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Evolutionary perspective

Interspecific competition in small rodents: from populations to individuals

JANA A. ECCARD* and HANNU YLÖNEN
Department of Biological and Environmental Science, University of Jyväskylä, PO Box 35, FIN-40351 Jyväskylä, Finland
*(*author for correspondence, tel./fax: +358-14-602321; e-mail: jaeccard@cc.jyu.fi)*

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Abstract. The role of interspecific competition in shaping animal and plant communities has formed one of the major issues in ecology for decades. Small mammals, mainly rodents, have been among the model systems used for research on interspecific competition. Most studies within small mammal systems in the past have examined effects of competition on population attributes such as on population size, habitat use, or population dynamics. Population-level responses are the cumulative effects of individual responses, however, the influence of competition on individual life-history traits has rarely been studied. Research on life-histories may bridge gaps between population biology and effects of competition on individual behaviour. In this paper, we review recent research approaches to interspecific competition in rodents based on census data and species assemblages, that use regression analysis, time series analysis, removal and exclusion experiments, and showcase our own experimental research on the effects of interspecific competition on individual life-history traits in boreal voles.

Key words: competitive exclusion, *Clethrionomys*, habitat selection, interspecific competition, life-history, *Microtus*, review

Introduction

Small mammals have been used as a model system for studying interspecific competition in terrestrial systems. A detailed history of early studies of the effects of interspecific competition in small mammals has been compiled by Grant (1972). The described studies focussed mainly on habitat use, negative correlations between population sizes of presumed competitors, and to a lesser extent on individual behaviour (Fig. 1). Most studies used field census data, but Grant's review marks a time when small mammal research was shifting from observational studies to field or enclosure experiments. In later reviews on experimental studies on interspecific competition authors set more rigorous criteria for studies to be included for review in their articles, and very few small

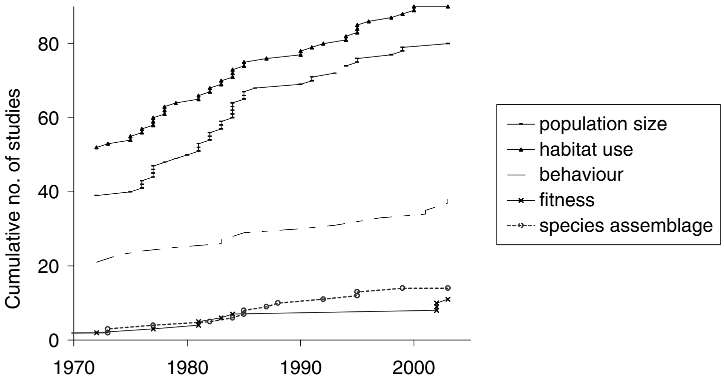

Figure 1. Historic development of the research focus in competition research in small mammals. The figure is based on the studies mentioned in a review on interspecific competition among rodents (Grant, 1972; 89 studies) and the author's own collection of articles on interspecific competition in rodents since then, comprising over 90 papers. Articles were gathered, however, not systematically. Studies can have multiple research foci (e.g. many studies of population size have also investigate habitat use) and both foci are included in the data, respectively. Early competition research focussed on population size and demography of two or more species until the mid 80's. Many of these studies were also investigating habitat selection and competitive exclusion of one species by another. Behavioural studies of the investigated communities accompanied this development in smaller numbers, most of these studies were staged in the laboratory. Study of species assembly and individual fitness are relatively recent developments in small mammal research.

mammal studies fulfilled the standards set by the authors. Connell (1983), using criteria such as the standard of journal, sufficient controls, similarity to natural conditions, and occurrence of interspecific competition, included eight small mammal studies, Schoener (1983) using the criteria field experiment and sufficient controls, found 18 small mammal studies, including Connell's choice of studies. A meta-analysis of Gurevitch *et al.* (1992), reporting experimentation on interspecific competition in the 1980's, included only one small mammal study. Thus a comprehensive review on experimental research on rodent competition since Grant's work is missing. Research on interspecific competition in small mammals meanwhile took other paths than experimentation, such as the increasingly sophisticated analyses of rodent census data. Most research on interspecific competition in small mammals since the 1970's focused on population-level responses to competition and to a minor extend on individual behaviour (Fig. 1). In this paper we provide an overview of approaches and methodology used in the research on interspecific competition research in rodents from 1970s to today on a population level (Section 'Population size and habitat use' of this paper), assemblages (Section 'Species assemblages') and an individual level (Section 'Research on individuals').

Population-level responses are cumulative effects of individual responses. Despite this the individual-level effect of competition on reproduction or survival has been mostly neglected in past research. Individual behavioural studies, on the other hand, may shed light on dominance relationships between species, but because of their short duration they rarely reveal information about the fate and fitness of individuals. According to recent understanding, interspecific competition should be manifested in the individuals of a species such that they suffer reduction in fecundity, survivorship or growth as a result of resource exploitation or interference by a second species (Begon *et al.*, 1996). Distinguishing individuals within a population consisting of adults and juveniles, reproducing and immature individuals, males, and females enables us to ask which individuals suffer the costs of competition – and consequently cause a decrease in fecundity or survival at the population level. This topic is also the key question of the present special issue of *Evolutionary Ecology*, and has, often been lacking in the research of interspecific competition in small mammals. In Section 'Effect of competition on life-history traits of individuals' we thus showcase a very recent experimental approach to studying the effects of interspecific competition on life-history variables of individuals, using our own research on boreal voles.

Population size and habitat use

Observations of negative correlation between population sizes of sympatric small mammal species provided early indications that interspecific competition could have consequences on population size and habitat use (see Grant, 1972 for review; Conley, 1976; Redfield *et al.*, 1977; Kincaid and Cameron, 1982; Gurnell, 1985). Species may as well use the same habitat, but segregate among strata within a habitat (Kincaid and Cameron, 1982; Ylönen, 1990) or can also segregate temporally and be active in different time windows (Ziv *et al.*, 1993; Ziv and Kotler, 2003 (this issue); Kronfeld-Schor *et al.*, 2001) in presence and absence of competitors. Spatial segregation into different habitats allows competing species to co-exist, and often conceals past and ongoing competition to the investigator.

Aided by regression analysis association of abundances of one species with abundances of other species can be studied from *census data*, using either a 'static' or 'dynamic' approach (reviewed in Shenbrot and Krasnov, 2002). The 'static' approach uses census data of population sizes at one point in time over many sites (e.g. Crowell and Pimm, 1976; Dueser and Hallet, 1980; Hallet *et al.*, 1983; Rosenzweig *et al.*, 1984, 1985). In co-existing rodent species, *density-dependent habitat selection* reduces competition coefficients and warps competitive isoclines to that the probability of co-existence is increased (Rosenzweig, 1981, 1991). Theories of habitat selection illustrate beautifully how density-dependent patterns of habitat utilisation can be used to measure interspecific competitive effects. Density-dependent habitat selection theories are based on an ideal free distribution of individuals of one species (Fretwell and Lukas, 1970). If individuals distribute ideal free, they should disperse to those habitats in which their fitness is maximised. Differences in habitat quality cause uneven distributions. The presence of competitor species can be seen as a reduction of habitat quality (Abramsky *et al.*, 1991). In experimentation, regression analysis allows for the comparison of census data with data after the removal of competitor species, or for comparison between enclosures with two competing species and one species alone (Abramsky *et al.*, 1991, 1994; Higgs and Fox, 1993; Thompson and Fox, 1993).

Experimentation in open populations mostly involved removal (or rarely the addition) of one species while monitoring the population size of another species (e.g. Abramsky *et al.*, 1979; Munger and Brown, 1981). Parts of the natural species assembly can also be excluded through a semi-permeable fence, i.e. by their body size (Heske *et al.*, 1994; Valone and Brown, 1995). Some removal studies faced the problem of fast re-immigration of the removed species (Schroeder and Rosenzweig, 1975). Often these studies found evidence for competition through an increase of population size in the absence of the competitor, and proposed exploitation of resources as a possible mechanism. (Gliwicz, 1981; Montgomery, 1981; Fox and Pople, 1984). Many open-population experiments, did not find effects on population sizes (Joule and Jameson, 1972; Wolff and Dueser, 1986), but habitat shift was a frequent response of the subordinate species to the removal or addition of a dominant species (Heller, 1971; Schroeder and Rosenzweig, 1975; Chappel, 1978; Holbrook, 1979; Montgomery, 1981; Abramsky and Sellah, 1982, Crowell, 1983). In enclosures with non-permeable fences, negative correlations between populations of presumed competitors were regularly observed (e.g. Krebs, 1976). Many studies found habitat selection and/or competitive exclusion in enclosures that offered a choice of habitat types, both with boreal rodent pairs (Grant, 1971; Morris and Grant, 1972; Hoffmeyer, 1973) or desert rodents (Price, 1978; Abramsky *et al.*, 1998). Counts of footprints (Kotler, 1985) have been used to indicate activity, habitat use and distribution of gerbils in presence or absence of competing gerbiline species, and indicated different microhabitat use (Abramsky and Pinshow, 1989; Abramsky *et al.*, 1990). Activity counts in two connected enclosures, permeable for the ideal free distribution of individuals of the subordinate species only, showed a non-linear dependence of the strength of interspecific competition on densities or activity densities of both competitors (Abramsky *et al.*, 1991).

Several types of community organisation models for co-existing rodent species have been proposed and illustrated with representative species pairs: distinct habitat preference (Rosenzweig, 1981; Brown and Rosenzweig, 1986), shared habitat preference (Pimm *et al.*, 1985; Abramsky *et al.*, 1990), and centrifugal community organisation (Rosenzweig and Abramsky, 1986). Models use non-linear zero-growth isoclines of both competitors and the isoleg, a set of points in density space of both competitors that separates optimal, strict habitat selection from mixed habitat use tactics of one species (Rosenzweig, 1981, for review; Rosenzweig and Abramsky, 1997). The habitat isodar (Morris, 1987) is the plot of densities in paired habitats such as that the expected fitness of an individual is the same in both habitat. Since densities of other species that cause a reduction in fitness of the focal species, they can change the shape of the isodar (Morris, 1989; Morris *et al.*, 2000) and thus be used to infer strength and nature of competitive interaction.

Time series of abundance data of two species can be analysed with a 'dynamic' approach (Shenbrot and Krasnov, 2002) to regression analysis (e.g. Abramsky *et al.*, 1991; Luo *et al.*, 1998; Morris, 1999). If several species are observed over longer time, time series analysis provides a powerful tool to investigate the importance of competition. Cyclic boreal vole population sizes of three co-existing species were used to show that interspecific competition may cause direct year-to-year negative density dependence on population sizes of some vole species (Hansen *et al.*, 1999). Interspecific density effects were not detectable in the 2-year delayed density dependence that is crucial for generating the characteristic cycles, which were attributed to species-specific trophic interactions. Many other authors attribute vole cycles to predator–prey interactions (Hanski *et al.*, 2001), however vole predators usually do not specialize on a single vole species, and may thus generate strong apparent competition (Holt, 1977) among co-existing vole species. The inclusion of interspecific competition in a predator–prey model has helped to explain several qualitative features of vole cycles (Hanski and Henttonen, 1996). Long-term data of a desert rodent system, where parts of the species assembly were excluded through a species-specific gates, showed that abundance of smaller granivorous species increased in absence of the largest granivorous member species, but other guilds, e.g. insectivorous species, were not affected (Heske *et al.*, 1994; Valone and Brown, 1995).

The application of regression models and time series analysis to different kinds of population data has firmly established that interactions of many sympatric species pairs are competitive and has also proposed models to explain the continued co-existence between competing pairs of species. The application of both 'static' and 'dynamic' of regression models to long-term community data may even distinguish between types of competition, e.g. exploitation and behavioural (interference) competition (Shenbrot and Krasnov, 2002). Often the complex regression techniques over different habitat types are however limited to two-species systems, and for more than two-species communities long-term data sets are required to investigate species interactions. Regression analysis based on ideal free distribution has been using the distribution of individuals in different habitats or with different competitor densities regardless of their sex or age (e.g. Abramsky and Pinshow, 1989; Abramsky *et al.*, 1991), neglecting a possible influence of social systems and relatedness (Morris *et al.*, 2001). Also sex- or cohort-specific interactions of parts of the competitor populations are possible, that may give indications about the nature of competition between species. These aspects have not yet been incorporated into the research on population sizes and habitat use.

Species assemblages

Authors in the 1970s gathered community data showing significant body size differences among co-existing seed eating desert rodents (Rosenzweig and Sterner, 1970; Brown, 1973; Brown and Lieberman, 1973; Hafner, 1977; Price, 1978). They were inferring an important role of interspecific competition in structuring the observed communities, preventing species with similar body size from occurring locally together and leading to character displacement (Brown and Wilson, 1956; Hutchinson, 1959). Community ecologists proposed a variety of assembly rules, many of them based on interspecific competition (Diamond, 1975; see Weiher and Keddy, 1999 for review). In a general backlash against the importance assumed for competition compared to other environmental factors, such observations were criticised to consist of indirect, circumstantial evidence which is subject to alternative explanations (e.g. Wiens, 1977; Connor and Simberloff, 1979; Strong *et al.*, 1979). Many argued that competition had been over-rated, and called for rigorous design in experimentation on competition (Connell, 1983; Schoener, 1983; Simberloff, 1982) and for the use of analytical tools such as null models, that would allow the istinguishing of random patterns from patterns generated by biological processes (Connor and Simberloff, 1979; Strong *et al.*, 1979; Harvey *et al.*, 1983).

In the research on assemblies of small mammals null models were also found useful. Fox' assembly rule was applied and debated for desert rodent communities. It proposes that interspecific competition leads to 'favoured states', an even representation of species in different functional guilds, that are sets of ecologically similar species (Fox, 1987; Fox and Kirkland, 1992; Fox and Brown, 1995). In desert rodent communities in North America, character displacement and Fox' assembly rules were shown to interact for a guild of granivorous desert rodents, suggesting that the co-existence of species of similar size was precluded by interspecific competition within the same ecological guild (Bowers and Brown, 1982). The use of modern computing technologies allows convincing comparisons on large geographical scales, and large numbers of communities, or high number of species per community. Kelt *et al.*

(1995), using data from 95 sites and Kelt *et al.* (1999), with data over 300 sites, found that desert rodent assemblages appear to differ in the underlying mechanisms in which communities were structured in the Americas (interspecific competition) and Asia (habitat selection). However, findings have also been challenged (Wilson, 1995; Stone *et al.*, 1996) claiming that the choice of species, scale, and their geographic ranges can produce biased results. Closely related mammal species, for example, can be found to overlap more than expected by chance on a large geographical scale (Letcher *et al.*, 1994). Arvicoline rodent communities in a removal experiment in Alaska were influenced by availability of preferred foods and by predation but less so by interspecific competition (Batzli and Lesieutre, 1995), community structure may thus be depending also on the productivity of habitat type. Therefore history, biogeography and resource distribution may play larger roles than thought in understanding the evolution of mammalian faunas.

Research on individuals

In species competing through interference, *behaviour* may give a clue about dominance relationships and asymmetric competition between species. Behavioural interactions between competing species remain difficult to study, since most small rodents have a rather cryptic and often nocturnal lifestyle. Apart from staged encounters (e.g. Grant, 1970) and rare direct observations (Mitchell *et al.*, 1990 in small enclosures; Heller, 1971, investigating diurnal chipmunks), most evidence on dominance of one species over the other has been indirect. Behavioural dominance of one species over the other has been indicated by inverse activity patterns (Brown, 1956; Kronfeld-Schor *et al.*, 2001), trap avoidance behaviour (e.g. Heske and Repp, 1985), or inverse foraging behaviour (Rosenzweig and Sterner, 1970; Ziv *et al.*, 1993; Ziv and Kotler, 2003, this issue). Radio-tracking provides a method of accurate following of habitat use, movements, temporal activity and interaction of individuals of two or more species (Kronfeld-Schor *et al.*, 2001; Maitz and Dickman, 2001). Some behavioural studies report habitat selection also in a laboratory setup (Grant, 1970; Stoecker, 1972; Hansson, 1983). Most studies report dominance of one species over the other, behaviourally expressed through either aggression (Grant, 1970; Heller, 1971; Conley, 1976; De Jonge, 1983; Wolff, 1985; Grey and Hurst, 1997) or avoidance behaviour of the subordinate species (Hoffmeyer, 1973; McPhee, 1984; Heske and Repp, 1985). The large number of studies reporting dominance and agression of one species towards another indicates that interference competition may be a common behavioural pattern among sympatric small mammal species. On the other hand, individual behavioural studies because of their short duration can rarely reveal information whether fate and fitness of individuals are influenced by a dominant competitor.

Few studies report individual fitness effects of interspecific competition on individuals. These studies consist of long-term capture-mark-recapture (CMR) studies or removal studies of open populations. CMR studies have documented lower survival and recruitment rates (Redfield *et al.*, 1977), and reduced reproductive rates (Viitala, 1977) in the presence of dominant competitors. Removal studies of open populations have reported reduced adult and juvenile survival (or possibly emigration as this is impossible to control for in open populations), reduced reproduction (Gliwicz, 1981) and differences in body size (Joule and Jameson, 1972; Montgomery, 1981) in the presence of competitors. Since these studies were conducted in open populations, they can not distinguish, whether observed differences in body size or reproductive patterns are a result of selective emigration or a change of individual's life-history tactics.

Effects of competition on life-history traits of individuals

Research on interspecific competition has addressed many important aspects of effects of a population of one species on the population of another species. Population-level responses to competition, however, are the cumulative effects of individual responses, and we think, that individual based, mechanistic aspects of interspecific competition in small mammals have been neglected in past research with very few exceptions. Behavioural studies are mostly too short to indicate fitness effects of interactions. We want to propose an experimental research approach that focuses on the life-history of individuals and its variations under competition and co-existence with other species. Life-history traits of individuals may help to explain population density changes and the interaction between species within communities. Inverse population sizes, for example, may be a product of individual processes, such as emigration, mortality, reduced reproduction, and may thus depend on the type of competition. The nature of fitness effects on individuals, can therefore also be used to distinguish between different types of competition. In the following section, we showcase research on the effects of interspecific competition in an experimental two-species system, using our own research on *arvicoline* rodents.

Life-history theory considers the schedule of reproduction and death in individuals, and can be a useful tool to describe fitness of individuals. Principal life-history traits are bound together by numerous trade-offs, such as between current reproduction and future survival, between current and future reproduction, or between the number and size of offspring (Stearns, 1992). The different ways of balancing these trade-offs in a variety of dietary, physical and social environments have resulted in a rich diversity of mammalian life history strategies (Bronsson, 1989). Voles in a boreal environment have a multivoltine life-history (many reproductive events) and most individuals can reproduce during only one season. If born late in the reproductive season, individuals have to delay their maturation and reproduction until the next breeding season over a many month long winter break with low survival chances.

Clethrionomys and *Microtus* voles are two very common vole genera of the old and new world. Population census studies had indicated competitive interaction between the two genera, and competitive exclusion of *Clethrionomys* by *Microtus* from habitats in which the former is doing well without the latter (Grant, 1972 for review; Henttonen *et al.*, 1977; Hansson, 1983; Löfgren, 1995). *Microtus*' dominance was also supported by experimental addition studies in enclosures (Grant, 1969; Hansson, 1983). The asymmetrical competition between the two genera could be explained using an evolutionary scenario following Hansson (1983): *Microtus* voles developed in ephemeral grassy patches within a sea of boreal conifer forest dominated by *Clethrionomys* voles. The omnivorous *Clethrionomys* can be potential food competitors for the nutritionally specialised *Microtus*, furthermore they are potential nest intruders. *Microtus* were thus selected for large body size and explosive reproduction in the small but productive grassy habitat patches to be able to competitively exclude *Clethrionomys* from these habitats. However, little is known about mechanisms of competition between these two genera, especially since their social system, diet, and the habitats they are most often found in, can vary considerably.

Our experiments were based on laboratory raised individuals of the Eurasian *Clethrionomys* – *Microtus* model pair, the bank vole C. *glareolus* and the field vole, M. *agrestis*. We developed a system for short-term experimentation on life-history traits in forced co-existence between the two vole species in large outdoor enclosures. Depending on season and the combination of individuals of the experimental bank vole population, effects of interspecific competition in all crucial life-history parameters, such as maturation, reproduction and survival can be followed (Eccard, 2002; Eccard and Ylönen, 2002a, in press; Eccard *et al.*, 2002). Effects of competition with the field voles on individual life-history traits of the bank voles, the subordinate competitor, were investigated in different field and bank vole densities. Performance of the individuals in survival, space use, growth, maturation, timing of pregnancies, offspring size and litter size were monitored. Experimental bank vole populations were released for a few weeks to the enclosures, and field voles, the competing species, were released to half of the enclosures. Bank vole females were removed to the laboratory at the end of their pregnancy in the field to investigate litters size and weight of pups conceived in the field. Behavioural and spatio-temporal interactions were followed by means of live-trapping (Eccard and Ylönen,

Table 1. Effects of competition of *Microtus agrestis* (left) and conspecific *Clethrionomys glareolus* (right) on main life-history traits of bank voles *C. glareolus*

Life-history traits of C. *glareolus* females	Increase of *Microtus* numbers		Increase *of* *Clethrionomys* numbers	
Survival				
Of breeding females	↓↓↓↓	a b w x	oooo	c f p z
Overwintered	o	x		
Year born	↓	x		
Of immature females	o	y	o	p
Of adults over summer	↓↓↓	w x		
Of adults over winter	o	r t		
Reproduction				
Pregnancy rate of breeding females	oo	w x	↓↓	e x
Maturation of weanling females	o	y	↓↓↓	e f g
Pregnancy of weanling females	o	y	↓↓↓	e f g
Offspring quality	ooo	w x y	o	q
Space use and behaviour				
Size of breeding territory	↓↓↓	w x	↓↓ but o	w h but c
Home range of juveniles	o	y	o	c
Winter home range size	↑	t	o	r
Avoidance behaviour summer	↑↑↑ but o	i j w but g	o	r
Avoidance behaviour winter	oo	k r	o	r
Initiation of spring breeding	o	r	delay	z
Maturation if juveniles	delay	y	delay	e f

Sources: (a) Hansson (1982), (b) Hansson (1983), (c) Bujalska and Grüm (1989), (d) Henttonen and 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 and 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), (w) Eccard and Ylönen (2002a), (x) Eccard (2002), (y) Eccard *et al.* (2002), (z) Eccard and Ylönen (2001).

Increase ↑ or decrease ↓ or no influence O of the selected trait in the presence of other species or conspecifics. A vote count from literature sources, symbols relate to the sources in the same order.

2002a), radiotracking (Halle *et al.*, 1999), activity recording (unpublished), and staged dyadic encounters (Köhler *et al.*, 2000).

The combined results of different experiments show, that the presence of field voles decreased survival of bank voles, and competition was identified as the primary variable affecting fitness (Table 1 left). The decrease was dependent on age, sex and breeding stage of the individual bank vole, with year born breeders suffering greater reduction of survival compared to over-wintered breeders or year born immatures (Fig. 2). The results suggested other life-history traits were affected than through density-dependence of con-specifics. While interspecific competition seemed to affect survival, intraspecific competition mainly affects maturation (Table 1, Bujalska, 1973, 1985; Löfgren, 1995; Tkadlec and Zejda, 1998; Prévot-Julliard *et al.*, 1999). However, survival effects of interspecific competition varied for different age groups of bank vole

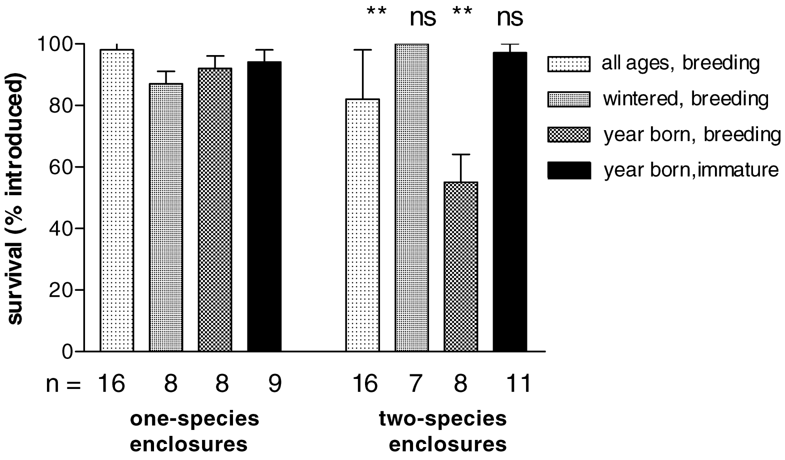

Figure 2. Effects of interspecific competition with field voles on the survival of bank voles of different age and breeding status. Combined results of different experiments with similar densities, comparisons in each category between one-species and two-species enclosures (students *t*-test). Survival of breeding females was reduced in two-species enclosures compared to one-species enclosures (Eccard and Ylönen, 2002a). Among breeding females, year born suffered a stronger reduction of survival than over-wintered (Eccard, 2002). Immatures survival was not affected by interspecific competition (Eccard *et al.* 2002).

females, and one may suggest that in the presence of a competitor it might be even advantageous for individuals to follow a different reproductive tactic than in its absence. In our system a year-born female bank vole should rather not breed during the summer of her birth in the presence of field voles. As an immature, her late summer and autumn survival would not be affected by the presence of field voles (Eccard *et al.*, 2002), and also her subsequent survival as an over wintered female in the next season would not be reduced (Eccard and Ylönen, 2002a). If she matured in the summer of her birth, she may face higher mortality through interaction with field voles (Eccard and Ylönen, in press). However, in a short-term experiment on maturation patterns of young females we found no adjustment of tactics due to the presence of field voles (Eccard *et al.*, 2002), but census data indicate an increase in maturation of bank voles in the absence of competitors (Löfgren, 1995). Since mortality seemed to selectively affect certain age groups of breeders, we suggest that the age combination of breeders may vary between populations in the presence and absence of competitors. If reproductive output differs between individuals of different ages (Boonstra, 1994; Morris, 1996) the age structure of a breeding population could affect the reproductive rate of populations.

The nature of interspecific competition between vole species may be indicated by the type of life-history variable affected. In our study system, we found no indications of resource competition during summer, since body weight of adults, litter sizes, and pup weights were similar between individuals in the presence and absence of competitors. These measures should have responded to food shortage (Cole and Batzli, 1978; Boutin, 1990). On the other hand, the mortality of some age groups increased in the presence of competitors. Mortality can increase through increased contact rates with superior conspecifics (Smyth, 1968; Gilbert *et al.*, 1986; Bujalska and Grüm, 1989) and seems to similarly increase with increasing contact rates with superior competitors (Eccard and Ylönen, 2002a). We thus suggest interference competition as the main mechanism affecting bank vole fecundity and survival during breeding season. Field studies, observing population development and space use, may also be combined with results on the individual, physiological responses to increased interference e.g. in the form of non-invasive stress monitoring (Harper and Austad, 2000; Eccard *et al.*, 2002).

In the boreal climate, short breeding seasons are separated by a 7–8 month long, non-reproductive winter break, during which aggressive interactions may be energetically very costly. *Microtus* and *Clethrionomys* voles are reported to co-exist during winter (Turner *et al.*, 1975). In a series of behavioural experiments in the outdoor enclosures both in summer and winter we found (Köhler *et al.*, 2000 and unpublished), that in mixed rodent communities as well as in single species populations, aggression levels in individual encounters are low during the non-breeding season. In spring at the onset of breeding higher aggression levels between species were observed. Thus the nature of competition may differ between seasons.

Conclusions

A wealth of population-level studies on the effects of interspecific competition on habitat choice and inverse population sizes exists for small mammals. An eternal focus is the study of effects of interspecific competition on population size and habitat use. Modern approaches have used sophisticated mathematical and modelling tools on population census data have firmly established the existence and importance of interspecific competition in many sympatric small mammal pairs and communities.

Population-level responses to competition, however, are the cumulative effects of individual responses, but the individual-level effect of competition on reproduction or survival has hardly been studied in past research. We would like to promote the inclusion of research on individual fitness into the studies of interspecific competition. Life-history research may be able to bridge investigations on individual fitness to population biology. While in open systems competitive exclusion and ‘the ghost of competition past’ often lead to the invisibility of interspecific competition, a very promising system to experimentally verify mechanisms and fitness consequences of interspecific competition may be forced experimental co-existence in enclosures. In addition to the short-term enclosure experiments introduced in this paper, more replicated long-term experiments which allow population growth over breeding season and follow survival over winter are needed. Though only a poor surrogate of complex systems, investigations of dispersal and dispersal thresholds in captive two-species systems may help the understanding of avoidance processes in open population systems.

Research on the effects of interspecific competition on individuals fitness and physiological costs could be a fruitful direction to elucidate the intricacies of interspecific competition. We hope that life-history theory provides a tool to connect effects and mechanisms observed from the individual-level to population-level effects.

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