäinen sosiaalinen säätely estää nuorten yksilöiden tulemisen sukukypsiksi. Ainoastaan talvehtineet naaraat ja osa lisääntymiskauden alussa syntyneistä naaraista lisääntyvät, mutta suuri osa nuorista ja varsinkin myöhemmin kesällä syntyneistä yksilöistä jää immatureiksi. Nämä syntymäkesänään lisääntymättömät yksilöt joutuvat odottamaan vuoroaan seuraavaan kevääseen, mikäli selviävät pitkän talven yli, jolloin suuri osa populaatiosta kuolee. Tyypillistä lisääntyvän populaation ikärakenteelle on sen kaksihuippuisuus; lisääntyjiä ovat joko erittäin vanhat talvehtineet yksilöt tai vain muutamia viikkoja vanhat nuoret naaraat. Ensimmäisen lisääntymisen ajoitus on yksi merkittävimmistä elinkiertopiirteistä, ja se vaikuttaa voimakkasti muihin elinkiertopiirteisiin, kuten koko elinaikaiseen poikastuotantoon ja eliniänodotukseen. Näin on varsinkin erittäin voimakkaasti vuodenaikaisessa ympäristössä, jossa pitkä ja ankara ei-lisääntymiskausi seuraa suhteellisen lyhyttä lisääntymiskautta. Yksilöiden kaksi lisääntymisstrategiaa, eli lisääntyä joko hyvin nuorina tai suhteellisen vanhoina, heijastuu erityisen voimakkaasti lisääntymispopulaation ikäjakaumaan varsinkin loppukesästä. Koska lisääntymistehokkuus vaihtelee nuorten ja vanhojen yksilöiden välillä, eri-ikäisten lisääntyvien naaraiden lukusuhde heijastuu koko populaation lisääntymistehokkuuteen.

Tässä väitöskirjassani olen tutkinut metsämyyrän, *Clethrionomys glareolus*, elinkiertopiirteiden vaihtelua muuttuvissa ympäristöolosuhteissa. Metsämyyrä on nimensä mukaisesti metsähabitaattia suosiva laji, jonka populaation sosiaaliselle rakenteelle on luonteenomaista lisääntyvien naaraiden territoriaalisuus. Metsämyyränaaraiden elinkiertopiirteisiin vaikuttavina ympäristömuuttujina tutkin talviravinnon määrää ja laatua, oman lajin populaatiotiheyttä lisääntymiskauden alkaessa ja kilpailevan lajin, peltomyyrän *Microtus agrestis*, populaatiotiheyttä lisääntymiskauden aikana.

Lajienvälinen kilpailu on eliöyhteisöjen yksi tunnusomaisimpia piirteitä. Väitöskirjatutkimukseni pääpaino onkin kahden myyrälajin kilpailu ja kilpailun vaikutus "heikomman" lajin, metsämyyrän, elinkiertopiirteisiin. Kilpailukokeet tehtiin suurissa neljänneshehtaarin ulkotarhoissa, joissa kaikissa oli rakenteeltaan samanlainen metsämyyräpopulaatio, ja lisäksi puoleen tarhoista kussakin kokeessa muodostettiin kilpaileva peltomyyräpopulaatio. Peltomyyrä on ruohovartisten kasvien syöjä ja metsämyyrä pääosin siemensyöjä, mutta myös luonnontilanteessa lajien populaatiot kohtaavat pääasiallisten elinalueidensa reuna-alueilla, varsinkin molempien lajien samanaikaisten huipputiheyksien aikana. Peltomyyrän läsnäolo samoissa tarhoissa heikensi lisääntyvien metsämyyrien hengissäsäilymistä jo suhteellisen lyhidenkin koejaksojen aikana. Varsinkin nuorten lisääntyvien naaraiden hengissäsäilyminen heikkeni, mutta vanhat metsämyyränaaraat säilyivät myös kilpailutilanteen alaisuudessa hyvin. Kuitenkin niiden naaraiden lisääntyminen tehostui, jotka pystyivät kilpailupaineen alaisuudessa säilymään hengissä. Eli samaan aikaan kun lisääntyvien lajitoverien lukumäärä pieneni, jäljelle jäävien lisääntymismahdollisuudet paranivat kilpailevasta lajista huolimatta. Tämä ilmiö osoittaa sen, että metsämyyränaaraiden lisääntymistä sääteli ainoastaan lajinsisäinen territoriaalisuus, eikä toisen lajin kilpailupaine. Lisääntymättömien nuorien eläinten säilyvyyteen ei peltomyyrän kilpailu vaikuttanut. Voidaan siis olettaa, että lajin sisäisestä sosiaalisesta säätelystä johtuva lisääntymisen siirtäminen on nuorten naaraiden edun mukaista myös lajienvälisen suhteen kannalta. Lajienvälinen kilpailu voi kuitenkin vaikuttaa heikomman lajin, metsämyyrän, populaatiotiheyteen kahta kautta, vähentämällä lisääntyvien yksilöiden lukumäärää ja vaikuttamalla ensimmäisen lisääntymisen ajankohtaan additiivisesti lajinsisäisen säätelyn lisäksi.

Väitöskirjani toinen pääteema oli metsämyyrän talvehtimisen ja keväisen lisääntymisen ajankohdan tutkimus. Tässä kokeessa, josta osa tehtiin tarhaolosuhteissa ja osa aitaamattomilla metsäpopulaatioilla, manipuloimme ravinnon laatua ja tarjontaa keskitalven ja kevään ajan. Lisäravintoa saaneet metsämyyrät aloittivat lisääntymisen aiemmin riippumatta ravinnon laadusta. Kaikissa ravintomanipulaatiopopulaatioissa lisääntyvien naaraiden lukumäärä oli erittäin merkittävä lisääntymisen ajoittumista säätelevä tekijä. Vaikka oletimme, että hyvä habitaatti ja ravinnontarjonta olisi mahdollistanut tehokkaan lisääntymisen, niin hyvillä laikuilla territorioiden puute ja lajin sisäinen säätely estivät kaikkien talven yli säilyneiden naaraiden aikaisen lisääntymisen. Myös tämä koe osoitti lajin sisäisten tiheydestä riippuvien sosiaalisten prosessien tärkeän merkitykseni, vaikka lisäravinnon merkitys oli myöskin selkeä.

ZUSAMMENFASSUNG

Die Lebensgeschichte (life history) von Individuen wird durch die Stammesgeschichte ihrer Art bestimmt, kann aber mit Umwelteinflüssen variieren. Viele Bestandteile einer Lebensgeschichte sind kompromißartig untereinander verbunden (trade-offs), so zum Beispiel das Körperwachstum mit frühzeitiger Vermehrung, die gegenwärtige Vermehrung mit der zukünftigen Überlebenschance oder die Grösse der Nachkommen mit ihrer Anzahl.

Wühlmauspopulationen können starken Bestandsschwankungen unterliegen und haben ein grosses Vermehrungspotential. Bei hohen Dichten werden viele der im Sommer geborenen Tiere durch innerartliche soziale Regulationsmechanismen an ihrer Geschlechtsreife gehindert und können sich folglich nicht fortpflanzen. Diese Tiere erreichen die Geschlechtsreife erst im nächsten Frühjahr, sofern sie den Winter überleben. Aus diesem Grunde treten in Populationen zwei grundsätzliche Reproduktionsmuster auf: Individuen reifen entweder heran, wenn sie erst wenige Wochen oder aber wenn sie schon viele Monate alt sind. Das Erst- Reproduktionsalter ist aber ein entscheidendes Merkmal der Lebensgeschichte und kann viele andere Merkmale beeinflussen, wie die Nachkommenzahl über das gesamte Leben oder die Lebensdauer. Diese beiden unterschiedlichen Reproduktionsmuster spiegeln sich auch in der Altersstruktur der adulten, sich reproduzierenden Tiere im Spätsommer wider. Da junge und alte Wühlmäuse unterschiedliche Reproduktionsraten haben können, spielt der Anteil der jungen unter den reproduktiv Aktiven eine entscheidende Rolle für die Reproduktionsrate der Gesamtpopulation.

In meiner Doktorarbeit habe ich an der *Rötelmaus Clethrionomys glareolus*, einer territorialen, waldbewohnenden Wühlmausart, die Reaktionen von wichtige Merkmalen der Lebensgeschichte auf verschiedene Umwelteinflüsse untersucht. Dafür wurden Nahrungsangebot, Dichte der Tiere und Konkurrenz zu einer anderen Wühlmausart, der Erdmaus *Microtus agrestis* zu verschiedenen Jahreszeiten manipuliert.

Konkurrenz zwischen Arten ist ein bestimmender Faktor in der Ökologie von Artengemeinschaften. Ein Grossteil der Experimente in dieser Arbeit beschäftigt sich mit den Auswirkungen der Konkurrenz der beiden genannte Wülmausarten auf die Lebensgeschichte der Rötelmaus, die die unterlegene Art ist. In den Experimenten wurden Populationen von Rötelmäusen in Gehegen gehalten, und in der Hälfte der Gehege befanden sich zusätzlich Erdmäuse. Erdmäuse sind Graslandbewohner, es überschneiden sich in fragmentierten, anthropogenen Landschaften jedoch die Lebensräume der beiden Arten. Bei Anwesenheit von Erdmäusen überlebten die Rötelmäuse schlechter als bei deren Abwesenheit. Besonders verringerte sich das Überleben junger, reproduzierender Weibchen, während alte Weibchen nicht beeinträchtigt waren. Bei hohen Erdmausdichten war das Überleben stärker reduziert, auf der anderen Seite waren die Reproduktionsraten der überlebenden Rötelmäuse höher als bei niedrigen Erdmausdichten oder gar ohne Erdmäuse. Das zeigt, dass Reproduktionsraten einzig innerartlich reguliert werden; selbst wenn die

ausserartliche Konkurrenz stark ist, werden freiwerdende Territorien von überlebenden Rötelmausweibchen genutzt. Das Überleben von Jungtieren vor der Reife wurde durch ausserartliche Konkurrenz nicht beeinträchtigt. Es könnte deshalb von Vorteil für sommergeborene Individuen sein, dass sie ihre Reifezeit in die naechste Saison zu verlegen. Auf diese Weise kann zwischenartliche Konkurrenz ähnlich der innerartlichen das Reproduktionsalter von Individuen verändern. Konkurrenz zwischen Arten kann durch niedrige Überlebensraten und durch Veränderung des Reproduktionsalters das Populationswachstum einer unterlegenen Wülmausart beeinflussen.

In einem weiteren Experiment dieser Arbeit wurde das Nahrungsangebot für Rötelmäuse über Winter und Frühling manipuliert. Wenn die Tiere grosse Mengen Nahrung zur Verfügung hatten, begann die Vermehrung früher im Jahr, unabhaengig von der Qualität der Nahrung. In allen Nahrungsmanipulationen spielte die lokale Dichte der Tiere dennoch eine entscheidende Rolle. So war es manchen Tieren bei hohen lokalen Frühjahrsdichten in guten Überwinterungshabitaten nicht möglich, mit der Reproduktions zu beginnen, da alle Brutterritorien bereits besetzt waren. Auch dieses Experiment zeigte, dass Reproduktionsraten innerartlich reguliert werden. Die Schwellenwerte für diese Regulation sind aber vom Nahrungsangebot abhängig.

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Original papers

I

Initiation of breeding after winter in bank voles: effects of food and population density

by

Jana A. Eccard & Hannu Ylönen

Canadian Journal of Zoology 2001, 79: 1743-1753

II

Direct interference or indirect exploitation?
An experimental study of fitness costs of interspecific competition in voles

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III

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IV

Effects of competition and season on survival and maturation of young bank vole females

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Jana A. Eccard, Ines Klemme, Taina J. Horne & Hannu Ylönen

Evolutionary Ecology 2002, in press

V

Interspecific competition in small mammals: Performance of the subordinate species along a gradient of competitor densities

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