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Inhalt

Introduction

Ever since Charles Darwin (1859) and Alfred E. Wallace (1903) wrote their unifying theories of evolution explaining the diversity of life, it is widely accepted that design follows the force of natural and sexual selection leading to evolutionary adaptation. Natural and sexual selection as designing mechanisms remove those variants, which cause their bearer a lower probability to represent its own genes in future generations (reduced inclusive fitness). Thus, evolution directed individuals towards adaptation and optimization in form and behavior with regard to the actual natural conditions and constraints (Maynard Smith 1982). Its goal is to achieve maximum inclusive fitness, in terms of transferring a maximum amount of individual genes into the next generations (Dawkins 1976). Prerequisites for this are high survival chances through sensitive behavior, efficient foraging strategies and effective reproductive strategies.

A way to study the adaptation of animals is to use optimality models that are designed to be applied to particular species and include parameters that can be readily measured (Parker and Smith 1990). These models aim to keep the analysis and conceptual conclusions as simple as possible and provide an adaptive explanation for the observed behavioral decisions (Salmon 1967).

To work with optimality models, a set of discrete strategies has to be defined, simplifying the plausible but complex behaviors that animals usually express. A strategy set is defined as a range of variants over which selection is supposed to be optimizing (Maynard Smith 1982). For example, an active animal has many simultaneous or sequential options to choose from to reach a source to forage. Many pathways of decision making finally lead to the achieved aim. All of these can be associated with different risks and/or opportunities. Thus there can be several strategies to cope with the task of gathering food, which can be more or less successful and promise varying rewards. These individual strategies can be limited by physiological and environmental constraints.

However, an animal is usually confronted with a large variety of options through the periods of activity or through the stages of life or within a complete lifecycle. There may be different types of prey available, different sources to explore or other individuals might become opponents or potential partners (Danchin et al. 2008). The value of each option can be flexible, according to the individual's status (e.g., sex, age or body condition and reproductive state) and external factors (e.g., season, temperature, time of the day, etc). Choices must be made, favoring some options over others. There is seldom a chance to optimize one strategy without accepting a confinement or a cost in some parameters.

Thus, any choice should be based on carefully calculated costs and benefits associated with any particular option. Herein embedded are severe conflicts: the trade-off between safety and the risk of predation, between starvation and nutrition and between reproductive isolation and inclusive fitness. As not all factors contributing to inclusive fitness can be maximized at the same time, animals should be able to estimate extrinsic factors (food provisioning, predator density, distance to sources or nest sites, season and temperatures) and individual parameters (hunger state, reproductive state) and carefully balance their needs to find an optimum.

How the external factors and intrinsic parameters affect individual decision making and what rules are applied to find the optimal strategy is still a challenging area of research that is based on 50 years of optimality research:

From the ideal free distribution theory (IFD) to the marginal value theorem (MVT) and the optimal foraging theory (OFT)

A way to study optimality and adaptation is to analyze foraging behavior in the context of the ideal free distribution theory and the optimal foraging theory (OFT).

The ideal free distribution theory (IFD) (Hutchinson and Macarthur 1959, Fretwell and Lucas 1969), assumes that an individual has the ideal knowledge of the environmental quality and its continuous food provisioning and moves unrestricted in this environment at no cost (Fretwell 1972). According to these assumptions, animals should distribute themselves in patterns that maximize energetic intake for every individual. Any type of interference between individuals or the influence of any external factor is omitted. Starting from these assumptions, we can add factors that restrict animal behavior and influence individual decision making (see I.M. Hamilton in Stephens et al. 2007 for review). Including restricting factors can help to explain individual behaviour under natural conditions, because individual behaviour is far from being optimal, influenced by interference, competition, predation and resource availability.

When researchers started to investigate foraging behavior in the mid-seventies, foraging and predation where treated separately. The idea, that energy maximization had the main impact on decision making predominated (Charnov 1976, Charnov et al. 1976). Early studies assumed that predators depressed their own food provisioning by exploiting sources (food patches) (Charnov et al. 1976) and based their patch leaving decision on the value of the actual patch compared to the marginal value of all available food in their habitat (resources landscape). Thus the lines of argumentation followed the rules of the IFD theory. Questions of individual behavior, optimization and predator-prey relationships where investigated as though they acted on different scales. Even the first edition of *Behavioural Ecology* (Krebs and Davies 1978) contained individual chapters on foraging, on predator-prey relationships and antipredatory defense strategies. It was not until the 1980´s of the last century that foraging behavior and risk through predation were linked together, for example by investigating the factors “habitat quality” and “predation risk” in a two factorial set-up and showing the emergent effects of multiple factors (e.g. for bluegills (*Lepomis macrochirus*) by Werner et al. 1983), or as in a study on black-capped chickadees (*Parus atricapillus*), which indicated that individuals sacrifice energy gain to reduce time of exposure to predation (Lima 1985).

Today, multiple factors are considered linked to decision making under predation risk, including, for example, unequal competitors (Sutherland and Parker 1985, Shochat et al.

2004), interference and uncontinuous energy flow in habitats (Tregenza 1995, Shochat et al. 2004), the risk of injuries (Berger-Tal et al. 2009) and costs of missed opportunities (Olsson and Molokwu 2007). Thus, an integrative approach to behavior is used that allows analyzing decision making in a combined context of the extrinsic and intrinsic factors.

The tendency to regard an animal as an interacting individual with the ability to assess pros and cons of different options needed the implementation of alternative currencies, for example, how animals compare and balance units of energetic gain und safety (Moody et al. 1996) or how they estimate the energetic equivalences of predation risk or mate search (Nonacs 2001, Hugie and Grand 2003). This was done by either translating all currencies into the expected influence on the inclusive fitness (Brown 1988, Brown 1992, McNamara and Houston 1994) or by assuming factors as being constant and further disregarding them. Such studies still relied on critical assumptions of the IFD theory, for example, the complete knowledge of the environmental resources. How animals actually assess their own and their environmental status and gather their knowledge of the environment, including the risk of predation, is now the focus of researchers. For example, the Bayesian forager approach (Olsson 2006) is a promising attempt to explain foraging decisions. It is assumed that animals benefit from gathering information and thus constantly update themselves while foraging or being active. This concerns the permanent evaluation of the value of food patches (Olsson and Holmgren 1998) as well as the level of risk while active (Bell et al. 2009) or the evaluation of combinations of many ecological parameters (Olsson and Holmgren 1999). Thus, animals can base their decisions on changes of risk or states compared to a prior risk or state by obtaining continuous estimates of the respective parameters and carefully balance the allocation of effort to vigilance or alternative activities.

Optimal foraging and predation risk

With the idea that animals integrate many ecological parameters into their calculation when making a decision, the way was open to indirect analyses of the perception of risk by observing animals in standard situations such as the resource exploitation (Olsson et al. 2001, Morris and Mukherjee 2007). For example, to evaluate if and how animals perceive predation risk, their allocation of time to different foraging activities could be analyzed instead of directly observing defense behavior or having to encounter an animal with its predator (Olsson and Molokwu 2007).

The classical approach to study the impact of predation risk on optimal foraging behavior is to analyze the use of foraging stations. These stations and their environment were deliberately manipulated in their risk of predation by reducing cover or by simulating the presence of a predator (e.g., with odor probes, artificial silhouettes, etc., (Korpimäki et al. 1996, Borowski 1998, Jacob and Brown 2000, see Brown and Kotler 2004 for review, Eccard et al. 2008)). First results showed that the energy invested into resource exploitation should be related to 1) the perceived predation risk at the foraging station, 2) the energy that has to be invested to gain food and 3) the value of other opportunities as mate choice or territory defense (Brown 1988, Brown 1992, Brown et al. 1994). According to these factors, the harvest rate H at a source has to satisfy the energetic (metabolic) costs of foraging (C), the costs of the predation risk (P) and the costs of missed opportunities (MOC) while foraging: $H = C + P + MOC$ (Brown 1988). So a resource patch should be left when the harvest rate drops under the energetic equivalent of these three factors.

Experimental evaluation of this formula was mainly done by analyzing giving-up densities (the food left after an animal has exploited a source, GUD) at non refilling sources. In such sources, food is mixed into a medium (for example grains in sand) leading to exponentially diminishing returns over time of exploitation. While at the beginning energy gain at such stations is high, the ratio of invested energy to returned energy declines, eventually forcing the animal into a patch-leaving decision.

Mainly studies of exposure of small mammals to mammalian (Koivisto and Pusenius 2006) or avian (Kotler and Blaustein 1995) predators or their scents (Kats and Dill 1998) while foraging were conducted to identify the effects of single factors on patch leaving decisions. However, comparisons of activity allocation under 1) simultaneous or sequential exposure to different predators (predator facilitation (Kotler et al. 1992)), 2) emergent impact of multiple predators (Sih et al. 1998) or 3) different levels of illumination or daytimes have also been a fertile ground for research (Clarke 1983, Price et al. 1984, Daly et al. 1992).

In most of these studies, the missed opportunity costs as well as the metabolic costs were assumed to be constant. Nevertheless, these studies have led to new interpretations of decision making in small animals. Instead of the pure maximization of energy gain, the trade-off between risk and foraging and other opportunities was seen to be the driving force of individual behavior. It became evident that individuals can deal with temporal variation in danger and allocate activities and duties accordingly (Sih 1992, Lima and Bednekoff 1999). Additionally, they include their personal state (body condition, reproductive state) into the calculation (Nonacs 2001, Kotler et al. 2004) and can act and decide on frequent updates of the environmental conditions and levels of risk or sources (Olsson and Holmgren 1998, Olsson and Holmgren 1999, McNamara et al. 2006, Bell et al. 2009).

Still, this body of research sometimes relies on critical assumptions or assumes important factors influencing animal behavior to be constant:

Open problems:

1) The optimal foraging theory relies on the assumption that all animals perfectly know their environment and the resource levels provided by sources in their environment. This implies that animals can differentiate between high and low quality habitats and align the perceived risk accordingly. The perception of risk is easy to test by artificially manipulating the environment and making it deliberately heterogeneous in environmental factors like ground cover. It is evident that individuals can differentiate between habitats of different predation risk via indirect cues (like cover reducing avian predation) and actively choose the safer places still containing enough food to survive. However, many prey animals live in vast homogeneous landscapes (dessert, fields and

meadows). Additionally, they are confronted with at least one predator that uses the same scales (for example, the least weasel (Sundell and Ylönen 2004), for example snakes and / or avian predators, the risk of which is hard to assess before the actual attack (Jedrzejewski et al. 1993, Kotler et al. 1992). Thus, for prey animals, which travel in environments with no cover or homogeneous cover, the threat by avian predation should be homogeneously distributed, and so should be the risk of predation by same-sized predators (because no safe retreats exist). For these conditions, no experimental evaluation or validated model exists. For rodents, the above mentioned predators are unpredictable in their movements and whereabouts, seldom heard or seen before attacking. Thus, there is no choice between habitats of different quality, but strategies should have evolved to adopt foraging and activity patterns to the perceived overall level of risk. These strategies should include the minimization of travelling and exposition to predators, as travelling is more dangerous than any other activity (Norrdahl and Korpimaki 1998).

2) The ideal free distribution theory and the special case of the optimal foraging theory have both been the focus of critical articles, regarding the testability of the assumptions that have to be made when applying the theories to actual problems of animal behavior. One problem is the intermixture of currencies when using formulas that sum up dimensionless variables like predation risk or the multiple variables of missed opportunities and costs of metabolism in terms of energy (Haccou and Vandersteen 1992). The solution to this is either translating all variables into one currency, which was actually done by Brown by translating all variables into units of fitness (Brown 1988, McNamara and Houston 1994) or what is still done most often: assuming metabolism and missed opportunities costs as being constant and disregard the two in further analysis of the results. This resulted in a trend to completely disregard factors influencing an animal's metabolism or its evaluation of the missed opportunities. For example, body weight, age and, most severely, the sex of a tested group of animals is often ignored (Kotler 1984, Jedrzejewski et al. 1993, Borowski 1998, Abramsky et al. 2004, Koivisto and Pusenius 2006). On the other hand, authors often assert the failure of the theory to explain patch residence time, where animals usually show an overestimation of patch quality, resulting in patch residence times that are longer than expected from the models predicting the maximization of the overall energy gain (Forkman 1991, Kamil et al. 1993, Nonacs 2001). These problems can be solved by taking other costs into account that might contribute to the value of a source as, for example, a meeting point with the other sex or the chance of meeting predators when travelling between sources. Males might well associate more with travelling and feeding in terms of missed opportunities (like territory defense or multiple mating chances) than females, especially in promiscuous, multivoltine or polygynous species. Thus males should show more risk-prone or aggressive behaviors than females which usually results in male biased mortality rates (Dickman et al. 1991, Clutton-Brock and Parker 1992, Bryja et al. 2005, Clutton-Brock 2007). Taking the sex, age or reproductive status of the investigated individual into account by

treating these as factors might explain high variation of data and will give valuable insights into individual status dependent behavior and decision making.

3) Various factors constrain the free movement in natural environments. There is a vast group of animals that are bound to a certain site, because of a limited number of breeding places, for example, or because they are committed to provide parental care. This includes another dimension of decision making: animals providing parental care have to include the value of their offspring and the potential predation risk for the offspring by nest predators. Choosing a safer habitat or another time window is no option in these cases. This might lead to a completely different evaluation of the value of food sources compared to other opportunities. For example the distance of a source to the nest site might gain importance, while the chance of meeting mating partners might be of no interest to an animal that is lactating or pregnant. Thus, the analysis of foraging strategies should include the actual (reproductive) status and with it additional values like current or future offspring of an animal and the social context it lives in as factors.

The above mentioned problems lead to the design of experiments that should provide adaptive solutions as parts of my PhD project:

1.) As a basic framework, I analyzed foraging strategies in risk-homogeneous landscapes. I asked the question, whether animals adapt their foraging strategies according to the overall level of perceived risk when no choice is given between habitats with different qualities. An artificial landscape was presented, consisting of foraging places of equal risk and an equal risk of travelling between these was provided. 25 foraging stations in a 3 x 3 m grid simulated a landscape of homogeneously distributed resources which could be exploited by the animals. The short and long-term strategic changes to homogeneously distributed odour samples of a least weasel were analyzed and combined with a simulation of homogeneously distributed avian predation risk. In this two-factorial setup (risk by weasel predation high / low and avian predation high / low) foraging decisions and activity parameters were investigated. An animal's response in foraging strategies should differ when different classes of predators are presented (avian or ground predation), according to the cues given by a predator species (olfactory, acoustic, optic or none). Olfactory cues provide information about immediate danger according to the amount of volatile compounds still present and could thus evoke changes of temporal patterns, whereas a high level of avian risk (estimated by missing cover from avian predation) could evoke changes of movement patterns to be as inconspicuous as possible. This experiment led to two published papers, one first authored by Thilo Liesenjohann, one by Dr. Jana Eccard. They form the first two chapters of this thesis.

2.) In a second experiment, foraging as a function of missed opportunities was investigated. Depending on the sex, social system, reproduction mode, and reproductive investment, the perception of risk should be influenced by the status of an individual. To test if the sex plays a role in assessing environmental qualities and opportunities, same sized and sexual active males and females of the common vole (*Microtus arvalis)* were simultaneously exposed to different levels of predation risk, and their allocation of effort to foraging and other activities was evaluated. This led to a submitted manuscript being the third chapter of the thesis.

3.) In order to analyze whether indirect predation pressure via a nest predator (the common shrew, *Sorex araneus*) influences the foraging decisions of lactating bank vole mothers (*Myodes glareolus*), an outdoor study at (and together with) the Konnevesi Research Station / University of Jyväskylä in central Finland was conducted. This study was replicated in summer and autumn to analyze the effect of different food provisioning in different seasons on the type and strength of interference of the two species.

These studies lead to two manuscripts with various coauthors. The first deals with the use of foraging stations and temporal adaptations by lactating bank vole mothers under direct avian and indirect predation pressure by a nest predator in two different seasons. The second analyzes changes in habitat use, recruitment and body weight under the same pressure (firstauthored by Monique Liesenjohann). These submitted manuscripts are chapters 4 and 5 of the thesis.

Einleitung

Seit Darwin und Wallace ist anerkannt, dass die kontinuierliche Veränderung der Umwelt Lebewesen dazu zwingt, sich permanent zu entwickeln und neu anzupassen (Darwin 1859, Wallace 1903). Das bedeutet, in einem sich entwickelnden, dynamischen System ist eine permanente Weiterentwicklung unerlässlich. Nur sie garantiert eine zumindest gleichbleibende Fitness relativ zu dem System in dem sich eine Art eingenischt hat (van Valen 1973). Auf die plötzlichen oder allmählichen Veränderungen der Umwelt stellen sich Individuen durch Adaptationen ihres Verhaltensrepertoires ein (phänotypische / neuronale Plastizität, Nespolo 2000, Ozgul et al. 2009). Es kann sich aber auch ein Prozess der Koevolution über lange Zeiträume entwickeln, in dem sich Arten durch zufällige genetische Mutation und Rekombination entwickeln und sich dadurch anpassen oder aussterben (natürliche Selektion, Endler 1986, Gross 2008). Individuelle Plastizität und Koevolution sind Optimierungsprozesse mit dem Ziel, so lange wie möglich zu überleben und sich erfolgreich zu reproduzieren (Dawkins 1976). Die kurzfristigen und flexiblen Verhaltensadaptationen von Individuen mit dem Ziel der optimalen Anpassung an die vorgegebenen Umstände sind Gegenstand vieler Studien der Verhaltensforschung und werden häufig in einem System untersucht, das eine lange Geschichte der gemeinsamen Koevolution aufweist. Hierzu zählen die Beziehungen zwischen Tieren (z.B. Räuber-Beute-Systeme, intra- und interspezifische Konkurrenz) aber auch die optimale Anpassung an abiotische Faktoren (Temperatur und Ressourcenlage).

Die Antwort auf die Frage, welche Parameter optimiert werden, hat sich durch zunehmende Erfahrung mit Optimalitätsmodellen und komplexeren statistischen Analysemethoden stark gewandelt: In den siebziger und achtziger Jahren wurde davon ausgegangen, dass Tiere nur eine Option maximieren, klassischerweise die Nettoenergieaufnahme, und alle ihre Strategien daraufhin ausgerichtet sind (MacArthur and Pianka 1966, Charnov 1976, Charnov et al. 1976, Krebs and Davies 1978). In den folgenden zwei Jahrzehnten wurden immer mehr Faktoren in Studien integriert und analysiert, um Verhaltensstrategien im Sinne von Optimierungsprozessen so gut wie möglich zu verstehen und um aussagekräftige, integrative Modelle erstellen zu können. Hierbei spielte zum Beispiel der Einfluss verschiedener Prädatoren sowie von Umweltfaktoren und deren Wechselwirkungen mit Strategien der Nahrungsaufnahmen eine besondere Rolle (Sih 1980, Clarke 1983, Kotler 1984, Lima 1985, Brown 1988, Lima and Dill 1990, Kotler et al. 1991, Brown 1992, Kotler et al. 1992, Lima 1992, Korpimäki et al. 1996, Lima 1998). Heute wird angenommen, dass Tiere sowohl zeitliche als auch räumliche Muster erfassen (Bell et al. 2009, Eccard and Liesenjohann 2008), ihre eigenen Erfahrungen in Entscheidungsprozesse einarbeiten (Liesenjohann and Eccard 2008, McNamara et al. 2006, van Gils 2010) und äußerst flexibel auf Änderungen eingehen können (Olsson and Molokwu 2007). Ebenso sind sie in der Lage verschiedene, simultan auftretende Prädatoren zu erkennen und ihre Strategien entsprechend anzupassen (Liesenjohann and Eccard 2008, Morosinotto et al. 2009, Sih et al. 1998).

Probleme der ideal freien Verteilung (ideal free distribution, IFD) und der optimalen Nahrungsaufnahme (optimal foraging theory, OFT)

Optimalitätsmodellen liegen die Theorien der ideal freien Verteilung (ideal free distribution, IFD, zusammengefasst in Tregenza 1995) und der optimalen Nahrungsaufnahme (optimal foraging theory (Charnov 1976)) zugrunde. Sie sind jedoch nicht uneingeschränkt für die Interpretation von unter natürlichen Bedingungen aufgenommen Daten verwendbar (Haccou and Vandersteen 1992, Cezilly and Benhamou 1996, Griffen 2009). Die Grundlagen dieser Theorien können nur in künstlichen Versuchen untersucht werden, sie kommen in der Natur nicht vor und sollten deshalb kritisch getestet werden. Hierzu zählen die Annahmen der freien und uneingeschränkten Verteilung von Individuen in Abhängigkeit von der Ressourcenlage, sowie die freie Wahl zwischen Habitaten unterschiedlicher Qualität (zum Beispiel nach der heterogen verteilten Ressourcenverfügbarkeit oder zeitlich und räumlich heterogen verteiltem Prädationsrisiko). Zusätzlich wird vorausgesetzt, dass alle Tiere die zur Verfügung stehenden Quellen und ihre Ergiebigkeit kennen. Es wird auch davon ausgegangen, dass Tiere sich des Prädationsrisikos ihrer Umgebung bewusst sind und dementsprechend den trade-off (die Allokation von Zeit und Energie zu einer bestimmte Option) zwischen Prädationsrisiko und Nahrungsaufnahme optimieren. Andere Alternativen (Paarungspartner suchen, Revier verteidigen) oder metabolische Kosten wurden dazu bisher als Konstanten zusammengefasst und in der Dateninterpredation ignoriert. Um die Allokationsfähigkeit von Individuen zu testen, wurden bisher Habitate mit unterschiedlichen Graden von Prädationsrisiko und Nahrungsverfügbarkeit angeboten und den Tieren eine aktive Wahl überlassen in wie weit sie Nahrungsaufnahme und / oder Sicherheit optimieren (Brown 1988, Kotler and Brown 1990, Brown et al. 1994). Der Fall, dass Tiere in Habitaten mit homogener Risikoverteilung leben, sei es, weil das Habitat extrem monoton ist, oder weil die Tiere das Risiko nicht abschätzen können oder sei es, weil der Prädator die gleiche Größe hat und es somit keinen sicheren Raum gibt, wurde bisher nicht untersucht. Ebenso wurden bisher Individualparameter wie das Geschlecht, das Alter oder der reproduktive Status vernachlässigt. Alle diese Parameter können jedoch die Entscheidungsfindung und die Gewichtung von Optionen beeinflussen. Auch die Interaktionen zwischen Individuen, inklusive der Ausbeutung gemeinsamer Ressourcen oder die indirekte Prädation wurden wenig im Hinblick auf ihre Auswirkungen auf Optimierungsprozesse und Futtersuchstrategien berücksichtigt.

Eine Methode zur Untersuchung der Allokationen von Zeit und Energie in Abhängigkeit vom Prädationsrisiko ist die Analyse der Nutzung von künstlichen Futterstationen in denen Futter in ein Medium (z.B. Sand) gemischt wird. Diese Futterstationen stellen eine endliche Ressource dar und die Futterdichte nimmt während der Ausbeutung ab, so dass die Effizienz (gefundenes Futter pro Zeiteinheit) abnimmt (Brown 1988, Charnov 1976). Das hat zur Folge, dass das Verhältnis von gewonnener zu investierter Energie mit der Zeit schlechter wird und die Tiere gezwungen sind, die Quelle zu verlassen und eine andere Futterstelle zu suchen (Grenzwerttheorem, marginal value theorem (Charnov 1976, Mcnair 1982, Wajnberg et al. 2000). Wann eine Ressource verlassen wird, kann von dem individuell empfundenen

Prädationsrisiko abhängen, und zwar dem relativen Verhältnis des empfundenen Risikos an der Futterstelle und dem Risiko auf dem Weg zur nächsten Futterstelle. Ein hohes Risiko an der Futterstelle führt zu frühem Verlassen, ein hohes Risiko auf den Wegen zwischen ihnen führt zu einer längeren Verweildauer an der Ressource. Diese Entscheidung wird außerdem durch den Gesamtressourcenlevel, durch die Kosten für Alternativen, die während des Fressens nicht wahrgenommen werden können, und durch metabolische Stoffwechselverluste beeinflusst (Brown 1988, Kacelnik and Todd 1992, Nonacs 2001). Diese Kosten für alternative Chancen und Metabolismus sind häufig diffus und werden als Konstanten zusammengefasst. In den alternativen Optionen sind jedoch wichtige statusabhängige Faktoren versteckt. Aufgaben wie das Verteidigen des Territoriums oder die Suche nach Paarungspartnern gehören hierzu, sind jedoch völlig unterschiedlich je nach Geschlecht und Sozialsystem. Diese alternativen Aufgaben können massiven Einfluss auf die Einschätzung der Wertigkeit einer Futterquelle haben und große Variation verursachen, wenn Populationen in ihrer Gesamtheit untersucht werden ohne das Faktoren wie zum Beispiel das Geschlecht oder der Status (zum Beispiel hungrig oder satt (Berger-Tal et al. 2010)) mit analysiert werden. Auch der Metabolismus kann innerhalb und zwischen Individuen stark schwanken (zum Beispiel drastisch steigen bei laktierenden Weibchen), auch er kann also die Gewichtung von Entscheidungen beeinflussen.

Auf der Grundlage dieser der Einfachheit halber bisher vernachlässigten Parameter und Grundannahmen wurden Fragestellungen erarbeitet, die einen Einblick in die Verhaltensoptimierung unter homogener Risikoverteilung und / oder bei statusabhängiger Entscheidungsfindung geben sollen.

Fragestellung:

In der vorliegenden Doktorarbeit wurden drei Themenkomplexe bearbeitet und anhand von Labor- und Freilandversuchen mit Rötel- (*Myodes glareolus*) und Feldmäusen (*Microtus arvalis*) untersucht:

1.) Homogene Risikolandschaften:
  - Haben Tiere ihre Nahrungssuchstrategien an Habitate angepasst, die sich durch gleichmäßig verteiltes Risiko auszeichnen? Hierbei wurde die Frage beantwortet, wie Tiere sich verhalten, wenn es nicht die üblicherweise angenommene Alternative gibt, in sichere Habitate zu wechseln. Stattdessen müssen Tiere räumliche und zeitliche Strategien bei der Ausbeute von Futterstellen entwickeln, in denen Parameter mit großem Prädationsrisiko minimiert werden und in denen der Grad des Gesamtrisikos eines Habitats eingeschätzt werden muss. Hierfür wurden künstliche, 3 x 3 Meter große Indoor-Arenen mit gleichmäßig verteilten Futterquellen geschaffen und der homogene Gesamtrisikolevel diese „Habitats“ mit Hilfe von Deckung (simulierte Luftprädation) und Streuproben (simulierte Bodenprädation) manipuliert.

2.) Alternative Aktivitäten und Chancen:

- Welche Parameter spielen neben der Prädation eine Rolle bei der Optimierung von Nahrungssuchstrategien? In Abhängigkeit von dem Sozialsystem in dem ein Tier lebt, können die Kosten für eine Option je nach Geschlecht unterschiedlich abgewogen werden. Es wurde getestet, ob Männchen und Weibchen unterschiedliche Futtersuchstrategien verfolgen. Bei Männchen könnten alternative Optionen wie das Verteidigen von Territorien und das Monopolisieren von mehreren Weibchen einen Einfluss auf die Allokation von Zeit und Energie haben. Bei Weibchen hingegen könnte der Schutz des Nachwuchses ein wichtiger Faktor sein. Hierfür wurden Männchen und Weibchen in Aussenarenen simultan getestet und der Risikolevel sowie die Risikoverteilung (homogen vs. heterogen) manipuliert.

3.) Abschätzen indirekter Risiken:

- Entwickeln Tiere, die an einen Ort gebunden sind und sowohl direkter als auch indirekter Prädation ausgesetzt sind, besondere Strategien der Nahrungssuche? Hier muss nicht nur das eigene Risiko kalkuliert werden, sondern auch das potentielle für den eigenen Nachwuchs. Aufgrund der Bindung zum Nest stellt hier ein Ausweichen in andere Habitate keine Option dar. Gezeigte Nahrungssuchstrategien müssen also auch die Wertigkeit des Nachwuchses für die eigene Inklusivfitness berücksichtigen. Hierfür wurde das Nahrungssuchverhalten laktierender Wühlmausweibchen untersucht, während sie einem potentiellen Nestprädator ausgesetzt waren. Es wurde die Nahrungsaufnahme aus künstlichen Futterstellen in ¼ ha Aussengehegen der Universität Jyväskyla / Finnland untersucht. Neben der natürlichen Prädation durch Luftprädatoren wurde ein Teil der Gehege zusätzlich mit Spitzmäusen (*Sorex araneus*) besetzt, um eine Bedrohung für die Wühlmausjungen zu generieren. Dieser Versuch wurde in zwei Replikaten einmal im Sommer und einmal im Herbst durchgeführt, um den Einfluss der Nahrungsverfügbarkeit auf die Form der Interaktion der beiden Arten zu untersuchen.

Die in den folgenden Veröffentlichungen im Detail dargestellten Verhaltensanpassungen zeigen, dass die Risikostruktur des Habitats, der Status des beobachteten Tieres und die Interaktion mit anderen Arten in natürlichen Habitaten einen entscheidenden Einfluss auf die Verhaltensmuster und die gezeigten Ausprägungen des Verhaltensrepertoires haben können.

Original publications and submitted manuscripts:

I. Foraging under uniform risk from different types of predators
Liesenjohann, T, Eccard, JA
BMC Ecology 2008, **8:**19 doi:10.1186/1472-6785-8-19
Both authors contributed equally to the development of the methods and design, TL collected and analyzed the data, wrote and submitted the manuscript, JAE contributed valuable information to the statistical analysis and added important intellectual content to the manuscript.

II. Foraging decisions in risk uniform landscapes
Eccard, JA, Liesenjohann, T
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JAE conceived the experiment, analyzed the data, wrote and submitted the manuscript. TL performed the experiments and added valuable intellectual content to the statistical analysis and the manuscript.

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Both authors contributed equally to the development of the methods and design, TL collected and analyzed the data, wrote and submitted the manuscript, JAE contributed valuable information to the statistical analysis and added important intellectual content to the manuscript.

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The study was conceived and designed at round tables by all contributing authors; all coauthors helped in the acquisition of data and added content to the manuscript. TL performed the statistical analysis, wrote and submitted the manuscript.

V. From interference to predation: type and effects of direct interaction between granivorous and insectivorous small mammals
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I. Foraging under uniform risk from different types of predators

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Abstract

Background

Many animals live in environments where different types of predators pose a permanent threat and call for predator specific strategies. When foraging, animals have to balance the competing needs of food and safety in order to survive. While animals sometimes can choose between microhabitats that differ in their risk of predation, many habitats are uniform in their risk distribution. So far, little is known about adaptive antipredator behavior under uniform risk. We simulated two predator types, avian and mammalian, each representing a spatially uniform risk in the artificial resource landscapes. Voles served as experimental foragers.

Results

Animals were exposed to factorial combinations of weasel odour and ground cover to simulate avian and/or mammalian predation. We measured short and long term responses with video analysis and giving-up densities. The results show that previously experienced conditions cause delayed effects. After these effects ceased, the risks of both types of predation caused a reduction in food intake. Avian predation induced a concentration on a smaller number of feeding patches. While higher avian risk caused a delay in activity, the weasel odour shortened the latency until the voles started to be active.

Conclusions

We show that the voles differed in risk types and adjusted their feeding strategies accordingly. Responses to avian and mammalian risk differed both in strength and time scales. Uniformity of risk resulted in a concentration of foraging investment and lower foraging efficiency.

Background

Predation influences the ecology of a prey species by directly increasing mortality and by altering prey behaviour indirectly (for reviews, see [1-3]). Antipredator behaviour includes foraging decisions [4], microhabitat shifts [5, 6] , and activity shifts [7, 8]. In all situations investigated, essential trade-offs exist between antipredatory behaviour and other fundamental activities, like foraging and mating [8, 9].

Depending on the type and persistence of risks, the behavioural responses to short and long pulses of risk vary and include shifts of feeding effort to either safe periods (the predation risk allocation hypothesis [9]) or safe habitats [10-12]. However, what if there are no safe times and places to forage? If risk increases suddenly, animals can reduce activity, which lowers the energetic reserves of the individual [13]; however, if high risk is frequent or persistent, animals still need to feed and cannot continually avoid the risky periods [9]. In these cases, they should either posses permanent defences (e.g. chemicals or physical adaptations) or show behavioural adaptations. Due to the huge range of rodent predators, physical adaptations might not be as promising as behavioural plasticity. Thus, the difference in antipredator behaviour between high and low risk situations should decrease if periods of high risk are persistent [9]. Instead of allocating their effort to safer times, the animals might react by applying alternative feeding strategies.

In studies with heterogeneously distributed predation risk, rodents have been found to trade food in favour of safety by using safer microhabitats, indicating that animals consider relative levels of risk [14, 15]. However, little is known in cases where risk is distributed uniformly in space and time. For example, in non-fragmented environments, an assessment of avian predation might not be possible and must therefore be assumed to be omnipresent. Furthermore, prey can face predators of the same locomotory type and body size as themselves, resulting in a uniform distribution of predation risk with no place for the prey to hide. For rodents, the least weasel *Mustela nivalis* (Linnaeus, 1766) is one such example of an omnipresent predator [16, 17]. Behavioural adaptations to these types of persistent risk uniformity are poorly studied. Our own studies on foraging in risk homogeneity have suggested that foragers concentrate their feeding effort in few locations and accept lower feeding efficiency ([18]; Eccard and Liesenjohann 2008, under review). We interpret this trade-off in the context of local foraging decisions [8, 19] and extrapolate the sum of local foraging decisions to a landscape level. Brown [8] extended Charnov´s marginal value theorem [19] to show that foragers balance harvest rates with metabolic costs, predation risk, and opportunity costs. These studies focus on local differences in predation risk by assuming that the metabolic and opportunity costs are constant. However, under uniform predation risks, the local predation risk in different food patches does not vary and the metabolic costs are also assumed to be constant among patches. Thus, foraging decisions depend on the costs of other activities besides foraging in a local patch. For example, the opportunity costs might be low under high uniform risk; since other activities and other animals underlie the same high risk as the forager, the foragers exploit patches to low quitting-harvest rates. In low risk situations, alternative opportunities like territory defence and mate search might gain importance because all animals underlie the same conditions and overall activity will be higher under low risk. Thus, the distribution of feeding effort over a greater area might be a consequence of high activity and engagement in multiple opportunities.

Even though most animals live in environments with multiple predators (e.g., hawks and owls, canids or snakes [20]), surprisingly few studies have assessed the conflicts arising from life under the threat of different types of predators ([21-24], but see Sih (1998) [24] for a review). Behavioural responses that reduce mortality from a predator type may expose the animal to greater mortality from a second predator type [19], so a predator-induced shift of habitat may send prey into “the jaws, talons or fangs of another species of predator” [22]. Small mammals face more than the problem of two predators in different microhabitats; they have to deal with different types of predation at the same time. Most studies dealing with more than one predator have regarded their effects as additive, which is difficult to address in a biological and statistical sense [24]. For example, the availability of cover [25] and scents of mammalian predators [26] heavily alter foraging behaviour [27] and can change with the season [28] or the time of a day [29, 30]. How these factors interact when occurring simultaneously in uniform risk landscapes remains unstudied.

An individual has to decide when and where to forage and, in order to maximise fitness, has to take a given risk context into account. Animals respond adaptively to changes in predation risk and exhibit several strategies to minimise their exposure to predators [22, 31, 32]. Therefore, foraging decisions can be used as an indicator of how animals perceive their environment [8]. We investigated the foraging behaviour of small mammals in depletable food patches and simulated two types of uniform risk, avian and mustelid. Avian predation risk was manipulated by ground cover (first factor, either high or low), whereas mustelid predation risk was manipulated by the presence of an odour of a least weasel (*Mustela nivalis*) (second factor, odour present or not). Foragers were exposed to high or low avian and mammalian predation risk levels in a 2x2 factorial set up.

In high risk situations, animals should tend to avoid travelling between sources and value known food resources more than uncertain findings. Additionally, the option of fulfilling alternative tasks becomes less attractive because opportunities like mate search or territory defence are linked to a greater exposure to predators.

We predict that, under high, uniformly distributed risk, animals will concentrate their foraging effort to fewer trays and expect different temporal scales for the two risk types. Responses to mustelid predation are expected to be observed on a short time scale because predator odour is a reliable sign of predator presence [27]. The risk by avian predation is difficult to estimate for a ground dwelling rodent. Birds of prey can cover plains very quickly, and their presence or absence is almost unpredictable for the prey [31]. Therefore, we expect that, in higher avian risk treatments, the avian predation risk is perceived as a constant threat over the entire experimental time scale and should also lead to a concentration of effort. We aim to dissect short term and long term responses by the video analysis of short term responses, such as foraging delay and behaviour in the first foraging bout after application of odour treatments, medium term responses such as concentration of effort and number of bouts in the first six hours after a change of treatment, and long term changes by comparing the first and second day of a treatment. With the factorial set-up, we further aim to discover interactions among the two risk types.

Methods:

Animals

Twelve wild caught male bank voles (*Myodes glareolus,* (Schreber, 1780)) served as experimental foragers. The animals were randomly assigned to three groups, because only four test arenas were available. Each animal of a group of four was tested for a total of 18 days. The first four individuals were tested in March, individuals 5-8 in April, and individuals 9-12 in May 2006. One was excluded during the experiment due to the absence of a response to any of the treatments. Animals were habituated to the experimental arenas and to the required mode of feeding from seed-trays for 4 days followed by an experiment where only ground cover was manipulated for six days (reported in [33]). After this experiment, all animals were kept under ground cover (wire mesh) for two days to provide similar starting conditions and independence from former experimental groups for the experiment reported in this paper. Animals were habituated indoors to a 12:12 hour L: D cycle, which was adjusted until darkness started at 12.00 to ensure activity during the treatment phases. Animals were weighed prior to each experiment, after the habituation phase, and after each experiment. All animals lost weight in the four-day habituation phase prior to experiment one, and their weights were constant for the duration of the experiment (mean initial body weight ± 1SE: 25,9 ± 3,3 gr., Mean weight loss: 2, 6 ± 1, 4 gr.). Consecutive groups contained breeding states from sexually inactive animals (March) to animals in an intermediate state in the second group (April), followed by fully sexually active animals (May). This difference among the groups was accounted for by including a three-level factor “season” into the statistical model.

Arenas and treatments

Indoor arenas of 9 m^2 contained a 5 cm high layer of sand and were surrounded by 100 cm high steel walls. Each animal was provided with a shelter consisting of a small (12x7 cm, 4 cm high) box in the middle of the arena throughout the whole treatment sequence. Above each arena, infrared cameras were installed using a 50W red-light bulb per arena.

We utilized a 2x2 factorial design examining the effects of predation (present or absent) crossed with ground cover (present or absent):

The presence or absence of predator odour was used to simulate predation risk by a terrestrial predator. Cage bedding of a least weasel (*Mustela nivalis*) was distributed before each observation period over all seed trays, making all feeding stations equally dangerous. The odour donor was a male least weasel fed a diet of *Microtus arvalis* and *Myodes glareolus.* Every fourth day, the cage bedding was removed and frozen at -20° until used in the experiment. As a control, we used clean, frozen cage bedding.

The presence or absence of ground cover, simulating low or high avian predation risk. For cover, we provided a wire mesh of 1cm mesh size that was installed on small stilts 4 cm above the ground and through which we were able to video tape movements.

The four combinations of the two treatments were assigned to the 12 animals in 8 different orders, since the odorous treatments had to be applied simultaneously to all arenas within the research hall. In the first and third groups, combinations of odours were administered during the 2nd and 4th treatment, and, in the second group, the odours were administered during the 1st and 3rd treatment. Treatment orders differed among animals in each season; i.e., the four different combination orders applied in the first season were repeated in the third season. Treatments started at 12:00 am and lasted for two days (46 h). During two observation periods (OP) animals very digitally videotaped. The first OP started with the change of the treatment at 12.00 and lasted 6 hours, the second started 24 hours later and lasted again 6 hours. Variables from the videos of the OPs are later compared within and between treatments (see Statistics). Treatment conditions were changed on days 1, 3, 5, and 7 between 10-12:00 am. After the OPs, all seed trays were sifted and the cage bedding was removed if necessary.

Foraging grids

Foraging decisions can be measured using artificial, non-refilling food patches with declining harvest rates over patch exploitation. Theory predicts that a forager will stop depleting a patch when the benefits of the harvest rate no longer justify energetic-, predation- and missed opportunity costs while foraging (based on the marginal value theorem [19, 31, 34]) . In the patch, the giving-up density (GUD) of food relative to substrate can be measured [31].

During the observation periods, 25 feeding stations were evenly distributed in the arena in a 5x5 grid. The feeding stations were 5 cm high and were dug into the sand, with 50 cm between feeding stations. Each feeding station contained 400 ml of sand and 0.2 gr. of millet. Thus, a total amount of 5 grams of food was provided per observation period (6 hrs). Since the animals consumed a maximum of 30 % of the food provided, different feeding strategies (either sampling a high number of trays with a high harvest rate or depleting a low number of trays to a low food level) were possible.

Between the observation periods, the animals were kept under treatment conditions with 10 food patches with even food distribution that were removed three hours before each observation period.

Statistics:

To analyse the delayed effects of the previous treatments on the intake and use of trays in the first and second observation periods (OPs) of the current treatment, we used a linear mixed model (lmm) and included the observation period (day, 2 levels) with a first order autoregressive co-variation model of repeated measurements. We used the second, third, and fourth treatment combinations and added the risk relation to the respective earlier treatment quality as a factor (higher, lower, or same risk). The dependent variables were intake and number of used trays in OP 1 (or OP 1). Higher risk was assumed if avian or mammalian risk levels increased while the other was constant or if both were increased; however, a lower risk was assumed if avian or mammalian risk levels were decreased while the other was constant or if the risk levels of both factors were decreased. The same risk level was assumed if the risk level of one factor increased and that of the other factor decreased. The current treatment was included into the analysis as a three level factor (high risk: both predation types present; medium: either avian or mammalian risk present; or low: no risk present).

Foraging decisions were identified with landscape-wide measures based on GUDs in trays over the entire OP. Decisions were analysed as follows: the total consumption was used as an indicator of perceived risk, the number of seed trays visited (as indicated by food prints) was used as a measure of tray exploration, and the concentration of effort (i.e., the percentage of food collected from the 5 most depleted trays) was used as a measure of the spatial concentration of effort. Behaviour was analysed using the video material. We used the number of activity bouts of the entire OP as a measure of overall activity. A bout was defined as an activity period outside the shelter which lasted at least 5 minutes and was divided from the next bout by 30 minutes of inactivity. Additionally, we analysed the number of trays used in the first bout and the delay of activity after onset of the experimental night as indicators of short term effects.

We analysed dependent variables with linear mixed models for the effects of odour treatment (2 levels), avian predation risk (2 levels), season (3 levels), and position of treatment in experimental sequence (4 levels) within individuals with the lmm procedure using SPSS 15 (SPSS Inc., Chicago, Illinois). Animals were used as subjects and treatment order as repeats. Response variables were log transformed to obtain homogeneous variances if necessary. If no homogeneous variances could be achieved, non-parametric Friedman and Wilcoxon tests were applied.

The main effects and the 2-way interactions of the fixed factors (odour, avian risk and season) were inspected in the first model. Non-significant interactions ($p>0.05$) were subsequently removed until the most parsimonious models were obtained. The position of the treatment in the experimental sequence had no effect on any of the models and was removed from all reported models.

Results:

Delayed effects as a result of predation risk allocation:

In the first observation period (1st OP) of a treatment, food intake and the number of trays used were strongly influenced by the relative risk of the previous treatment and interaction between the current and previous treatments (Table 1). After the higher risk treatments, the voles consumed more food and used more trays than after the less dangerous treatments (Table 1). In the second OP, only the risk level of the current treatment explained the intake and the number of seed trays used.

To further analyse effects of persistent risk treatments only, we analysed the second observation period by itself.

Behavioural changes during a treatment due to uniform risk distribution:

Over all treatments, the animals decreased their food intake by one half when the animals were shifted from the safest treatment combination (low avian risk, no mustelid odour 0.67g ± 0.45) to a combination with both risks (0.32g ± 0.3). Food intake was reduced by both high avian and mustelid predation risk with no interaction (Table 2, Fig 1A). Under the increased avian risk, food intake was reduced by 35 percent (low: 0.64g ± 0.41, high: 0.44g ± 0.31,) while the application of mustelid odour reduced food intake by 26 percent (without: 0.62g ± 0.36, with: 0.46g ± 0.36). Note: All values are means ± 1 SD.

The number of trays used and the concentration of effort were only affected by higher avian predation risk but not by weasel predation risk (Table 2, Fig. 1B+C). With cover, 24±8 trays were visited, while without cover, 11 ± 7 trays were visited. Even though the concentration of effort was highest in the treatment group with both risk factors present (72 % ± 16 were foraged from the 5 most used trays), only avian predation increased the concentration significantly from a mean of 55 % ± 23 with cover to a mean of 65 % ± 19 without cover (Table 2).

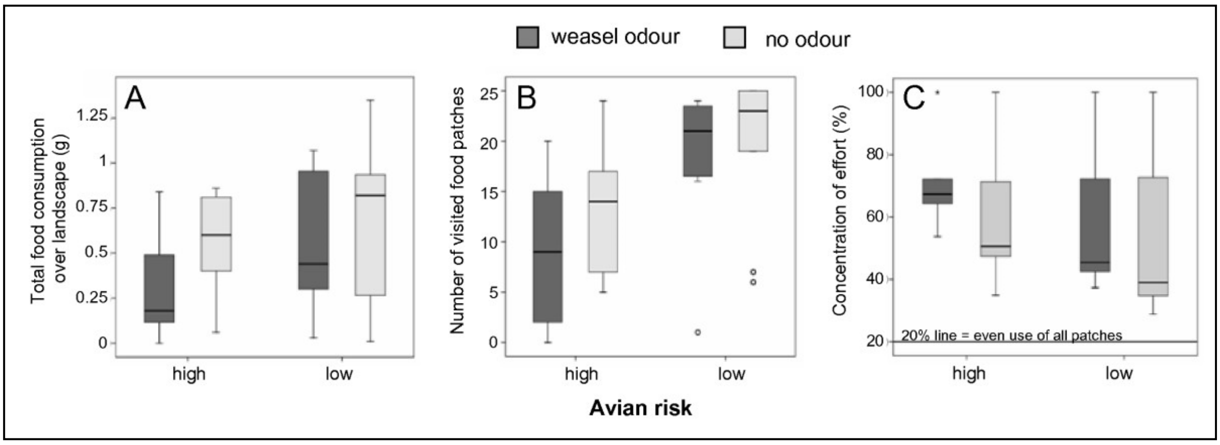

Figure 1 A-C: Food consumption and distribution of feeding effort of 11 bank voles in a 6 hr long observation period, effects of high or low avian predation risk and weasel odour.

A: Food intake (gram millet). B: The number of used trays C: Concentration of effort (percentage of food taken from the five most depleted trays (20% of trays)).

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During the first bout after the application of experimental conditions, animals used 11 ± 9 of the 25 trays, but the number of trays visited differed between the four treatment combinations within animals (Friedman test chi2 = 9.95, p = 0.019, Figure 2C). This difference was due to the reduced number of trays visited by the voles when they were exposed to the mustelid predation risk in combination with high avian predation risk (7±6) when compared to the number of trays visited in the absence of mustelid predation risk in the presence of high avian predation risk (15 ± 7) (post hoc test (Wilcoxon) Z = 2.31, p= 0.021). The two other treatments showed no significant difference (all Z < 1.5, p > 0.1).

Video analysis revealed that the length of delay and the number of bouts were each dependent upon both the avian and weasel predation risks (Table 2, Figs. 2A+B). The highest number of bouts occurred when only avian predation risk existed (3.7 ± 2 bouts), whereas the lowest number of bouts occurred when only the weasel odour was present (2.9 ± 1.4 bouts). The longest delay until foraging occurred when no cover was provided and no weasel odour was presented (157 ± 89 minutes). Surprisingly, the shortest delay until foraging occurred when only the weasel odour was presented (82 ± 60 min). Furthermore, the number of bouts varied between the groups tested in different seasons. In the early season, a mean number of 4 ± 2 activity phases were counted. In the second season, 3.1 ± 1.7 phases were counted. In the third season, 2.5 ± 0.8 phases were counted (Table 2).

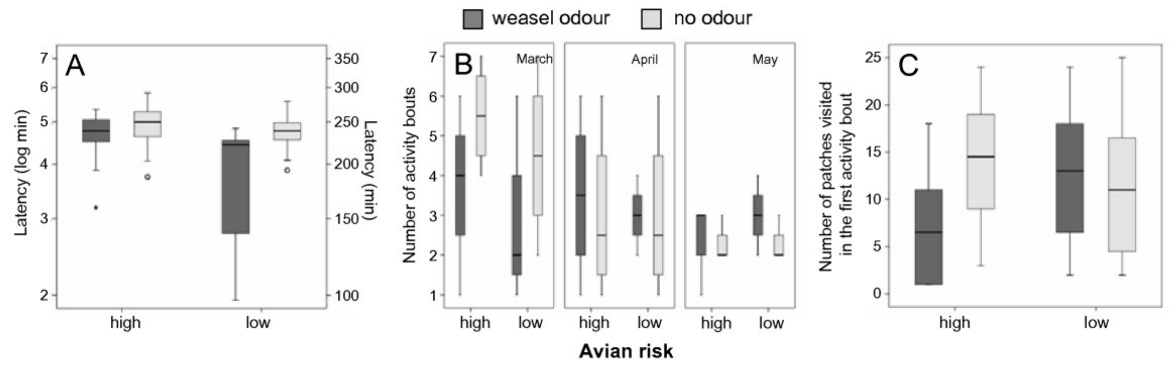

Figure 2 A-C: Behavioural observations of foraging behaviour of 11 bank voles under avian and mammalian predation risk in three different months.

A: The delay of activity after the application of odour treatments. B: Number of bouts within a 6 hr observation period. C: Nr of visited trays in the first foraging bout.

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Discussion

Strategic foraging patterns in risk uniform environments

Foraging decisions under predation pressure have mainly been studied in settings where prey animals were offered a choice of feeding stations that differed in predation risk [14, 15, 35]. Prey usually shift foraging activity to safer habitats, but many natural habitats are risk uniform. Predation risk can be evenly spread across the habitat, such as when predator and prey are of similar body size and locomotion type [17] or the habitat is structurally uniform.

We created a risk uniform habitat in experimental arenas and showed that foragers changed their feeding strategy by concentrating their effort on fewer trays under increased uniform risk. Since trays were not refilled over the observational period, foragers yielded and accepted diminishing returns over time. Consequently, foragers under uniform predation risk are less efficient. This trade-off can be interpreted as balancing the harvest rates to the predation risks and opportunity costs [8]. In a uniform high predation risk, the opportunity costs of other activities other than foraging in a local patch are low since other activities and other animals underlie the same high risk. Therefore, animals exploit patches to low quitting-harvest rates, while dangerous travelling is avoided.

Temporal allocation

The effects of the previous treatments dominated the effects of the current treatments during the first observation period (OP) if the previous treatment posed a higher risk (Table 1). This effect indicates that the animals compensate by increasing their feeding rate and supports the predictions of the predation risk allocation hypothesis [9]. According to Lima and Bednekoff [9], the duration of low and high risk periods should affect the amount of antipredatory behaviour allocated to the respective periods, and, at some point, animals have to counterbalance for earlier missed feeding opportunities. If animals avoid foraging during periods of high risk, their energetic resources decrease if high risk situations become persistent, and their nutritional demands will surpass their fear of predation. Voles, just as any other homeothermic small animal, can not interrupt their food intake too long [36] because they need to maintain a favourable energy balance. In our experiment, voles adjusted their feeding strategies to the persistent risk level and predation type only after a day had lapsed. Thus, in constantly shifting environments, special behavioural adaptations can be explained by the influences of previous conditions. If animals start their activities with a memory of the prior state of the foraging and risk landscape, their decision making might be based on three different factors: their own condition (depending on the former activities), their memory of the last environmental state, and updates of current changes in the actual state of environment and food resources, representing a Bayesian forager [37, 38] that is regulated by its internal state of nutrition.

Specific responses to different types of predation

In the second observation period, the avian predation risk level had already persisted for at least 24 hours. Weasel odour was applied at the start of each observation period, and it affected short term behaviour and reduced the number of visited trays in the first bout. However, over all bouts in the six hours, the difference was no longer visible.

Uniform avian predation risk significantly reduced the food intake of the voles (Table 2, Fig. 1A), increased their concentration of effort (Fig. 1C), increased their delay in activity (Fig. 2A), and reduced the number of used feeding stations (Fig. 1B) when compared to the same animals under lower uniform risk levels.

The importance of avian predation risk is that it is the most invariant result in studies of risk heterogeneity [8, 31, 39]. Birds of prey have large home ranges and scan the ground out of sight of their prey. As such, voles have to treat avian predation risk as a constant. The prey seem to be unable to adjust feeding activities to the proximate cues of avian presence, but they are able to adjust to the overall perception of the environmental quality in terms of cover and refuge. This is supported by the long delay of activity in the avian risk treatment groups.

The responses of voles to cues that indicate the presence of a weasel have been demonstrated earlier, including spacing behaviour [40] and feeding behaviour [41]. The least weasel is about the same size as its prey, is able to move as voles do [16], and follows voles into their burrows [17], which cause a uniform distribution of weasel predation risk. Weasel presence also alters the temporal patterns of vole activity [14]. Support for weasel odour effects in our experiment comes from the strong reduction of overall food intake (Fig. 1A) with the weasel treatment. On a short time scale during the first of all activity bouts after the distribution of fresh weasel odour, voles reduced their explorative activities if avian predation risk was high at the same time, as indicated by the number of used trays (Fig. 1B). A short delay until the start of activity and general boldness were also observed in fish that were raised under conditions with a predator threat, as compared to those fish raised without the presence of a threat [42]. This may be interpreted as a sign of alertness under constant predation pressure.

Interactions

Our 2x2 factorial set-up allowed us to check for (emergent) multiple predator effects (MPE [24]). According to Lima [43], the addition of predation risk to an already risky situation (no cover and weasel odour in our case) should not cause prey to use time for predator scanning but rather to shift to a concentration of foraging investment. Supporting this model, the foragers in our study reduced the number of foraging patches in reaction to simulated mustelid risk only if avian predation risk was already high, this can be seen as an emergent effect which only occurs when two types of predation occur simultaneous. Additionally, animals reduced their food intake under persistent risk of avian predation and the renewed risk of mammalian predation. These responses lead to a minimum intake when both predation types are present, whereas each of the predation types alone produces a similar reduction of intake (Fig. 1A, boxes 2 and 3). Although we found additive effects of the two predation types in the food intake, the combination of both predation types did not differ from the sum of their single effects (no emergent effects) in this variable. A further reduction of time spent foraging (indicated by a delay of activity) allowed the animals to reduce metabolic needs. Thus, two or more types of predation (representing “trophic species” [24]) can produce additive and emerging effects, depending on the type of risk that is represented through these predators.

Effects of season:

Our experiments were conducted over the progression of spring. Even though animals were kept under artificial light conditions, we cannot exclude effects of an internal clock of the animals [44] and their change of sexual status. These factors could have changed the relative importance of parameters like mate search or territory defence, which could explain the significant interaction with season (Fig. 2B).

Conclusions

Our study has shown that voles adapt their feeding strategies to the perceived levels of uniform risk and that their feeding strategies are specific for different classes of predation. They changed feeding strategies according to the type of risk on spatial and temporal scales. Additive and emergent effects of the two risk types were found, but no multiplicative effects. This might be due to the small margins and energy spares that small mammals have, which do not allow additional reduction of activity at a certain benchmark. The animals adapted their spatial distribution of feeding effort to the uniform distribution of risk. With all places being equally unsafe, animals concentrated their effort to very few trays. Thus, foragers were able to perceive risk homogeneity over the entire landscape and adapt foraging strategies to reduce their risk. Because voles are capable of adaptive strategies to risk uniformity, it stands to reason that voles experience such landscapes of fear under natural conditions and have evolved optimal feeding strategies to deal with permanent uniform risk distributions.

Authors' contributions

TL participated in design of the study, collected data, performed parts of the statistical analysis and wrote and drafted the manuscript. JAE conceived the study, participated in the design of the study, and performed parts of the statistical analysis. She revised the manuscript and added important intellectual content.

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OP	Variable Factor	Food intake (g)			Number of used trays		
		df	F	p	df	F	p
1	Current treatment	2,24	1,11	0,35	2,27	0,2	0,84
	Previous treatment	2,24	2,75	0,084	2,27	3,98	0,03
	Curr. treatment * Prev. treat.	2,18	4,31	0,03			
2	Current treatment	2,17	7,76	0,04	2,20	6,82	0,006
	Previous treatment	2,17	0,05	0,96	2,20	1,67	0,21
	Curr treatment * Prev. treat.	2,10	2,14	0,17			

Table 1: Delayed effects of previous treatments on current treatments
The relative risk of the previous treatment (three risk levels: higher, lower, or same risk) compared to the present treatment (three risk levels: high, medium, or low) shows a significant impact on the variables obtained after a change of treatment. During the first observation period (OP 1, 0-6 hours after change of treatment), the previous and current treatments interact significantly. In the second OP (24-30 hours after change of treatments), only the current treatment causes the significant effects. 11 bank voles served as experimental foragers.

Variable Factor	Intake (g)			Number of Trays			Concentration of Effort (%)			Number of bouts			Latency (log(sec))		
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Weasel Odour	1,24	8,20	0,008	1,23	0,12	0,73	1,19	2,800	0,110	1,6	14,07	0,009	1,8	7,92	0,022
Avian Predation Risk	1,30	1,40	0,001	1,31	0,19	0,008	1,32	5,500	0,026	1,10	7,180	0,022	1,11	6,11	0,031
Season	2,9	1,25	0,332	2,10	7,90	0,83	2,10	1,400	0,280	2,8	1,740	0,239	2,50	0,004	0,95
Avian Pred. x Season										2,10	8,930	0,002			
Weasel Od. x Season										2,6	20,41	0,006			

Table 2: Behavioural responses of bank voles foraging in a risk-uniform landscape.
Treatments were weasel odour (present or absent) and avian predation risk (ground cover present or absent) in an ongoing season (three months). The most parsimonious linear mixed models are shown. Non-significant factor interactions were removed.

II: Foraging decisions in risk-uniform landscapes

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Summary

Behaviour is shaped by evolution as to maximise fitness by balancing gains and risks. Models on decision making in biology, psychology or economy have investigated choices among options which differ in gain and/or risk. Meanwhile, there are decision contexts with uniform risk distributions where options are not differing in risk while the overall risk level may be high. Adequate predictions for the emerging investment patterns in risk uniformity are missing.

Here we use foraging behaviour as a model for decision making. While foraging, animals often titrate food and safety from predation and prefer safer foraging options over riskier ones. Risk uniformity can occur when habitat structures are uniform, when predators are omnipresent or when predators are ideal-free distributed in relation to prey availiability. However, models and empirical investigations on optimal foraging have mainly investigated choices among options with different predation risks.

Based on the existing models on local decision making in risk-heterogeneity we here extrapolate predictions to a landscape level with uniform risk distribution. We compare among landscapes with different risk levels. If the uniform risk is low, local decisions on the marginal value of an option should lead to an equal distribution of foraging effort. If the uniform risk is high, foraging should be concentrated on few options, due to a landscape-wide reduction of the value of missed opportunity costs of activities other than foraging. We provide experimental support for these predictions using foraging small mammals in artificial, risk uniform landscapes. In high risk uniform landscapes animals invested their foraging time in fewer options and accepted lower total returns, compared to their behaviour in low risk-uniform landscapes. The observed trade off between gain and risk, demonstrated here for food reduction and safety increase, may possibly apply also to other contexts of economic decision making.

Introduction

Ecological theory assumes, that animals have adapted to their environment by optimising behavior in order to maximise fitness. Foraging behavior is often used as a paradigm of optimal behavior [1]. While foraging, a forager may itself become prey to another forager and it is pivotal to reduce the risk of being killed or seriously injured by predation to increase the forager's fitness. Foragers should thus not only maximise their gain but also minimize predation risk by making decisions on where to forage and when to leave a patch [2, 3].

Antipredatory adaptations to foraging behavior have largely been studied in risk-heterogeneous environments, such as desert ecosystems with a choice of microhabitats [4] or in habitats deliberately made risk-heterogeneous, for example by mowing [5]. In such situations foragers value patches in safer locations higher than in unsafe locations, which can be measured by the quitting harvest rate [6]. Meanwhile, many environments are relatively uniform in their risk distribution, i.e. predation risk is evenly spread over space from the prey's perspective and all patches are equally unsafe. Environments can be risk uniform by their uniform structure, or risk uniform independent of habitat structures if the predator matches body size and locomotive ability of the prey and prey can thus not hide from predation. Further, risk uniformity may occur if predators follow an ideal free distribution in relation to prey availability, then risk will tend to be uniformly distributed among patches. Indeed IFD theory would suggest that risk uniformity should be very common in natural systems [7].

In this paper we will introduce predictions for risk-uniform landscapes and discuss the role of opportunity costs and travelling risk. We will then present data from experimental foragers in artificial, risk-uniform landscapes under controlled laboratory conditions that support our predictions.

Risk-uniform landscapes

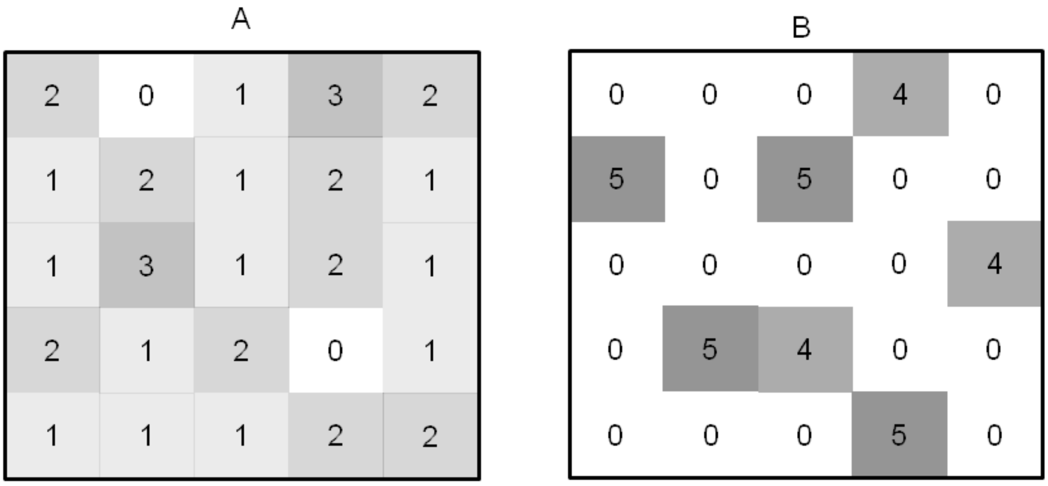
When comparing between risk-uniform landscapes we have to compare between environments. Such between-environment comparisons were done earlier to assess the importance of mean resource level [8] including mean fitness value of an environment [9], however, predation risk in these models/experiments varied among patches within the environment. We here compare among environments with different risk levels that have a uniform resource distribution and a uniform risk distribution among the patches within the environment.

We base our considerations on the marginal value theorem (MVT, [10]) with depletable resources that are depressed by their exploitation. Foragers should leave a patch as soon as the return rate from this resource drops below the average return rate of the habitat. Here we extrapolate this local decision rule to a conceptual landscape consisting of many depletable options. The investment pattern resulting from many local decisions by a forager switching among options would be evenly distributed among the options (Fig. 1A). Since the mean return rate of the habitat decreases with depletion, the even distribution of investment patterns over time should in theory slowly drain the resource level of the habitat.

With an extension of the MVT it is possible to include the local predation risk into optimality models on patch depletion [2], stating that a forager should leave each resource patch when the return rate is no longer greater than the sum of the energetic costs, predation costs, and missed opportunity costs (MOCs) of foraging. Predictions follow, that if two patches share the same energetic cost of foraging and the same return rate function, then any differences in patch residency should reflect differences in patch specific risks of predation. Consequently, measurements of patch residency are used to compare predation risks among patches [2, 11], and can be used to map the forager's perception of differences in predation risk across landscapes [12].

Applying Brown's model [2] to an environment where metabolic costs of foraging and the predation risk is constant among patches, a forager could also base its local decision on patch residency on the MOCs inherent to the forager in his environment. The MOCs include fitness costs of not engaging into other, fitness- increasing alternative activities such as mate search, territory defence or recovery and are constant for any forager in a given environment. Among environments though, MOCs depend on habitat richness, but also on feeding in and travelling between patches and on the survival rate in the habitat [8, 13]. Thus, MOCs also have a predation risk component. We therefore predict, that if predation risk is uniformly low, animals will engage in other activities than foraging. The patch residency, with constant costs of foraging and constant predation risk among options should then reflect the costs of missed opportunities. Both quitting return rate and missed opportunity costs in low risk contexts therefore are high, which is reflected in an early and frequent leaving of patches. This prediction differs from predictions and observations in risk-heterogeneous environments, where locally relatively low predation risk results in low local quitting harvest rates [2, 11]. If we extrapolate our prediction of frequent leaving and use of many patches to a risk-uniform landscape level, variance in foraging effort among patches will be low and animals' local decisions will create foraging landscapes with an even distribution of foraging effort.

If risk is uniformly high, exploration of new food sources as well as social and sexual activities make potential prey animals conspicuous and vulnerable and thus increase predation risk. Animals should therefore invest little in alternative activities and only conduct the absolute necessary minimum activity of foraging. Further, social or sexual interactions are reduced because conspecifics reduce activity too, due to the same high predation risk. If predators distribute themselves towards the availiability of prey, as predicted from ideal free distribution [7] the predation risk affects all conspecifics equally. Opportunity costs of missing other activities are therefore low and reflected in low quitting return rates, i.e. a long local investment. This contradicts the effects of *local* high predation risk in risk-heterogeneity where quitting harvest rates are high with high local predation risk [2, 11]. Thus, high investment in single options under high uniform risk may increase disproportionately, increasing the variance in foraging effort among patches. Extrapolated to a risk-uniform landscape level, foraging effort results in a landscape with high and isolated peaks while other options remain untouched (Fig. 1B).



A

2	0	1	3	2
1	2	1	2	1
1	3	1	2	1
2	1	2	0	1
1	1	1	2	2

B

0	0	0	4	0
5	0	5	0	0
0	0	0	0	4
0	5	4	0	0
0	0	0	5	0

Figure 1. Predicted distribution of total investment.

The same total investment (sum of cell values) into a resource landscape with (A) uniformly low risk where investment is evenly spread among options or (B) uniformly high risk with distinct investment peaks (B). Higher number and darker color indicate a higher local investment.

Small mammals and risk-uniformity

The meaning of risk-uniformity depends on the size of the organisms, its mobility and the scale of microhabitats and habitat structures. For small mammals that we used as experimental foragers in our experimental system, agrobiomes with monocropping often exceed the scale of small mammal territories and can thus be risk-uniform in their avian predation risk. Small predators of rodents, such as snakes or mustelids match their rodent prey in size and locomotion type [14] and may distribute themselves according to prey availability in space and time [7]. Rodents cannot hide from such omnipresent predators, which therefore produce a uniformly distributed predation risk over the entire landscape. Some foraging patters produced in rodent-mustelid systems [15, 16] are difficult to understand within a risk-heterogeneous approach. In the study of Eccard et al. [16] in a large enclosure experiments, rodents increased their foraging in artificial food patches and depleted these to lower levels in the presence of mustelid predators than in the absence. Patterns can possibly be explained using the risk-uniform landscape approach to foraging we propose here.

Methods

Experimental foragers in risk-uniform landscapes

Foraging behaviour of 12 male bank voles (*Myodes glareolus*) was investigated in an artificial resource landscapes with uniformly spread predation risk. In an 9 m^2 indoor arena covered with dry sand we offered 25 food patches (15 cm diameter, 0.2g millet/0.4l sand) in a 5x5 grid with 40cm distance, and a central nest box. Ground cover was provided by a framed metal lattice ($4m^2$ with 1cm x 1cm cells). We approached foraging decisions as the shape of a 3-dimensional investment landscape resulting from the (2-dimensional) position of a resource patch and the local investment into each patch defining the third dimension.

Each animal was tested in two temporally separated treatments under either uniformly safe or uniformly risky conditions. In the "safe" treatment we covered the foraging grid, potentially protecting the forager from attacks by birds of prey. In the "risky" treatment no ground cover was provided. Attacks by birds of prey are unforeseeable and unavoidable, for most prey species the avoidance of open ground is an apparently invariant result in foraging studies with antipredatory behaviour of rodents [11]. Thus, even without a hawk in the research hall the subjective perception of predation risk is higher without cover than with cover for a ground dwelling mammal. Each individual was subjected to both risk levels for 2 days each, allowing pair-wise comparisons within individuals among risk levels. Animals were divided into two groups with reversed order of treatments in the two experimental phases. Phases lasted for 2 subsequent days in which data were gathered during 6 evening hours, with 4 days habituation to the arena and a 2-6 day break between phases.

From both experimental phases we obtained depletion levels of food for all patches. During the second experimental phase animals were filmed to establish the relation of patch residency (invested time) and depletion levels (Fig. 2A). Local patch use followed the classical patterns [10] of diminishing returns with increasing patch residency (Fig. 2B).

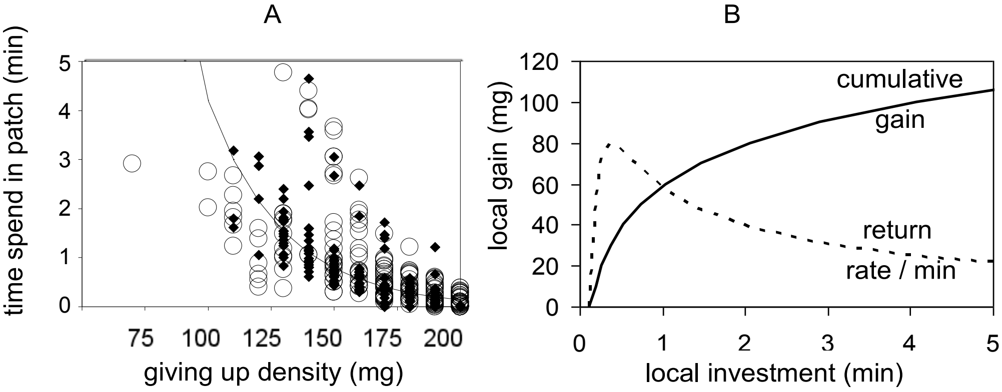


Figure 2: Local gain and investment (patch residency)

(A) Observational data on patch residency from a video analysis of foraging bank voles (11 animals, 22 trials, 369 experimental patches with initial food density of 200mg, open circles: safe risk-uniform conditions, diamonds: risky uniform conditions) and predictions (line) of patch residency by the measured amount of food left over in the patch (giving up density) with an exponential model:
time = -272sec*e(-7327,6*gud(mg)) with R2 = 0.571, F = 491; p < 0,001. (B) Predictions for cumulative gain (solid line) and diminishing returns (rate per minute, dashed line) over patch residency based on the model in A.

We analyzed spatial distribution of the invested time over the entire resource landscape with RangesVI, a GIS-based location analysis program [17] and determined the number of patches where

50% of the time was spent (cluster analysis). Choice of percentage for cores was arbitrary. Similar results as presented for 50% cores were also obtained for 30% and 80% cores. Spatial clumping of investment was calculated relative to distance between locations (Kernels contour analysis, Fig. 3).

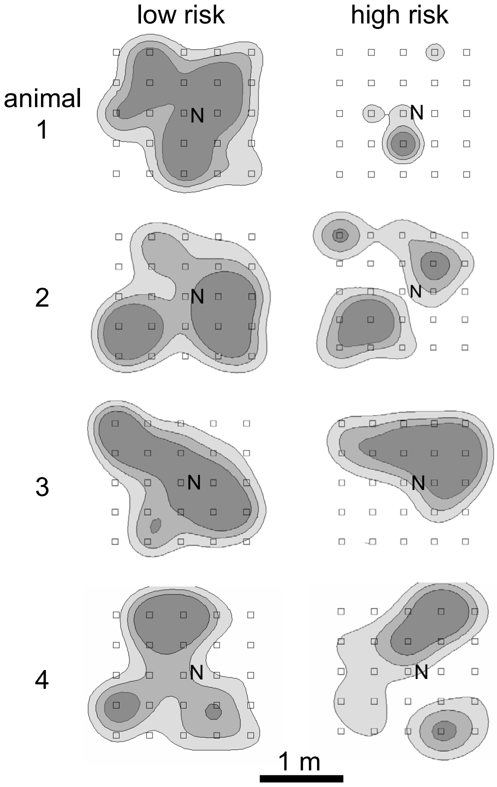


Figure 3: Distribution of time investment

Four exemplary foragers (male bank voles) at their first day of foraging under safe (left) and risky (right) conditions. Investment is displayed as 50% (darkest), 75% (lighter) and 95% (lightest shade) Kernel contour cores based on location density (time investment) and distance between locations.

Preliminary analysis with repeated measures ANOVA models revealed, that day (2 days per treatment) as inner subject repeats, treatment order (2 levels, between-subject factor), progressing season (covariate) and weight loss during experiment (covariate) were not explaining variance. We therefore concluded the analysis using within-animal means of the two days for each of two risk treatments, and compared among risks with paired t-tests within subjects where appropriate (tests for normality and homogeneity of variances) and non-parametric Wilcoxon tests otherwise.

One may argue, that artificial landscapes were not truly risk uniform in their distance to safety, i.e. either central nest box or the arena wall. We therefore analysed the proportional use of the 9 patches near the central nest (their preference would be indicated by proportional values >1) in relation to the 16 patches closer to the arena walls (their preference would be indicated by proportional values <1).

Ethical note: Animals were captured by live trapping from premises of the University of Bielefeld (Germany) and were returned after the experiment to the capture grid. Animal care and housing complied with institutional guidelines. Permissions by Umweltamt Bielefeld (360.12.06.01.3) and Gesundheits-, Veterinär- und Lebensmittelüberwachungsamt Bielefeld (530.42).

Results

Experimental foragers (n=12) invested similar length of time in foraging into the resource landscapes in both risk treatments (690 ± 376 (mean ± SD) seconds in uniform high risk and 660 ± 399 seconds in uniform low risk; Wilcoxon signed rank test, Z = -0.2, p = 0.875). Meanwhile, the total amount of food removed from the experimental grid was lower under uniform high risk (0.51 ± 0.25g) than under uniform low risk conditions (0.72 ± 0.29g, t = 2.5, p = 0.028).

Individuals' gain function per patch did not differ among risk treatments (ANCOVA of GUDs by residence time (data of Fig. 2A) with no interaction of risk(factor) and time(covariate, log transformed): F interaction (1, 355) = 1.4, p = 0.237, individual was added as a random factor, F: risk treatment (1, 355) = 2.9, p = 0.088; F log(time) = 542.8, p < 0.001).

In the high risk treatment, less patches were used for foraging: 50% of foraging time was invested into 24% ± 12% of patches under high risk and into 40% ± 20% under low risk conditions (paired t-test, t = 5.6, p = 0.0001). This resulted in a smaller area of investment cores under high risk (0.35 ± 0.15 m^2) than under low risk (0.62 ± 0.15 m^2, t = 2.6, p = 0.023, with similar number of cores: risky: 1.6 ± 0.6 cores, safe 1.6 ± 0.5 cores, t = 0.0, p = 1.0, Fig. 3).

There were no behavioural indicators that locations differed in perceived local risk relative to safety. Proportional use of patches closer to the nest or to the wall did not differ from 1, one-sample t-test with n= all 24 trials, t=1.1, p = 0.281; and with n=12 trials in high risk treatment, t=0.97, p=0.354).

Discussion

In summary, under uniformly high risk animals invested the same foraging time into fewer patches as under low risk conditions and, by exploiting these with diminishing returns over time, accepted lower total returns from the landscape. The experimental results support our predictions for distinct investment patterns between levels of uniform risks. Predictions may further be supported by our results from field experiments with rodents under a uniform mustelid predation risk [16] where artificial food patches were exploited to lower levels in the presence of weasels than in their absence.

In our experiment reported here, foragers under uniform, low risk behaved as predicted by the marginal value theorem on diminishing returns [10] and distributed their effort as to maximise their returns. Foragers under uniform high risk concentrated their effort to very few options and exploited these consequently (Figure 3) despite diminishing returns. This behaviour minimizes the risk associated with other activities outside feeding in the chosen location which are probably also characterized by increased predation risk. With other activities reduced, their missed opportunity costs are devaluated. With its strategy of distribution of investment, the animal potentially depresses the overall return from the resource landscape. This general trade off between gain and risk, demonstrated here for reduced food gain and increased safety from predation, may possibly apply also to other economic decision contexts in biology, psychology or economy with uniform risk distributions.

Alternative explanation for our results in the riskier treatment could be an increased risk in travelling among patches (1) or an increased vigilance while foraging (2). First, the risk of predation may function to increase the danger while switching patches, compared to a continuation of foraging in the current patch. In a natural habitat with large distances between patches this explanation may hold – animals may leave scent trails or produce noise while traveling, or by moving increase the chance to encounter a predator. In the small scale of the experimental landscape the explanation can be refuted, since distances between patches were short relative to the size of patches and relative to the forager's mobility. Our data further showed that foragers did not prefer the patches closer to safety, another indication for that distance between patches was not relevant at the investigated scale. Furthermore, risk treatment (cover or open) was the same for the patches and the matrix between them in our experiment so that risk should not differ among feeding and travelling. As a second alternative explanation, vigilance during foraging in the riskier treatment could have reduced the gain function. In our analysis of gain per patch (Fig. 2a) we could not find a difference in the gain function between the risk treatments and therefore have little support for this alternative explanation.

In conclusion, high risk levels in a risk-uniform landscape can produce foraging patterns different from low risk levels. Further, patterns cannot be directly anticipated from theory based on risk-heterogeneity. Thus, decisions in uniform risk should be included in a comprehensive theoretical framework on foraging decisions under predation risk.

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III. Sex specific foraging strategies – do missed opportunity costs cause differences in male and female foraging strategies

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Abstract:

The risk of predation can have major, sometimes terminal, effects on the life history of prey animals. Thus, evolutionary responses to increased risk are strong and include habitat choices, timing and duration of activity phases. Allocation of time and effort to other activities than foraging such as mate search, display behavior and territory defense is a crucial task and accounts for the expected inclusive fitness of an individual. In most species, males are the more active sex engaged in the described behaviors, so predation becomes a non-random mortality factor and causes male-biased mortality rates in natural populations. Meanwhile, little is known on how the selection on activities related to alternative opportunties also affects foraging decision of males and females.

To analyze differences of male and female strategies of allocation of effort to foraging and alternative opportunities, both sexes of the common vole (*Microtus arvalis*) were tested simultaneously under increasing levels of risk of avian predation. We manipulated the risk of travelling and foraging in a factorial setup, which allowed us to separate the assessment of risk while moving between sources as well while foraging at a source. We expected differences to became visible, because for males the costs of missing opportunities (such as mating and territory defense) remained high in high risk scenarios. For females, no additional preoccupations exist and they can optimize their foraging behavior to maximize survival chances. Activity patterns of 24 voles, including foraging behavior and spatio-temporal patterns were monitored.

Results show, that males start their activity bouts earlier after events of disturbance and allocate more time to roaming in the arena, even when travelling is dangerous. Females allocate more time to foraging behavior in save situations, even though the total intake remains the same in both sexes. This might indicate that the high reproductive skew in males together with valuable opportunities contributes to risky strategies to outcompete other males. Thus, excess male mortality can be a result of sexual selection for traits that enhance reproductive success.

Introduction

Male-biased mortality is widespread in the animal kingdom and well investigated. Many studies on this topic focus on promiscuous mammal species (Clutton-Brock and Isvaran 2007). Explanations are based on sexual selection theories and the evolution of high potential reproduction rates of males compared to females (Clutton-Brock and Parker 1992). These ultimate reasons may explain the costs for growing larger in species with sexual size dimorphisms (Ricklefs and Scheuerlein 2001), reduced immunocompetence and enlarged parasite loads (Moore and Wilson 2002), and the high chances of males of engaging in risky behaviors like roaming and dispersal or physical combat (Magnhagen 1991, Norrdahl and Korpimaki 1998, Kraus et al. 2008). These constraints shape the species specific survival rates of males and females.

Especially prey species face a severe trade-off between foraging activity, reproduction and predation risk (survival). Rodents for example, as multivoltine income breeders, produce extremely high population densities and in these situations, animals have to engage in risky behaviors, including large dispersal distances and high mobility (Norrdahl and Korpimaki 1998), fighting with territory owners (intraspecific stress Chitty 1952) or searching for several mating partners (Gwynne 1987, Moore 1987). In promiscuous, polygynous rodent social systems, these factors mainly affect males (Spitz 1974), especially big males or subadult, roaming males (but see (Cushing 1985)) for estrous females and predation risk). This is supported by studies on Microtus species were males of all sizes predominate in pellets of diurnal avian predators (Beacham 1979, Halle 1988). Additionally, the more conspicuous and bigger sex has a higher vulnerability to predation and in Microtus species; younger animals or the most mobile animals are more vulnerable than experienced ones or those with a reduced activity (Longland and Jenkins 1987, Norrdahl and Korpimaki 1998). In these social systems, males are forced to be active and risk-prone, because the cost of missing for example a mating partner is directly reflected in a reduced lifetime reproductive success.

Though predation pressure is strongest on active males, it is not known if parameters of foraging behavior in rodents are expressed differentially between males and females for example if costs of missed opportunities create different foraging patterns in males. Within males, a high reproductive skew exists, resulting in few very successful males (those who are able to monopolize females and hold a territory) and those with poor success (due to missing experience or small body size or a small number of suitable territories). Thus, the costs of missing any opportunity of mating or defense can be extremely high in case the resident male is outcompeted by an intruder. Females on the other hand are either lactating or pregnant or both during the whole season, thus there are only very days when females are in estrus so that females usually are engaged in no riskier behavior than the mere search for food.

Owing to several aspects of the social system and behavior, common voles (*Microtus arvalis* (Pallas et al. 1778)) provide an excellent model species to analyze which behavioral adaptations distinguish males and females and cause the exceptional male-biased mortality rates. Common voles live in homogeneous meadows, with male homeranges (~800m^2)

overlapping several female homeranges (~300m^2) and females being potentially polyandric. For females get into a postpartum estrus, chances to reproduce occur repeatedly during a reproductive season. Thus, despite extremely low survival probabilities for males (Spitz 1974) (resulting in a female biased operational sex ratio at the end of the summer (Bryja et al. 2005)), territory defense and regular visits of females might pay off in terms of enhanced inclusive fitness. Differences among behavior of sexes can be expected to be large, for males try to mate with several females and thus have to defend a territory and be very mobile and active during the breeding season. Females on the other hand defend small territories (if at all (Boyce and Boyce 1988a)), and can afford to reduce travelling in environments of high risk (Boyce and Boyce 1988b) since they are visited by the males. Here we test, if these differences are accompanied by different foraging strategies.

To analyze parts of the complex behavior of males and females, we tested sexual active male and female field voles in small outdoor arenas and exposed them to different levels of risk. Our treatments manipulated the perceived risk of avian predation at foraging stations or while travelling to foraging stations in a factorial set-up in arenas with central nest stations. We tested males and females simultaneously in eight adjacent arenas, presuming that all animals identified potential mating partners and opponents via acoustic and olfactory cues.

For the males have preoccupations other than foraging, the costs of missing these opportunities in inactive phases are high, whereas females can afford to maximize survival chances by inactivity. We therefore assume that:

1) Males travel in high and low risk scenarios more than the mere distances between the nest and the foraging stations, because missed opportunity costs are high for males and more travelling means higher chances of meeting females or opponents. Females might reduce travelling activity in any scenario with a high risk of travelling or foraging to reduce exposure to predation
2) Males should perform longer activity bouts than needed for foraging to enhance chances for mating or territory defense at any landscape of risk. In high risk conditions, females should go for short bouts to minimize exposure and delay activity to potentially safer time windows
3) Males should show shorter phases of delay after a change of predation risk to enhance chances of reproduction and outcompete other males. Females should let more time pass by before becoming active again to make sure, that the actual cause of risk has moved on.

Material and Methods:

Animals:

12 male and 12 female wild captured field voles (*Microtus arvalis*) were kept under laboratory conditions 2-4 month prior to the experiment. All animals were adult and sexually active but there was

no difference in body weight between males and females (mean weight 22.9 ± 4.2 gram, t-test: t=-1.21, df = 22, p=0.24). One animal failed to feed from the foraging stations and had to be excluded.

Set-up:

Animals were released into experimental arenas of 4*2 meters. Arenas were surrounded by metal walls of 30 cm height on a concrete floor in otherwise empty outdoor aviaries. The animals were housed in small homeboxes in the middle of the arena and were provided with two foraging stations at either end of the arena. Foraging stations consisted of trays of 30cm*20cm*5cm (l*w*h) and contained 2 liters of sand. Into each station 2 grams of millet were mixed in the sand.

By covering the floor and the foraging stations with wire mesh on 2cm props we created an environment of relative safety from avian predation for a habituation phase of three days. This set-up allowed us video-filming from above and to monitore animal movements. In this phase, animals learned to exploit the trays and that exploitation leads to diminishing returns over time, further, changing between the two stations leads to a higher intake at the less exploited tray. For these resources are not refilling, exploitation results in lower returns over time and forces the animal into a patch leaving decision. This should be based on the perceived level of risk and potential energy gains at alternative sources (Brown 1988) based on the Marginal Value Theorem by Charnov (1976)). Trays were refilled once a day. The amount of food left in these trays after being used by an animal (giving up density GUD), provides a reliable estimate of the perceived risk while foraging or travelling. This is a well-established method to analyze risk-dependent foraging decisions (Brown 1988, Brown and Kotler 2004, Strauss et al. 2008).

The experimental run lasted five days with each day having a different level of exposure to predation (Fig. 1) with the following specifications in random order for each animal:

1) Floor and Foraging stations were covered with wire mesh – full safety.
2) No cover was provided – foraging and travelling between the trays and homebox is dangerous.
3) Foraging stations are covered, distances between trays and homebox are uncovered – foraging safe, travelling risky.
4) Only floor between house and patches is covered – travelling safe, foraging risky.

5) One half of the arena is covered (treatment condition for a different experiment, not analyzed here).

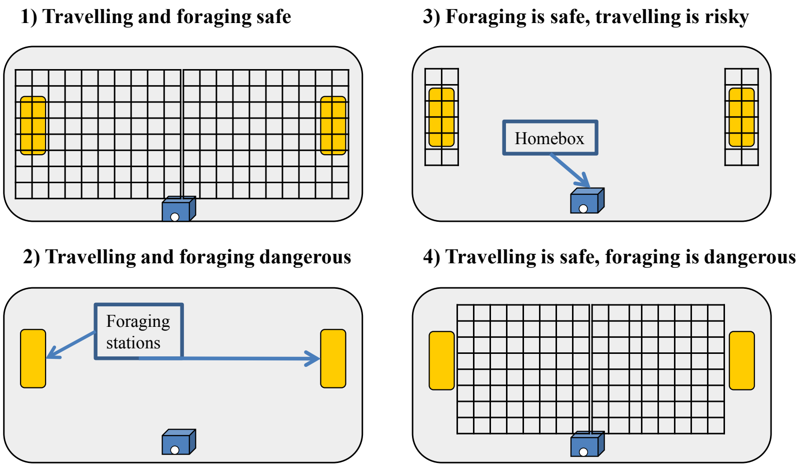

Figure 1: Setup and Treatment

Arenas were 4x2 meters, any 2 shared one wall and were charged with a male or a female vole. Wire mesh cover on props was provided according to the randomly assigned treatment. Foraging trays were placed at either end of the arena, video cameras were mounted above each arena.

Treatment conditions were established at 10.00 pm at the day before the first treatment. At 4.00 pm the next day trays were refilled with 2 grams of millet and mixed. The observation period lasted for 6 hours until 10.00 pm. Behavior of the animals was video-taped. Above each arena, infrared cameras were installed using a 50 W red-light bulb. After the observation period trays were sifted and the remaining grains were dried and weighted.

The next treatment condition was installed immediately after the observation period . We provided 4g millet seeds in both trays during the non observation phases. Again at 4 pm trays were refilled with 2 grams of milled and behavior was monitored as above. Thus, before the measurement in a new treatment, 18 hours in this new treatment had passed. This was done to avoid measuring the delayed effects of the previous treatment (Liesenjohann & Eccard 2008) directly after a change of treatments.

Statistics:

Videos were analyzed to get temporal and spatial behavioral patterns. A linear mixed model with animals as subjects and order of treatment as four step repeat within animal was used with 2 factors: **cover of foraging stations (yes/no)** and **cover of travelling matrix (yes/no).** Sex was used as a fixed factor in each model. Significant interactions were separately analyzed for simple effects using paired t-tests. Reported are the most parsimonious models. Variables are: **Total time active**, **total intake**, the **number** and **length of activity bouts**, the **number of tray changes, time spend foraging** and **delay of activity** after onset of treatment. Additionally a **skew** of investment was calculated to analyze the acceptance of lower returns in risky conditions. The skew is the percentage of food taken from the deeper exploited tray and should be between 50 (if both trays were depleted equally) and 100 (if the animal used only one tray). Variables with heterogeneous variance with a significant Levine's-test were log transformed and achieved homogeneous variances. All statistics are listed in table 1, all descriptives are summarized in table 2.

Results:

The **total time active** did not differ between sexes and treatment conditions. But the total amount of food the animals harvested (**intake**) from the trays was strongly depending both the risk while foraging and while travelling (Fig. 2A). If both were at high risk, the lowest intakes were found, while at low risks the intake was maximized, conditions with cover on either trays or matrix evoked intermediate harvesting amounts.

The **skew** was influenced by an interaction of the two main treatments. An increase in travelling risk generally increased the skew (Fig. 2B). Within high travelling risk were no effects of foraging risk, while within low travelling risk, the skew was reduced when foraging risk was high compared to lower foraging risk.

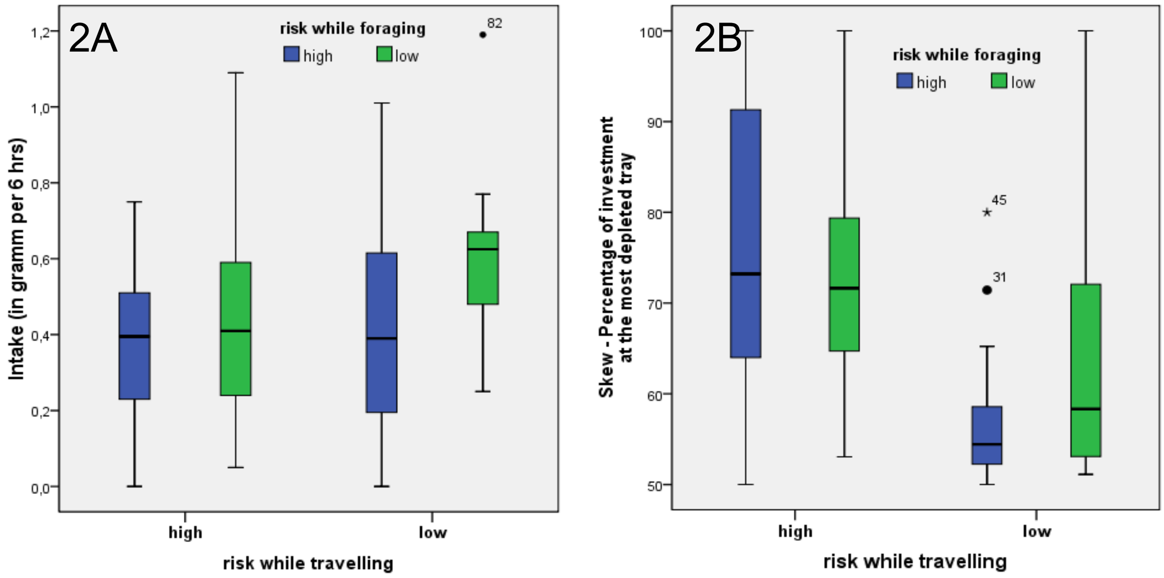

Figure 2A & B: Intake and skew

2A: All animals adjust their intake according to the applied treatments. There is no effect of the sex, both sexes feed most when travelling and foraging is safe, and feed less when either condition gets worse. **2B:** The skew, the percentage of food taken from a single tray is affected by an interaction of the two treatment factors: All animals invest more in a single tray when traveling is dangerous but produce almost even exploitation percentages when travelling is safe. The condition of the foraging places plays only a minor role but animals produce the most homogenous exploitation when travelling risk is low but foraging risk is high.

Activity bouts were longest when either one factor of travelling and foraging risk was high and the other low, and were shortest when both risks were either high or both low due to an interaction of both factors (Fig. 3A). Within high traveling risk the bouts tend to became longer in low foraging risk compared to high foraging risk, while in low traveling risk scenarios bout length is hardly affected.

The **number of activity bouts** depended as well on an interaction of the treatment combinations of risk of travelling and foraging: Within high traveling risk, the animals reduced the number of bouts when foraging risk was low compared to high foraging risk. When travelling was safe, animals tended to enhance the number of bouts when foraging risk was low compared to high foraging risk (Fig. 3 B).

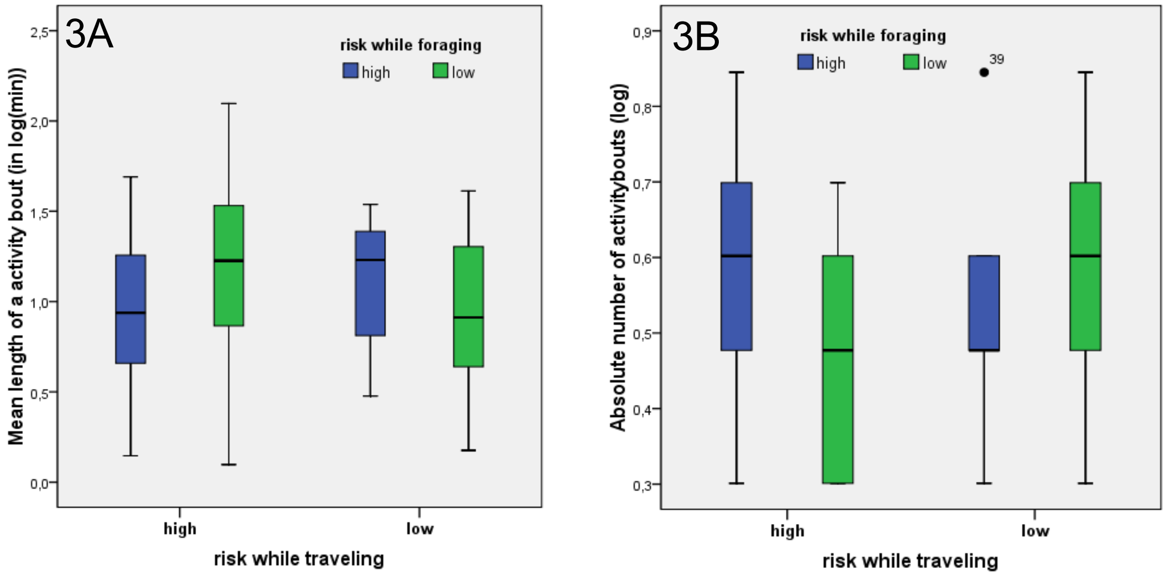

Figure 3A & B: Length and number of activity bouts

3A: Animals perform short activity bouts when conditions are risky and when conditions are completely safe (linked to high intake rates). Long activity bouts are performed when travelling is risky or when only travelling is safe. Both situations are linked to low intake rates. **3B:** The number of activity bouts is high in either completely dangerous or in completely safe conditions. If only one of the treatments is dangerous, animals perform a smaller number of bouts.

The activity variable **number of changes between trays** was influenced by a significant interaction of travelling risk and the sex of the animal. Males drastically enhanced the number of changes between trays when travelling risk was high and reduced changing activity between trays when traveling risk was low (Fig 4A). Females had equal number of changes independent of low and high travelling risk.

The actual time of activity **spend foraging** was depending on an interaction of the sex and the risk level at the foraging stations. While males kept their time allocated to foraging constant over high and low foraging risk, females invested more time into foraging when foraging risk was low compared to high foraging risk (Fig 4B).

The **delay of activity** after the experimenter’s disturbance in order to prepare the observation period was depending on the sex of the experimental animals. Males restarted to be active significantly earlier than females (LMM, F_{sex}= 4.56, p= 0.035, $delay_{males}$= 63.2 ± 63.8 minutes, $delay_{females}$=95.5 ± 79.8 minutes, Figure 4C).

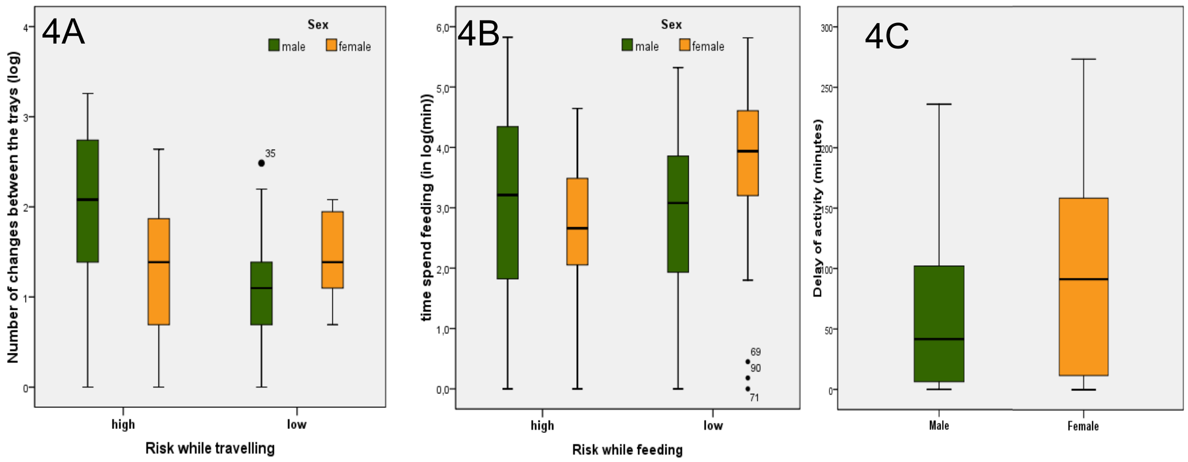

Figure 4A - C: Intake, skew and delay of activity

4A: Males are significantly more active when travelling conditions are dangerous while females stay on a low level of changes between trays independent of travelling conditions. **4B:** While males allocate the same amount of time to foraging behavior independent of any treatment, females grant significantly more time to foraging when the risk while foraging is relatively low. The traveling risk plays no role for the allocation of time to foraging behavior. **4C:** The resumption of activity after a disturbance, in this case the change of treatment at four o´clock, is not depending on any treatment but due to the mere difference between the sexes. Females spend a significantly longer time inactive than males.

Discussion:

Vole species are the most abundant small mammal species throughout Europe and form the basis of a variety of carnivore food chains (e.g. Korpimaki and Norrdahl 1991, Korpimaki et al. 1991). As well avian as mammalian predators depend on voles as most frequent source and have evolved effective hunting strategies which have the potential to regulate prey population densities (see Sundell 2006 for review). As response to this extremely high predation pressure, we expect antipredatory adaptations such as inconspicuousness and reduced mobility (Norrdahl and Korpimaki 1998), reduction of scent marking (Wolff 2004), delayed body growth (some predators select for larger body size (Longland and Jenkins 1987)) and effective, time saving foraging strategies (Eccard and Liesenjohann 2008). Unfortunately, most of these measures reduce mating success and act contrary to the overall aim of enhancing inclusive fitness. The trade-off between reproduction and survival might be different between males and females, since intra-sexual selection for mating partners is higher in males than in females (Luque-Larena et al. 2003, Mills et al. 2007). Males have to try to be more active and dominant than other males to increase their fitness. Cautious strategies can be immediately reflected in reduced reproductive success, thus the costs for missing any opportunity related to reproduction are extremely high. Thus, high, male-biased mortality rates are common in promiscuous species especially in the breeding season (Clutton-Brock and Isvaran 2007, Kraus et al. 2008).

Our study analyzes sex-specific adaptations of foraging behavior of common voles to different levels of predation risk at foraging places and while travelling between the nest and the foraging places. According to the points stated above, males should try to connect additional tasks to the essential duty of foraging to reduce the costs of missed opportunities while foraging. A males´ behavior should thus be not as sensible to increasing predation risk as a females´, because it should be graded by the additional chances that can be carried out.

We could show that the total intake, the skew of investment and the length and number of activity bouts are affected by both high and low risk while travelling and foraging, however, independent of sex. Nevertheless, the activity variables of changes between trays, time spend foraging and delay of activity are affected by an interaction of a distinct risk factor and the sex of the animal or the sex only.

Sex-independent Changes in foraging strategies as an answer to predation risk:

The total intake of both sexes was depending on the experimental treatments (Fig 2A). Thus the energy expenditure of males and females was equal due to the same body weight and same status (adult, sexual active but, in case of the females, not lactating or pregnant). Therefore foraging strategies were not confounded by the higher needs of one sex, which would lead to more ineffective foraging strategies of one sex (e.g. sexual segregation due to size dimorphism (Spaeth et al. 2004, Markman et al. 2006)). As demonstrated already in earlier studies, the total intake is simply reduced in risky conditions and could represent the attempt to delay foraging activities in potentially safer timeframes (Lima and Bednekoff 1999, Jacob and Brown 2000).

According to this, the total time spend active was likely to depend on the treatment conditions as well, because it should be related to the time needed to explore the foraging stations and the time needed for travelling between these (Charnov 1976, see Stephens 1986 for further reading, Cuthill et al. 1994). But the length of the activity phase was not depending on any treatment or sex; instead it seems to be a rather fixed period. The fact, that the animals invest the same time but achieve lower intake rates in dangerous conditions, suggests, that foraging becomes either ineffective in risky conditions due to high amounts of time allocated to vigilance and slower and more cautious movements (Lima and Bednekoff 1999), or time is spend with alternative activities like searching for alternative (safer) food sources.

A hint that foraging becomes ineffective is given by the skew, which is affected by the travelling risk. Dangerous travelling produces high skews. Thus, animals exploit one tray deeper than the other and accept diminishing rewards over time. This is in accord with other studies (Charnov 1976, Jacob and Brown 2000, Eccard et al. 2008, Liesenjohann and Eccard 2008), performed by both sexes equally and is interpreted as strategy to avoid risky traveling, or a perception of lower missed opportunity costs due to the overall high risk.

Interestingly, although the total times spend active add up to the same length, the animals split it into different segments according to the treatment: Most striking is the difference when travelling risk is high. As long as foraging risk is low, the animals come out less often, but stay longer active. As foraging gets dangerous, animals come out more often and perform shorter bouts (3A&B). On the other hand, when travelling risk is low, animals shorten the length of their activity bouts and come out more often when foraging risk is safe, too. This means that animals display opposite strategies, depending on the risk while travelling and foraging. In completely risky environments multiple short bouts might have the aim to obtain a continuous estimate of risk (Bell et al. 2009), check for improvements of the situation over time (as a "Bayesian forager", (Olsson 2006, Olsson and Molokwu 2007)), to leave a minimum amount of scent markings (Boonstra et al. 1996) but yet to keep a favorable energy balance (Lima and Bednekoff 1999). The same pattern is expressed in completely safe environments but predation cannot be the reason. This pattern can be explained by the fact that it is not costly to check out several food sources, mating partners and other missed opportunities. The situation changes as either foraging or travelling gets dangerous. When travelling is dangerous, safe foraging places increase in value, resulting in long but few foraging bouts (Olsson and Holmgren 1999). When only foraging is dangerous, changing between patches pays in terms of effective patch use and updates of predation risk.

These results show that all animals are well aware of the costs of travelling and foraging under high and low risk and include the value of the alternative resources into their decision making. These essentials of risk sensitive decision making and optimal foraging behavior affect both sexes. In this case the missed opportunity costs are only represented by the gain at the alternative food source, the worth of which is only determined by its level of safety of staying at it or travelling to it.

Different activity patterns of males and females

Due to the different missed opportunity costs of males (territory defense, search for females and multiple mating with multiple females) and females (neither pregnant nor lactating, mainly maintaining body condition) we expected the two sexes to react different to a foregone threat or an existing risk scenario and both sexes to assess the risks of travelling and foraging differently (e.g. for fiddler crabs though the females is the travelling sex here (Booksmythe et al. 2008)).

Evidence for this difference is the males´ early resumption of activity after the change of treatment. Since in males reproductive skew is high, it may pay for a male to get active as soon as possible after a disturbance because it might be the first to enhance territories or to encounter a female. Thus evolution should drive the length of delay to find the equilibrium between the shortest possible lag without putting oneself to much at risk in case the disturbance was produced by a predator. Consequently, males are more often found in risky sites than females (Trebaticka et al. 2008). In the case of the females, this equilibrium depends on the decreasing nutritional state and the risk of predation and thus activity can be delayed much longer until nutritional needs forces the females to seek for food (state dependent resumption of activity (Gotceitas and Godin 1991)). Females are known to react stronger to predatory cues by body mass changes and increased corticosterone concentrations, leading eventually to reduced breeding success (Tidhar et al. 2007), so they should carefully balance their exposition to predator cues.

The role of missed opportunities in male and female decision making can be evaluated from the sex-specific assessment of travelling and foraging risk. Males allocate time spend foraging independent of the risk while foraging (Fig. 4B), females on the other hand stay significantly longer in the trays, when it is safe to feed there (sex specific optimization of habitat choice (Luque-Larena et al. 2002)). Meanwhile, there were no sex differences among the high intake rates in safe trays (Fig. 2a), indicating that females also stay in foraging places without foraging, whereas males keep their pace to get to the alternative opportunities (Fortier and Tamarin 1998).

On the other hand, the risk of travelling affected only the behavior of males, they increased the number of changes between foraging stations in the risky conditions, while females changes between trays were constant across traveling risks. For all prey animals the activity of traveling enhances the risk of attracting a predator; but only for males it contains the additional benefits of territory defense and visiting multiple females (Fortier and Tamarin 1998). These conspicuous activity patterns increase selection pressure over the progress of the reproductive season. Due to these strategies, the ratio of males to females changes dramatically until in late autumn, only 20-40 % of vole populations consists of males (see Bryja et al. 2005 for detailed analysis). For females have a 6 times higher probability of surviving the breeding period (Bryja et al. 2005), the odds to sire offspring and bring the individual genes into the next year, increase towards autumn for males. Thus, males should become even more risk prone late in the season, while females should stay on minimum homeranges for their own safety and to prevent infanticide (Fortier and Tamarin 1998). Thus the chance of siring offspring in a short lived promiscuous species seems to represent an invaluable option for males and is worth strategies of high risk.

Our results show that differences in behavior of males and females selected through different mating strategies and intra-sexual selection pressures also affect foraging strategies. We suggest that this is directly related to differences in missed opportunity costs between the sexes while foraging and travelling. It is also important to understand such different foraging strategies when investigating risk dependent foraging behavior in wild populations and further, to identify male and female foragers in natural populations since their coping with risk differs fundamentally due to sexual dimorphic constraints in travelling behavior.

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Table 1: Statistics of the linear mixed models and simple effects t-tests

Variable	**lmm** **travelling*foraging**	**lmm** **travelling+foraging**	**t-test for simple effects of travelling**		**t-test for simple effects of foraging**	
			Foraging safe	Foraging risky	Travelling safe	Travelling risky
Total time active	n.s.	n.s.	-	-	-	-
intake	n.s.	$F_{travelling}$= 4.35, p= 0.04 $F_{foraging}$ 5.9, p= 0.018	-	-	-	-
skew	$F_{travelling*foraging}$= 4.38 p= 0.041	$F_{travelling}$= 33.16, p= 0.00 $F_{foraging}$ = 0.16, p= 0.67	T=2.41 p = 0.015	T= 5.04 p< 0.001	T=2.03 p= 0.051	T=0.73, p=0.47
Length of activity bouts	$F_{travelling*foraging}$= 7.36 p= 0.009	$F_{travelling}$= 0.23 p= 0.63 $F_{foraging}$ = 0.84, p = 0.34	n.s.	n.s.	n.s.	T= -1.99, p=0.054
Number of activity bouts	$F_{travelling*foraging}$= 11.9 p= 0.001	$F_{travelling}$= 0.23, p= 0.39 $F_{foraging}$ = 0.78, p = 0.38	n.s.	n.s.	T=-1.94, p=0.06	t=2.42, p=0.02
Number of changes	lmm travelling*sex	lmm travelling + sex	Males High vs low travelling risk		Females High vs low travelling risk	
	$F_{travelling*sex}$= 9.85 p= 0.002	$F_{travelling}$= 4.44, p= 0.038 F_{sex} = 2.24, p = 0.14	t=3.41, p=0.001		n.s.	
Time spend foraging	Lmm foraging*sex	Lmm foraging + sex	Males High vs low foraging risk		Females High vs low foraging risk	
	$F_{foraging*sex}$= 4.51 p=0.037	$F_{travelling}$= 4.44, p= 0.038, F_{sex} = 2.24, p = 0.14	t=-0.52, p=0.61		t=-2.22, p=0.032	

Table 2: Descriptive statistics

Treatment Variable	**Low travelling and low foraging risk**	**Low travelling risk - high foraging risk**	**High travelling and high foraging risk**	**Low foraging risk - high travelling risk**
Time active (minutes)	37.4 ± 45.1	33.6 ± 20.7	32.0 ± 29.7	42.0 ± 33.5
Intake (gram/6hrs)	0.6 ± 0.18	0.42 ± 0.27	0.38 ± 0.2	0.47 ± 0.27
Skew (%)	63.8 ± 14.1	57.1 ± 7.4	76.6 ± 15.6	73.5 ± 12.2
Mean **bout length** (log min)	0.9 ± 0.45	1.1 ± 0.35	0.9 ± 0.5	1.2 ± 0.5
Mean **number of bouts** (log)	0.6 ± 0.14	0.51 ± 0.12	0.6 ± 0.14	0.5 ± 015
	Low travelling risk		**High travelling risk**	
	male	**female**	**male**	**female**
Mean **number of changes** (log)	2.5 ± 1.2	2.1 ± 1.5	3.3 ± 2.0	2.6 ± 1.3
	Low foraging risk		**High foraging risk**	
	male	**female**	**male**	**female**
Time spend foraging (log min)	2.8 ± 1.6	3.6 ± 1.7	3.1 ± 1.7	2.6 ± 1.4

IV. Do bank vole mothers risk their pups with own foraging behavior?

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Abstract

Potential prey individuals face the trade-off of nutritional demands and exposure to predation while active on foraging. For individuals with parental duties and a stationary nest site, temporal or spatial flexibility to avoid predators is further limited.

Nevertheless, lactating mothers have to leave their nest unguarded when foraging, which exposes the young to nest predators.

We investigated how mothers of altricial, nest-bounded young respond to the risk of nest predation in their own foraging decisions. We present a study on behavior of lactating bank voles (*Myodes glareolus*) confronting a nest predator, the common shrew (*Sorex araneus*). Mothers were released with their pups to outdoor enclosures, and shrews were added as risk treatment. We monitored the use of feeding stations around the central nest as measurement of activity and strategic foraging behavior. The experiment was repeated in summer and autumn to account for seasonal variance.

Voles adapted their strategies to shrew presence and optimized their foraging behavior according to seasonal constraints, resulting in an interaction of treatment and season. In summer shrew presence reduced food intake from the trays, while it enhanced intake in autumn. Additionally, shrew presence decreased the number of visited trays, and concentrated mothers' foraging efforts to fewer trays. Independent of treatment and season, mothers foraged more in seed trays far away from the nest.

These results indicate that females are not investing in nest-guarding but camouflaging the nest and its surroundings from cues leading a nest predator to the young. This is also manifested in the higher exploitation of fewer food patches, contrary to optimization of food intake, probably due to minimize movements in the vicinity of the nest.

Keywords

Myodes glareolus, optimal foraging, *Sorex araneus*, nest protection, seasonality, interference

Background

Individuals of prey species are confronted with the major trade-off of energetic requirements and exposure to predators. Most research has focused on single aspects antipredatory decision-making and optimal foraging (Lima and Dill 1990, Lima 1998). However, to single out distinct behaviours and relate them to a certain trigger is not easy. It has recently been discussed, that antipredatory behaviours have to be regarded as composites including a range of behavioural options and duties to compensate for predation risk (Lind and Cresswell 2005, Ajie et al. 2007). We here present a study on a common problem of an animal tied to a certain site. Constraints, that reduce an animal´s ranges to these sites can be various, and include limited resting sites or patchily distributed resources. Probably the most common reason constraining the movements is parental demands at stationary nest sites (Danchin et al. 2008). Especially mothers with altricial young face the dilemma of acquiring as much food as possible to meet the high energetic demands of its own and the litter (Gittleman and Thompson 1988) without exposing the young to risk of predation. Neither activity shifts nor leaving a habitat to avoid the risk of predation are options in such a case, and the risk of nest predation is not a single event but a permanent threat.

Only few studies in birds and fish deal with this problem (Komdeur and Kats 1999, Sasvari and Hegyi 2000) yet almost all individuals with parental commitments face the parallel threat of predation to themselves and to their young when these are left alone. Thus, strategic answers to predation risk should be evaluated according to the actual state of an animal, reflecting the emphasis on distinct stages in life history and reproductive cycle. Lactating female mammals for example, are most likely to react with adaptive strategies including nest-guarding, pup defence (Koskela et al. 1997) or by scaling down territory sizes, moving distances and frequencies (Desy et al. 1990). On the other hand, their energetic demands are extremely high (Gittleman and Thompson 1988).

In studies on foraging behaviour of wild mammals, the provisioned foraging resources were used less when risk was high or animals were far away from the nest site (Brown and Morgan 1995, Thorson et al. 1998). Reduction of travelling further reduces the probability of meeting a predator (Norrdahl and Korpimäki 1998). But in none of these the sex of the foraging individual was specified and taken into account.

Foraging strategies have been mostly analysed in situations, where a choice of habitats or food patches differing in risk of predation was offered to animals (Kotler and Blaustein 1995, Korpimäki et al. 1996, Jacob and Brown 2000). Animals tend to shift their foraging activities to either safer habitats or safer time frames. When the risk is distributed uniformly or poses a permanent threat, avoidance of risky times or change of habitats are not options. In these cases, animals change their spatial and temporal investment patterns by concentrating their foraging effort in fewer options and accepting lower total returns, compared to their behaviour in low risk-uniform landscapes (Eccard and Liesenjohann 2008). Additionally they defer their alternative opportunities (like territory defence / mate search).

Small mammals are subject to predation from a range of predators, as well mammalian as avian. Their ability to detect predators via olfactory, acoustic and visual cues allows them to decide about their immediate reaction to a given threat. These decisions are based on the perceived level of risk and type of risk (Jedrzejewski et al. 1993, Liesenjohann and Eccard 2008). Most small mammals including many rodent species are altricial with stationary nest sites. Many rodent species like the bank vole (*Myodes glareolus* Schreber 1780) have large litters and a post partum oestrus allowing them to give birth immediately after weaning the ongoing litter. This creates high nutritional demands on the mother during lactation and simultaneous pregnancy (Trebaticka et al. 2007). In many small mammal species, only females take care of their litter and females themselves and their young are subject to predation. This makes lactating females good subjects to study effects of antipredatory behaviour towards direct predation on the adult and nest predation on the offspring and their inclusive fitness consequences.

Here we present results of a study where bank vole mothers were exposed to a potential nest predator, the common shrew (*Sorex araneus (Linné 1758)*). Occurring sympatrically with voles across all boreal and temperate habitats, shrews can have impact on the voles spatial behaviour (Fulk 1972), they also predate on vole nestlings (Ruzic 1971). Though fighting and killing each other is known from larger American species (Maurer 1970, Getz et al. 1992), no european shrew has been seen killing adult voles and the larger voles seem to be successful in chasing shrews off. This study is presented in a risk-uniform framework, since shrews inhabit the same habitat structures as voles and are of similar body size and locomotion type.

The advancing season with changes in climate and resources as external factor alters foraging behaviour and reactions to predator cues (Hayes et al. 2006). With decreasing food availability in autumn, animals have to increase the search area to find enough food (Ostfeld 1985) and competition for shared resources increases. Declining food availability might change the interaction type between species (shown for birds by Marquiss 2007). Any food resources should become more valuable due to the ending of the growing season and gradual depletion of resources. In seasons with high resource provisioning, nestlings of voles and other small mammals are not a very rewarding target to shrew species. Approaching the nest might be even dangerous for shrews because a confrontation with the mothers is likely. However, when late in the season other food resources become scarce, preying on nestlings will be more rewarding for shrews. Nest-guarding by bank vole mothers was indicated in our previous study where we found that bank vole mothers decreased their summer home ranges in the presence of shrews (M. Liesenjohann et al. in prep.) probably by staying close to the nest or additionally to avoid encounters with shrews. On the other hand, female bank voles had to increase their home ranges in autumn, indicating reduced food availability and food competition with shrews. Further, in autumn the vole recruitment in the presence of shrews decreased either due to food competition with shrews or nest predation by shrews or both (M. Liesenjohann et al. in prep.).

In the present study, we investigated seasonal effects of shrews as potential nest predators on the foraging behaviour of lactating bank vole females. The lactating mothers lived in an environment of simultaneous risk of avian predators dangerous for the adult, but the risk for its young increases with time left alone. If the mother calculated this risk, we would expect her to forage closer to the nest site in shrew presence if she tried to physically defend her young. Further, we expected a concentration of effort on a smaller number of food patches to decrease movements and avoid shrew contact. Further, we expect mothers to use the feeding stations more in autumn than in summer because they become a more valuable resource, allowing them to keep the foraging bouts shorter and home ranges smaller.

Methods:

The study was conducted in 50 m x 50 m outdoor enclosures of the Konnevesi Research Station (University of Jyväskylä, Central Finland, 62°37´N, 26°20´E). It was split into two rounds, one in August and one in September 2007. Both rounds contained 3 control and 3 shrew treatment enclosure replicates.

Treatment of enclosures:

15-18 common shrews (*Sorex araneus*) were released into the treatment enclosures in the summer round (12-14 shrews in autumn); shrews were caught in the vicinity of the enclosures and immediately transferred into the enclosures. After the summer replicate 57% ± 37 of the shrews were trapped back from the enclosures (55% ± 30 in autumn). The number of shrews per enclosure had been included as covariate in the analysis but did not explain much of the variation. Therefore only shrews presence or absence was used as a factor in statistical analysis.

Experimental animals:

Three female bank voles (*Myodes glareolus*) with their 1-2 day old pups were released into each enclosure at 35-40 meters distance from each other. Females were equipped with radio collars (TW-4, Biotrack LTd., Wareham, UK) to identify their nest sites and home ranges.

Set-Up of feeding trial:

One mother per enclosure was randomly chosen as experimental animal. A grid of 4 x 4 feeding stations was installed with the nest site in the centre. Each station consisted of a plastic tray containing 1 gram of millet and two litres of fine sand. All trays were covered by a lid and had two entrances of 2 cm diameter. Millet was weighed in portions of 1 g ± 0.05 g and mixed into the sand. The amount of food left in these trays after being used by an animal (giving up density GUD), provides a reliable estimate of the perceived risk while foraging or travelling. This is a well-established method to analyse foraging decisions (Brown and Kotler 2004). As these resources are not refilled, exploitation results in lower returns over time and forces the animal to decide when to leave a patch. This decision should be based on the perceived level of risk and potential energy gains at alternative sources (see Brown (1988) based on the Marginal Value Theorem by Charnov (1976)).

After 3 days of pre-baiting, virtually all (91 ± 5.4%) stations had been used so all were sifted and mixed with 1 g of millet for the experimental run. Trays were recollected and sifted after 24 h. All grains were dried for three hours at 40°C and weighed to the nearest 0.01 g. Control grains were taken from the package and dried as well; all results were corrected for the mere weight loss due to the drying process (mean loss 6 ± 1 %).

Variables and Statistics:

Mean **Giving-Up-Densities of trays of short distance to the nest (n = 4) and trays of long distance to the nest (n = 12)** were compared within grids (paired Wilcoxon-test). The **proportion of visited short-distance trays** out of all visited trays (identified by digging traces and foot prints in the sand) was compared to the proportion of available short-distance trays relative to all available trays (4 out of 16 = 0.25, one-sample t-test).

The **total Intake** per 24 h and the mean **Giving-Up-Density of all used trays** were analysed with a 2-way ANOVA with **season** and **treatment** as fixed factors and their interaction. For simple effects of shrew treatment within season we used Mann-Whitney tests due to the reduced sample size. The **total number of visited trays** was compared among shrew treatments using a Mann-Whitney-test (Data not normally distributed, Kolmogorov-Smirnov-Test, df= 12, p=0.014). The **concentration of effort** is a measurement to describe investment patterns at feeding stations and was compared among shrew treatments (Mann-Whitney-test). It shows how much of the total intake is taken from the 4 most used trays. If all trays were exploited equally, a value of 25% would be expected. 100% would mean that the complete intake was taken from a single tray.

Results:

Spatial foraging patterns

Even though almost all trays were used, not all were exploited equally. Trays with a long distance to the nest were exploited to a deeper level (lower GUDs) than those being close to the nest (Mean GUD of trays close to the nest: 0.65 g ± 0.13g; long distance trays: 0.56 g ± 0.14, paired Wilcoxon-test Z = -2.134 p = 0.033; Fig 1A). A higher proportion of short distance trays were visited than expected by availability of short distance trays (0.41±0.16, one sample t-test, T = 3.24, df = 11, p = 0.09; Fig 1B). The proportion of short distance trays visited did not differ with shrew presence (Mann-Whitney-test, Z = 0.00, p = 1.00, Fig. 1B) or season (Z = -.655, p = 0.512 Fig 1B).

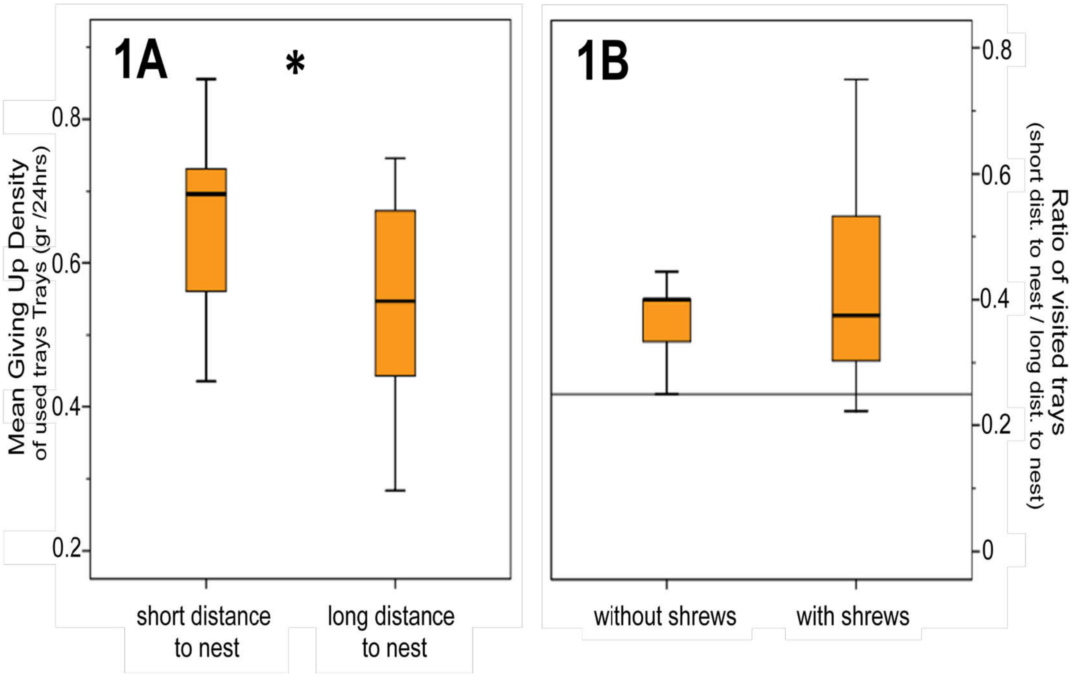

Figure 1 A & B: Spatial foraging patterns

1 A: Trays being twice as far away from the nest site are depleted to a deeper level than those close to the nest site. 1 B: The visited proportion of trays being close to the nest side is higher than expected by chance (reference line: 0.25) by the animals,). The use of the long distance and short distance trays is not depending on the shrew treatment.

Effects of shrew presence and season on foraging strategies

Both the **total intake per grid** and the **mean GUDs of the used trays** were influenced by a significant interaction between shrew treatment and season (Table 1). In summer, shrew presence tended to reduce total intake (Mann-Whitney-Test, N = 6, Z = -1.731, p = 0.083 Fig. 2A) whereas in autumn shrew presence tended to increased the intake (Mann-Whitney-Test, N = 6, Z = -1.852, p = 0.053 Fig 2A).

In summer GUDs were not affected by the treatment (Mann-Whitney-Test, N = 6, Z = -0.577, p = 0.56 Fig 2B), while in autumn the shrew presence induced a heavy use of feeding stations shown by the deep exploitation levels of used trays (Mann-Whitney-Test, N = 6, Z = -1.852, p = 0.043; Fig. 2B).

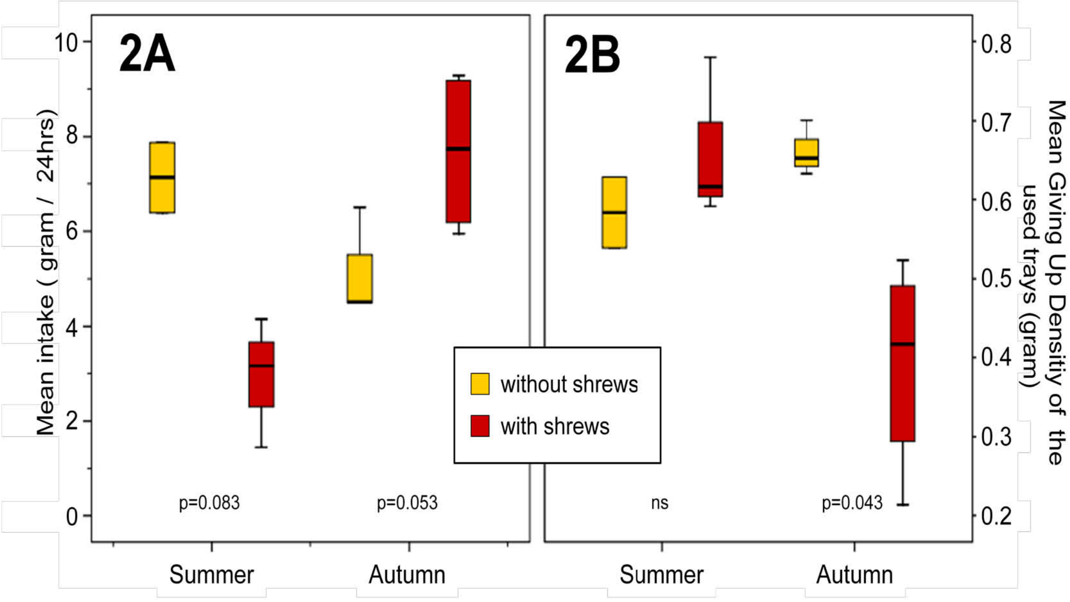

Figure 2 A & B: Interaction of treatment and season

The mean intake per grid and giving up density only of the used trays (GUD) is influenced by a significant interaction of the treatment and the season: **2A:** The intake from the trays is reduced by shrew presence in summer, but tends to be increased when shrews are present in autumn (interaction of shrew treatment*season: p= 0.013). **2B:** The GUDs slightly increase in summer when shrews are present, but heavily drop to deep levels of exploitation in autumn when shrews are present (interaction of shrew treatment*season: p = 0.037).

The total number of visited trays did not differ between seasons (Mann-Whitney-test for the number of used trays: Z = -0.249, p = 0.803). However, in the presence of shrews, a significantly lower number of trays was visited (mean number of visited trays without / with shrews: 14.4 ± 1.1 / 11.2 ± 2.6, Mann-Whitney-test, Z = -2.06, p = 0.039; Fig 3A).

Although the mean total intake did not differ between shrew treatments (Table 1) the animals in the shrew treatment **concentrated their effort** on a lower number of sources (mean % taken from the four most used trays without / with shrews: 44.2 ± 7.4% / 60.8 ± 16.7%, Mann-Whitney-test, Z = -2.19, p = 0.028). Under both treatments values were significantly different from the 25% value expected in an even use of all trays (one-sample-t-test, without / with shrews: T=5.85, P=0.010 / T=5.62, p=0.001; Fig. 3B) There was no difference in the concentration of effort among seasons (Mann-Whitney-test, Z = -.568, p = 0.570).

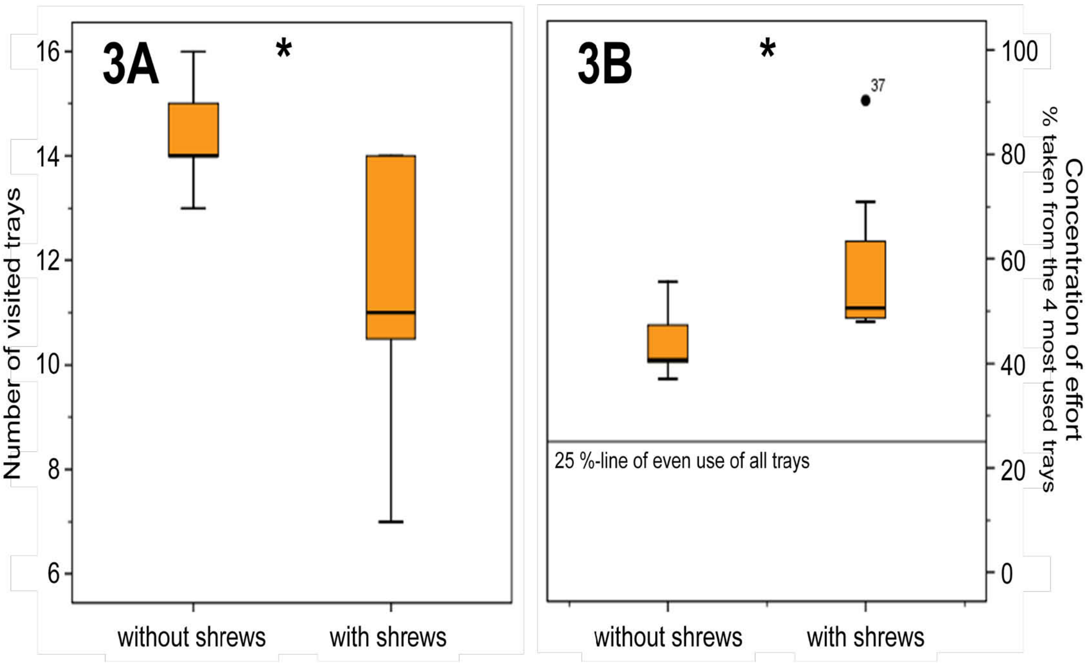

Figure 3 A & B: Influence of the treatment on foraging strategies

3 A: The number of used trays is reduced by the shrew treatment, but is independent of the season. **3 B:** The concentration of effort is influenced by the treatment, in shrew presence a higher amount of the total intake is taken from the four most used trays. Nevertheless both groups are significantly above the even use of all seed trays

Discussion

Strategic foraging patterns under predation pressure

In this study, we show that the lactating bank voles changed their foraging strategies due to the presence of a potential nest predator, the common shrew. Further constraints were set by the changing season. Mothers reduced their intake in the presence of shrews in summer but they enhanced the intake from the foraging stations in late autumn. Analogue to this, trays were depleted more in autumn when shrews were present, but there was no significant effect of shrew presence on the GUDs in summer. Shrews´ presence reduced the number of used seed trays, thus reduced travelling between patches and made the mothers to concentrate their foraging effort on a smaller number of trays. Independently of the season, mother depleted trays far away from the nest to deeper levels than those close to the nest site.

We here present a study of small mammals that have to leave the nest to forage while being under the constraints of parental duties. In addition to the nutritional demands of the pups and exposition to predators while searching for food, the mothers have to deal with a potential nest predator. This provides a fitness trade-off: On the one hand nest protection might be costly due to food deprivation (Hinch and Collins 1991) on the other hand nest protection against shrews or infanticidal conspecifics can enhance the survival probabilities of the pups (Jonsson et al. 2002, Ylönen and Horne 2002). Furthermore, for the adult forager the interaction with shrews is costly and can impair travelling and feeding activities (see Rychlik and Zwolak 2006 for shrews). Since voles and shrews use the same runways and tunnel systems and are of the same type of locomotion, the risk of encounter and the detection of the nest sites of the voles is high and uniformly distributed.

Behavioural strategies and life history decisions often depend on extrinsic factor like season (Kaitala et al. 1997). In our experiment, the total food intake, measured in form of mean giving up densities of the used trays, were affected by an interaction of season and treatment. In summer, the intake from the feeding stations was reduced in shrew presence (Fig. 2A), indicating the sufficient natural resources that allow the mothers to disregard the feeding stations. This interpretation is further supported by our telemetry results with smaller home ranges in summer under shrew presence (M. Liesenjohann et al. subm.). Voles have reduced movements and thus decreased the probabilities of encounters with predators and interfering competitors (Norrdahl and Korpimaki 1998, Nie and Liu 2005). Additionally the amount of reliable, conspicuous, olfactory cues in the vicinity of the nest site is reduced (Koivula and Korpimaki 2001).Low temperatures and lower densities of invertebrate food in autumn might force shrews to switch to alternative food sources, like vole pups, and enhance predation pressure. This was supported by our finding of reduced pup survival of the bank voles in autumn in the shrew treatment (M. Liesenjohann et al. subm.) But it might as well be caused by larger home ranges and reduced food intake of bank vole mothers. Reduced food availability may also explain bank voles foraging patterns reported in this experiment. In autumn, intake from the trays was higher in shrew treatments, indicating interference and/or food competition between voles and shrews. In this case, the provided feeding stations allow keeping smaller home ranges and thus longer inactive bouts to keep the nest above threshold temperatures and prevent nest predation.

Other foraging studies found, that provided foraging resources were used less when risk was high or animals were far away from the nest site (Brown and Morgan 1995, Thorson et al. 1998). In our study, feeding stations were depleted to a lower level when the distance from the nest increased and the probability of finding an alternativ source was lower (Fig. 1A & B). This can be explained by the fact that our feeding patches provided (1) a reliable food source and (2) a place with a relatively high level of safety by providing cover from avian predation. These two factors become more important with increasing distance to the nest site. This foraging strategy can be explained by two different approaches to optimal decisions of lactating mothers: either parental demands do not affect optimal foraging strategies and the mother maximises her own safety and intake depending on the distance to the nest. As an alternative explanation, the mother tries to avoid producing permanent scent marks in the direct vicinity of her nest site which allures mammalian predators (Banks et al. 2000, Sundell et al. 2008). It has been shown, that a variety of predators uses scent marks (Cushing 1985, Roberts et al. 2001) as cues and that the ultraviolet visibility of urine attracts avian predators

(Viitala et al. 1995) and thus enhances predation pressure around the nest site. This predation pressure is known to alter scent marking (Roberts et al. 2001), defecation behaviour (Boonstra et al. 1996) and strategies to camouflage nest sides (Mironov 1990). This adaptation is not depending on the shrew treatment but is a general strategy promising success under all types of predation. While the mother roams in an environment with homogeneously distributed risk, the risk of the pups of being attacked grows over time of being alone. This should force the mother to use the stations close to the nest more intense if she would trade foraging for nest protection (Andersson and Waldeck 2006). Apparently, the expressed behaviour constitutes a compromise between the duties of nest guarding and parental demands at the nest site on the one hand (after all, the animals use a grid of feeding stations which is relatively close to the nest site) and the need to forage and avoid scent marking near the nest on the other hand.

This latter composition of constraints is in line with the behavioural changes made due to shrew presence, the reduction of movement distance (smaller number of visited trays; Fig. 3A) and the adjustments of temporal investment at the feeding stations (concentration of effort and Fig. 3B). Less travelling events reduce the probability of meeting other animals (Norrdahl and Korpimäki 1998) thus females try to avoid costly encounters with shrews while foraging. To maintain intake from the trays, mothers invest more time and deplete the trays to a lower level when shrews are present. This makes foraging ineffective because the longer the animal depletes a non-refilling patch to gather food items the more energy has to be invested per unit of energy returned (Charnov 1976). This indicates, that the mother is not accepting high encounter probabilities to maximise nest protection time.

Conclusions

Our experimental results show that the mother adjusts her strategies to minimize the risk of leading predators with olfactory cues to her nest site. She further accepts inefficient foraging strategies to avoid encounters and reduce the probability of being detected by predators. These strategies are adapted to seasonal constraints of reduced food availiability and higher energetic demands in autumn.

Lactating bank voles were well able to adapt their foraging behaviour to shrew presence. These behavioural adaptations were different in summer and autumn, indicating that seasonal constraints (like food availability) provide a framework in which behaviour can be expressed in a flexible range of options. Here we suggest that behaviour adaptations are not only depending on the individual state but as well on individual demands and duties in different seasonal and risk contexts.

Authors' contributions

TL, ME, JE and HY contributed to the planning of the experiment and hypotheses, TL, ME, LT, JS and MH prepared and conducted the data sampling, TL analysed the data, TL ME, JE wrote the paper, LT, JS, MH and HY revised the manuscript and added important intellectual content .

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Table 1: Effects of Season and Treatment on Intake and Mean GUD

factor variable	treatment		season		season x treatment	
	$F_{(1, 8)}$	p	$F_{(1, 8)}$	p	$F_{(1, 8)}$	p
total intake per grid	1,6	0,24	1,9	0,21	17,3	0,013
mean GUDs of the used trays	1,9	0,2	1,7	0,23	7,3	0,037

Table 1: 2-Way ANOVA of the effects of the factors season and shrew presence on the total intake and exploitation levels.

V. From interference to predation: type and effects of direct interaction between granivorous and insectivorous small mammals

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V. From interference to predation: type and effects of direct interaction between granivorous and insectivorous small mammals

Abstract

Background

Indirect exploitative competition, direct interference and predation are important factors affecting species coexistence. These interaction types act not mutually exclusive, but may overlap and may also vary with season and life history state of the animals.

We studied the effect of interference and potential nest predation by common shrews (*Sorex araneus*) on lactating bank voles (*Myodes glareolus*) in two different seasons. These two species coexist and partially overlap in their diet and may interact aggressively in their common habitat. Additionally, shrews can prey on nestling voles. We studied bank vole mothers´ spatial and temporal adaptations to shrew presence during summer and autumn in outdoor enclosures in Central Finland. Further we focused on fitness costs, e.g. decreased offspring survival, which bank voles may experience in the presence of shrews.

Results

In summer interference with shrews decreased the vole mother's home ranges and they spent more time outside the nest, but there were no effects on offspring survival. In autumn with dissimilar environmental conditions (e.g. lower temperature, decreased food resources) we found decreased offspring survival in enclosures with shrews, potentially indicating nest predation by shrews or increased competition.

Conclusion

We provide evidence for a change of the interaction type between different seasons. In summer, sympatric voles and shrews seem to interact mainly by interference, whereas resource competition and / or nest predation by shrews on bank vole pups gain importance in autumn. Different food availability, changing environmental conditions and following energetic constraints in voles and shrews later in the year may be the reasons for the shift of the interaction type and its increasing effects on the inclusive fitness of bank voles.

Key-words: shrews, *Sorex araneus*, interspecific competition, interaction type, coexistence, behavioural adjustments, spacing behaviour, offspring survival, voles, *Myodes glareolus*

Introduction

Most studies on interspecific interaction have focused on indirect interactions like resource exploitation (e.g. Case and Casten 1979; Levins 1979; Armstrong and McGehee 1980). But the implications of direct interactions such as interference or predation have been neglected so far (Amarasekare and Nisbet 2001; Amarasekare 2002). Nevertheless, exploitation and interference, and interference and predation are often overlapping in nature and their effects are not easy to separate (Triplet et al. 1999; Smallegange et al. 2006; Scharf et al. 2008). The overlap differs with the species investigated and may further vary among life history stages of the animals (Walls 1990; Eccard and Ylönen 2003). For the type of interaction also depends on resource abundance (Harris et al. 2006), it should vary within different seasons as well (Shenbrot and Krasnov 2002; Hoset and Steen 2007, Eccard et. al unpublished).

Direct interactions – interference and predation

Interference among adult animals, e.g. interspecific territoriality, agonistic and aggressive behaviour can structure communities (Case and Gilpin 1974; Walls 1990; Kennedy and White 1996; Amarasekare 2002). To avoid negative overlaps with competitors, either in time or in space, animals respond by changing their habitat or activity periods (Ziv et al. 1993; Eccard and Ylönen 2003). Meanwhile, they accept confinements and negative effects e.g. time loss for other activities like foraging or the use of suboptimal habitats and diets (Laundre et al. 2001). Nevertheless, these behavioural adjustments can lead to a reduction of the impact of interference and to a balanced species coexistence (Walls 1990; Abramsky et al. 2001; Valeix et al. 2007).

Predation can be a mechanism and extreme case of interference which alters the competitors' ability to exploit any resource (Palomares and Caro 1999; Amarasekare 2002). The inferior species usually has a smaller body size than the predator and may suffer higher costs due to this asymmetrical interaction (Valeix et al. 2007). Larger species are therefore considered to have a higher impact in structuring communities than smaller species.

Nest predation is a special case of interspecific killing and can also occur between same sized species, e.g. rodents preying on bird eggs (Bradley and Marzluff 2003). Predators may even be smaller than their prey, e.g. shrews preying on voles (Getz et al. 1992) or their nestlings (Ruzic 1971). Hence, nest protection against predators or infanticidal conspecifics is essential for prey species in order to secure nestling survival (Lambin and Yoccoz 1998; Wolff and Peterson 1998). Therefore, individuals with parental duties face trade offs between foraging or staying in the nest to protect their offspring against intruders (Getz et al. 1992).

Interference and nest predation among shrews and voles

We studied interspecific interactions between shrews and voles coexisting in many habitats of the northern hemisphere. Little is known about species interactions and mechanisms driving their population dynamics. On a local scale populations seem to fluctuate successively (Huitu et al. 2004) but also coupled oscillations were observed (Eadie 1952; Henttonen et al. 1989).

Since voles and shrews use the same aboveground runways and underground tunnel systems, space limitation might be a reason for aggressive encounters. Additionally, shrews exploring vole tunnel systems have a high probability of encountering and plundering the easily accessible vole nest sites. Ruzic (1971) reported that during a common vole (*Microtus arvalis*) plaque in Germany 33 out of 36 monitored nests were destroyed by shrews. Therefore, the reproductive success of voles can be negatively influenced by the mere presence of shrews, but also by their function as nest predators of the vole's altricial young. Accordingly, we expect adaptations to have evolved in the voles' strategies of offspring protection. Indeed, some vole species (e.g. *Microtus pennsylvanicus and M. ochrogaster*) can defend their nests against larger shrews (e.g. the American short-tailed shrew *Blarina brevicauda,* Getz et al. 1992) by aggressive vocalisation and attacks or completely avoid each other (Fulk 1972). These two vole species only lost young while being away from the nest for foraging trips. None of the mentioned behavioural adaptations have been investigated for European species so far.

In our study system, the granivorous-omnivorous bank vole *(Myodes glareolus)* served as the focal species and insectivorous common shrews *(Sorex araneus)* as antagonists. Both species coexist in forests, forest edges and agricultural habitats and overlap in their common polyphasic activity patterns and to a smaller extent in their diet (Table 1).

We conducted two experimental runs with a one month break in between. Experimental runs in the midst of summer and autumn differed greatly in ambient temperature and vegetative decay due to the short fennoscandian summer (Table 2). The earlier replicate resembled best breeding conditions and the latter degrading autumn conditions with the last reproductive events of the season. Differing conditions should represent different resource availability between experimental runs (Eccard and Ylönen 2002; Ylönen et al. 2004).

Aims and Hypotheses

To analyse the effects of interference, we investigated patterns of activity (home range size, appearance outside the nest site and temporal adjustments). Further, we monitored recruitment rates of lactating vole females with their new born pups to study the role of nest predation by shrews.

We expect home ranges to decrease with increasing aggressive interactions (Viitala 1984; Eccard and Ylönen 2002), an effect caused by direct interference or nest predation.

A change of the activity patterns is hard to predict, it can either be expected, that voles enhance their appearance near the nest (e.g. for offspring defence or for predator inspection (Dugatkin and Godin 1992)). On the other hand, voles could avoid the vicinity of the nest to avoid the attraction of predators by scent marks and auditory cues (Boonstra et al. 1996). A change of temporal patterns depends on the voles´ assessment of the type of risk (Liesenjohann and Eccard 2008). If the voles react to an unknown type of risk, they might follow their "ancient predatory response of mammals, seeking safety in the dark" (Gliwicz and Dabrowski 2008), and shift their activity periods into the night. If the adaptation is specific for shrew species, temporal adjustment is not sensible, for shrews are active in short, unforeseeable bouts around the clock (Churchfield 1990).

If shrews act as nest predators, the recruitment rates of the bank vole mothers should be negatively influenced by shrew presence.

Further, we expect resource availability to have an effect on the change of the interaction type: with high resource availability for both species in summer we assume interference to be the only acting type of interaction. In autumn with declining resources we assume exploitation competition or even nest predation to become more important than interference.

Methods

Experimental field sites and populations

The experiment was carried out in large outdoor enclosures between August and October 2007 at field sites near the Konnevesi Research Station, Central Finland (62°37'N, 26°20'E). We conducted two experimental runs in summer and in autumn sequentially at two different field sites which differed in vegetation and due to the sequential design also in seasonal parameters such as day length (Table 2). Enclosures were ¼ ha in size and fenced by a galvanised metal sheet dug half a meter into the ground and extending 0.5-1 m above ground to separate populations and to prevent predation by terrestrial predators. Enclosures were not protected against avian predation. Each enclosure was equipped with 25 permanent trapping locations in a regular 5 x 5 grid with 10 m spacing. Each location had one multiple capture live-trap (Ugglan, GrahnAB, Sweden) inside a metal chimney for shelter. The general design of the study is additive, investigating whether interference and predation exists in this granivore-insectivore system and whether or how the shrew's presence affects the bank vole's behaviour or life history traits. In control enclosures we wanted to exclude any possible secondary effects due to intraspecific competition among bank voles and therefore disclaimed to add conspecific animals as density controls for shrews in treatment enclosures (see Connell 1983 for a comprehensive discussion on additive versus replacement designs).

We used populations of bank vole females consisting of lab-born and wild-caught over-wintered and year-born animals. Age groups and origin were equally distributed over replicates and treatments. All females were experienced mothers.

Common shrews were trapped from adjacent forests and fields. Because shrews are very sensible to trapping stress, we checked mealworm baited traps every hour and directly transferred the animals to treatment enclosures until reaching a number of 18 in summer and 13 shrews in autumn per enclosure. After the experiment, we trapped 9 ± 5 individuals (mean ± SD) per treatment enclosure of the originally released shrews and found no seasonal influence on shrew survival (Mann-Whitney-Test, $Z = -0.54$, $p = 0.629$). Their density after the experiment in summer was 4 fold (autumn: 3.2 fold) higher than densities reported for boreal grasslands in summer (max. 10 animals / ha, Hansson 1968)

Table 1 Ecological and specific characteristics of the two study species.

Species	Bank vole *(Myodes glareolus)*		Common shrew *(Sorex araneus)*	
Habitat	forest, forest edges (1)		grassland, woodland, arable land, hedges (2)	
Diet	granivore-omnivore: seeds, lichens, forbs, insects (3)		insectivore: insect imagines and larvae, earthworms, spiders (2)	
Activity rhythm	polyphasic (4) - ultradian (5)		ephemeral (5)	
Social system	*breeding season*	*nonbreeding season*	*breeding season*	*nonbreeding season*
	territorial	social	strictly territorial (2)	
Mean body size (mm)	80-135 (1)		60-88 (2)	
Mean body weight (g)	12-40 (1)		8.0 (6)	
Home range size (m2)	*summer*	*autum/winter*	*summer*	*autum/winter*
	300-1200 (7, 8)	300-500 (7, 9)	400-450 (2)	500-600 (2)

(1) Niethammer and Krapp 1982, (2) Churchfield 1990, (3) Hansson 1985, (4) Ylönen 1988, (5) Halle 2006, (6) Rychlik 2002, (7) Ylönen 1990, (8) Eccard and Ylönen 2003, (9) Ylönen and Viitala 1985, 1991

Table 2: Replicate characteristics and the seasons' abiotic parameters during the telemetry phase.

		summer	autumn
	time period	July-September 2007	August-October 2007
replicates	telemetry phase	15./16. August 2007	09./10. September 2007
	offspring trapping (days after birth)	22-25	22-25
	enclosures total N	6	8
	treatments	3 S + 3 SF	4 S + 4 SF
	enclosures used for telemetry	5 (minus 1 S)	7 (minus 1 SF)
	enclosures used for recruitment	6	8
parameters during telemetry phases	vegetation	homogeneous open grassland, saplings of alder, willow and birch	tall grasses, alder saplings
	abiotics		
	day length [h]	~16	~13
	temperature min [°C]	14,7	4,75
	temperature max [°C]	24	12,2
	rain [mm]	0	0
	humidity [%]	72,8	73,3

S = enclosures with shrews SF = shrew free enclosures

Experimental schedule and methods

Each replicate started with pairing bank voles in standard breeding cages in the laboratory of the Konnevesi research station (Table 3). After a pregnancy of 20 ± 2 (Mean ± SD) days, females gave birth to 5 ± 2 pups. Females and their pups were habituated to 30 cm x 30 cm x 20 cm wooden nest boxes for two days before transferring them to the enclosures.

Three females with pups were released in their nest boxes in every enclosure and placed with 40 m distance between each other. This is the maximum distance for three locations in the enclosures and was used because bank vole females are known as territorial breeders (Koskela et al. 1997). We checked nest boxes 24 hours after release to the enclosures. In summer 17% of the females and in autumn 42% died in the habituation phase and were replaced by other females and nestlings of the same age. The high autumn mortality is probably related to the natural autumn decline of reproducing cohorts in bank vole populations (Kaikusalo 1982). We had no loss of replacement females and their pups in summer and only one replacement female could not be trapped back after the autumn run. Mortality of females on enclosure level over the rest of the experiment was calculated only after the replacement of females on day 23 (Table 3).

Table 3: Study course of events.

Day of experiment	Event
0	Pairing of bank voles in the laboratory
0-19	Live trapping of shrews and introduction to treatment enclosures
19	Habituation of pregnant bank voles to nest boxes
20	Parturition in nest boxes
21	Radiotagging
22	Introduction of mothers + pups in nest boxes to enclosures
22-23	Replacement of females in case of deaths
23	Radiotelemtry (24 h, 2 fixes / h)
42-45	Live trapping of bank voles (mothers + offspring) and shrews

In the autumn run we placed temperature loggers (KOOLTRAK Inc. USA) at the inner lid of the nest boxes for the recording of the nest temperature. We analysed the data of survived females during the night of telemetry (12 hours) for having a nest usage control. The temperature in the nest boxes decreased by 3.9 °C (± 0.87 °C, mean ± SD, N = 6) per activity bout when the animals were outside the nest (44.0 ± 7.2 min, mean ± SD, N = 6). In summer, ambient temperature was too high to expect temperatur droppings and we therefore did not use the loggers.

Two lactating females per enclosure were equipped with radio collars (BIOTRACK, Wareham, UK) in the laboratory. Radio telemetry started one day after transfer to the field and lasted 24 hours per individual. Hand-held telemetry fixes were taken every half hour with the exact position (± 2 m) of each individual by using foldable Yagi antennas and RX-98 tracking receivers (Televilt, Sweden). Home range sizes were calculated by using RANGES VI software package (Kenward & Hodder 1996). To estimate the size of the main activity area we used 95% minimum convex polygons (MCP) excluding excursions far away from the nest. We used the percentage of fixes outside the nest as an activity index for each individual. An animal was defined to be outside its nest by getting telemetry fixes ± 1 m apart from the nest site and to be active by changing positions as detected by amplitude changes in the acoustic signal within a time frame of 2 minutes.

To test whether the temporal activity of the bank vole females during one 24-hour period was affected by shrew presence we calculated diurnal and crepuscular activity (Halle 1995) of each individual female based on telemetry data. The diurnality index was calculated by using the equation applied by Hoset and Steen (2007), and should be positive if the animal was mainly active during the day. We counted the number of active telemetry fixes per individual during day and night time for the individual's telemetry period; each corrected by the length of the tracked day time and tracked night time. The crepuscularity index relates to an individual's activity during sunset and sunrise, corrected by the number of active fixes during the whole telemetry period (24 h). The index is positive if an animal prefers being active during twilight compared to the other time periods of a day.

At the end of the experiment, bank vole mothers and their 22-25 days old juveniles were trapped back from the enclosures. Bank vole pups are weaned by their mothers before reaching an age of three weeks (Oksanen et al. 2001). Since pups were not individually marked, the recruitment data of offspring was analysed on enclosure level. We used the number of juveniles per surviving female from each enclosure as recruitment rate and body weights of juveniles as offspring condition.

Statistics

Survival of mothers is a dichotomous output variable (alive or dead). We used a *probit* regression model to analyse proportions of survival on the enclosure level using shrew's presence and season as independent variables. Recruitment of young (mean number of juveniles per surviving female) was analysed on the enclosure level. Telemetry data were analysed on an individual level from 17 individuals (8 females from 7 shrew enclosures, 9 from 5 control enclosures). In six cases (5 in summer, 1 in autumn) we had complete datasets from two females per enclosure, but because sample sizes were low, we treated them statistically as independent observations. This is justified since female's home ranges were small (30.05 +/- 11.3 m^2) compared to the distance between home range centers (40 m). Telemetry data were log-transformed before analysis. To test recruitment survival and female's telemetry data we used two-factorial, general linear models (GLM, table 4) with treatment (shrew presence or absence) and season (summer and autumn) as fixed factors. Reported are the most parsimonious models, non significant interactions are removed. Significant interactions were tested for simple effects using t-tests. For all statistical analyses SPSS for Windows 15.x (SPSS Inc.) was used.

Results

Home range size and appearance outside the nest

Both home range size (Figure 1A) and appearance outside the nest (Figure 1B) of the female voles were affected by an interaction of shrew presence and season (GLM, table 4). We therefore analysed simple effects of season and treatment separately using t-tests.

In summer lactating bank voles significantly decreased their home range size in shrew enclosures (23.0 ± 5.4 m^2) to 59% of the home ranges in enclosures without shrews (38.9 ± 6.7 m^2) (t = -0.3445, df = 7, p = 0.01). In autumn, female home ranges are not larger in shrew presence (121.8 ± 73.5 m^2) than in the absence of shrews (53.2 ± 26.4.m^2) (t = -0.189, df = 6, p = 0.11). In the shrew-free enclosures we did not find a seasonal effect on home range sizes (home ranges in summer / autumn: 38.9 ± 6.7 m^2 / 53.2 ± 26.4 m^2, t = -0,724, df = 6, p =

0.496) but in the shrew enclosures home ranges were smaller in summer (23.0 ± 5.4 m^2) than in autumn (121.8 ± 73.5 m^2) (t = -5.13, df = 7, p = 0.001).

Females in summer inhabiting shrew enclosures had a significantly higher percentage of telemetry fixes outside the nest (72.4 ± 13%) compared to females in enclosures without shrews (51.3 ± 2.7 %)(t = -4.084, df = 7, p = 0.005). Bank vole females in autumn on the other hand tend to spend less time outside the nest in shrew presence (percentage of telemetry fixes outside the nest shrews present / shrews absent: 22.7 ± 3.7 % / 28.7 ± 3.7 %, t = -2.3, df = 6, p = 0.061). As well in enclosures with shrews (percentage of telemetry fixes outside the nest in summer / autumn: 72.4 ± 13.9 % / 22.7 ± 3.7 %) as in enclosures without shrews (51.3 ± 2.7 % / 28.7 ± 3.7 %) lactating bank vole mothers reduced their time outside the nest in autumn compared to summer (shrew enclosures, t = 9.970, df = 6, p <0.001, no shrew enclosures, t = -10.987, df = 7, p <0.001).

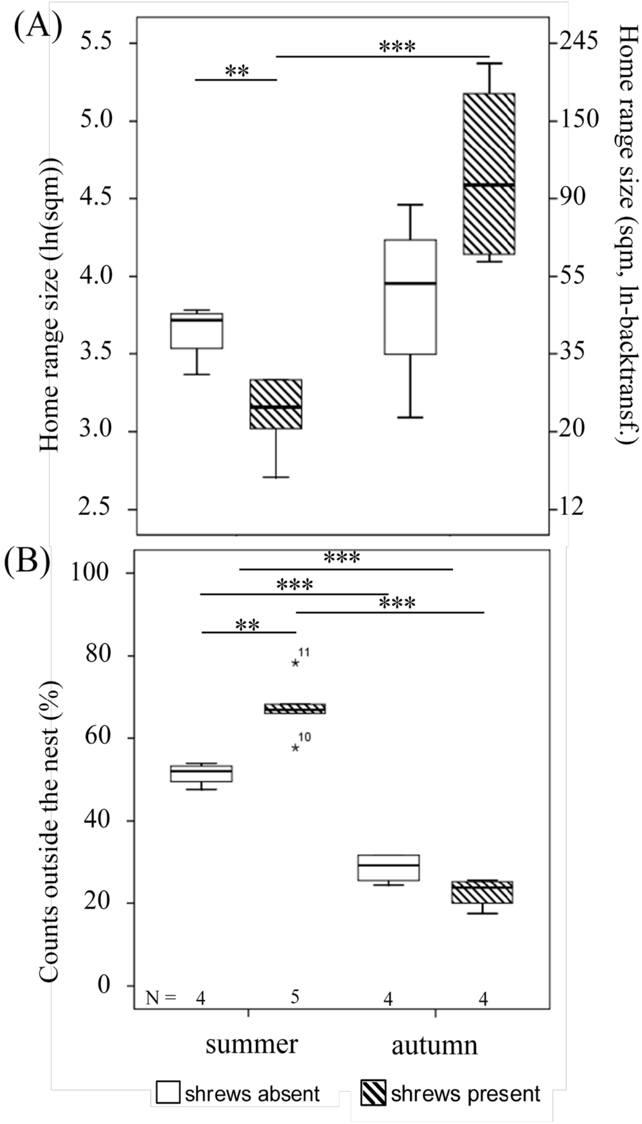


Fig. 1A Mean home range sizes (sqm) of lactating bank voles.

Home ranges are significantly enhanced in autumn. The significant interaction is a result of reduced homerange size in shrew presence in summer but an enhanced home range size in shrew presence in autumn. This shows the voles´ adaptation to the different type of interaction in different seasons, triggered by the resource availability.

Fig. 1B Proportion of number of telemetry fixes outside the nest.

A measurement of vole appearance outside the nest. The activity outside the nest is significantly enhanced in shrew presence in summer, but reduced in shrew presence in autumn. This results in the significant interaction of the two factors (see Table 4).

Asterisks indicate the results of the significant t-tests.

Both indices of diurnality and crepuscularity were not affected by shrew presence or season (GLM, table 4).

Survival and recruitment

The proportion of surviving vole mothers was not affected by season or treatment (*probit* regression, $\chi^2_{11} = 12.4$, p = 0.333, Figure 2).

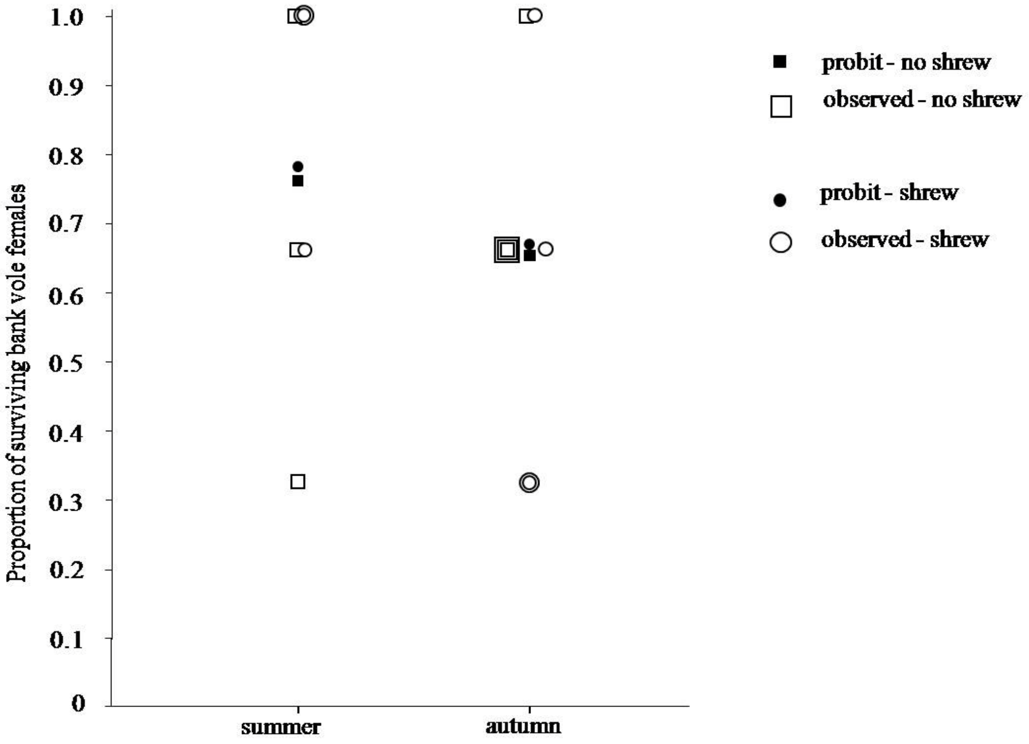


Fig. 2 Proportion of surviving bank vole females:

We used a probit regression model to analyse proportions of survival per enclosure for each season. Survival of adult females was not affect by the shrew presence and was not different between the two replicates

Recruitment was affected by an interaction of shrew presence and season (GLM, Table 4), we therefore analysed simple effects of shrew presence and season. There was no negative shrew effect on vole recruitment in summer (t = 0.414, df = 4, p = 0.7), but in autumn recruitment decreased in the presence of shrews compared to control enclosures (t = -3.073, df = 6, p = 0.022, Fig. 3A). Season had no significant effect on recruitment, neither in enclosures with shrews present nor in enclosures with shrews absent (all t-test n. s.).

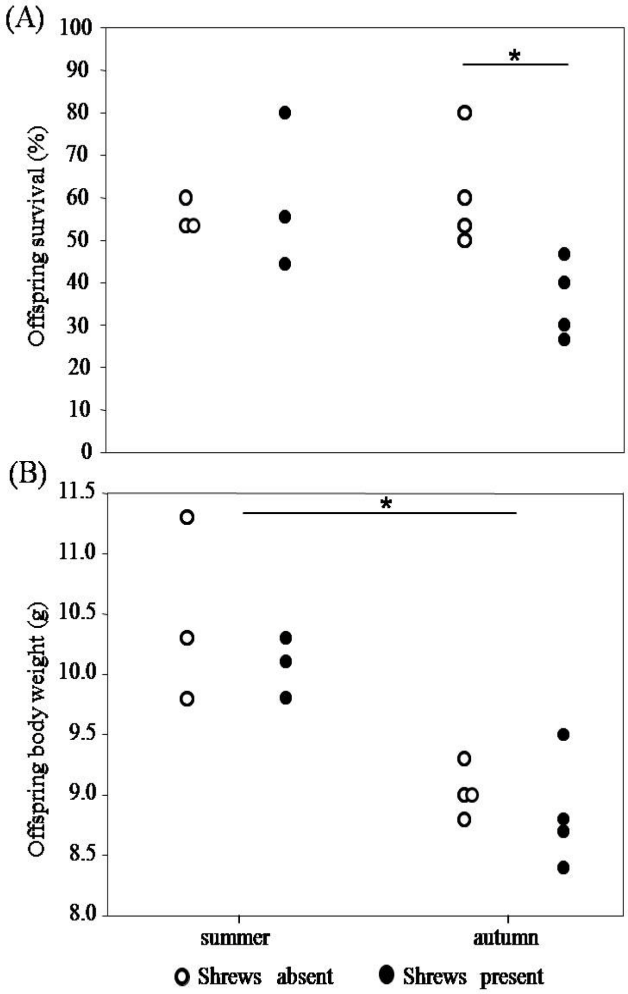
Fig. 3A Percentage of offspring survival in summer and autumn, for shrew and shrew free enclosures.

The significant interaction (see Table 4) is mainly caused by the significant reduction of offspring survival in shrew presence in autumn.

Fig. 3B Offpring body weight (g) in shrew and shrew free enclosures in summer and autumn.

Body weight is significantly reduced under the harsh conditions of the autumn season. Shrew presence has no effect on the body weight of the vole pups (see Table 4).

Asterisks indicate the results of the significant t-tests.



Juveniles were lighter in autumn (8.9 ± 0.3 g) than in summer (10.3 ± 0.6 g, Fig. 3B) but there was no significant effect of shrew’s presence or of the interaction of treatment and season on offspring body weight (GLM, Table 4).

Table 4 Statistics of the General Linear Models.

	shrew presence (df = 1)		season (df = 1)		interaction (df = 1)		
	F	p	F	p	F	p	error df
home range size	0.36	0.56	17.06	0.001	9.69	0.008	13
counts outside the nest	4.28	0.06	194.47	<0.001	20.69	0.001	13
diurnality index	0.76	0.39	3.47	0.083	1.521	0.24	14
crepuscularity index	1.97	0.18	0.94	0.35	0.58	0.46	13
recruitment	2.44	0.15	2.06	0.18	5	0.049	10
offspring weight	1.43	0.26	34.02	<0.001		n.s.	11

Presented are the most parsimonious models, showing only significant main effects and interactions. Non significant factors are removed. Varying error degrees of freedom are due to missing datasets in case of partial failure of enclosures.

Discussion

To analyse the type of interaction and its effects between two coexisting species, we exposed lactating bank vole mothers to a high density of shrews in outdoor enclosures. This was done in summer and replicated in autumn. We observed as well effects of shrew presence as of the season (summer / autumn). Home range size, appearance of vole mothers outside the nest, and offspring recruitment were influenced by a significant interaction of the treatment and the season, showing a change of the interaction type depending on different resource availability in the two seasons. While interference and potentially nest predation are responsible for the behavioural adaptations in summer, exploitation gains influence in autumn and intensifies the impact of interference and nest predation. To discuss the type of interaction in each season, the effects were separated according to the results of the t-tests.

Effects of the interaction types

Shrew presence caused smaller home ranges of bank vole females in summer, but not in autumn. Experimental field studies of forced coexistence in rodents have shown that avoidance behaviour can prevent detrimental effects due to direct interference (Mappes et al. 1995; Eccard and Ylönen 2002). Decreasing home ranges can therefore be an effective mechanism to relax interference. In our study, this pattern is only expressed in the summer replicate. Apparently, high food provisioning is a prerequisite for reducing home ranges without considerable costs. Koskela et al. (1997) have shown that the size of bank vole females' home ranges is at its smallest around parturition and connected to highest aggression levels towards intruders, in contrast to other reproductive phases. The presence of an interfering species may intensify this spatial behaviour. Observations from our experiment support the idea of home range and activity reduction as an answer to unknown potential predators to avoid costly encounters (Norrdahl and Korpimaki 2000). As an additional benefit, nest protection might be more effective when home ranges are smaller.

Females increased their exposure time outside the nest in the summer replicate when shrews were present. In autumn, shrew presence had no effect on the vole mothers′ appearance outside the nest. The pattern shown in summer might be threat inspection of the voles (sensu predator inspection, Dugatkin and Godin 1992) and an effective nest protection strategy within their home ranges and especially in the close vicinity of the nest. This meets findings of Getz (1992) who observed that vole females eject shrews when they draw near the nest site. In autumn, environmental factors seem to force the voles to stay in the nest (see below).

Vole mothers did not shift their activity phases as a response to the presence of shrews (no change in the crepuscularity and diurnality index), neither in summer, nor in autumn. As predicted, this is a behaviour to deal with a permanent threat, e.g. predators that have no distinct activity phases. A behavioural adjustment with the aim of temporal segregation from shrews would not be a promising strategy for voles, since the shrews′ frequent activity bouts are evenly distributed over day and night times (Churchfield 1990; Halle 2006).

In summer we found no effects of shrew presence on recruitment rate and offspring condition (weight), assuming that females were able to protect their offspring effectively during the sensitive nestling phase. This might be owed to sufficient food sources (seeds and invertebrates) around the nest sites during summer, which might be responsible for a good mother and offspring condition and nest maintenance. By sufficient nutritional provisioning, vole mothers were not forced to do long foraging trips and leave the nest unattended. The missing effect of shrew presence on the offspring's body weight supports the idea that voles can adapt their spatial and foraging strategies without suffering measurable costs for themselves or their young as long as food is abundant.

A reduced or even absent exploitation competition among shrews and voles due to abundant invertebrate food might be an additional explanation for the missing effect of shrew presence on pup survival in summer, shrews have simply no need to prey on nestling voles (Churchfield 1982).

In contrast to the summer run, bank voles in autumn suffered fitness costs (decreased offspring survival) in shrew presence. This effect may be caused by a combination of the three interaction types gaining importance in seasons with declining resource availability: (1) nest predation, (2) exploitation and (3) interference.

(1) The nest predation rate by shrews may have increased as a result of reduced availability of invertebrates. Bank vole pups may have become a valuable resource. It has been reported for several shrew species that they feed occasionally on vertebrates (e.g. on Muridae, Punzo 2003; on nestling common voles, Ruzic 1971). The American short-tailed shrew (*Blarina brevicauda*) covers its food demands particularly in fall and winter by feeding on meadow voles (*Microtus pennsylvanicus*) (Eadie 1952). Our own observations in different years suggest that young, summer-born shrews in seasons rich in food were not very prone to search

and attack vole pups. But in spring with low insect availability, overwintered shrews were very aggressive against vulnerable pups. (2) A general decrease of seed availability leads to an increased exploitation of common invertebrates in autumn by both, voles and shrews. Due to their high metabolic rates (Pernetta 1976), an average sized shrew as *Sorex araneus* requires about 100 invertebrate prey items (10 mm body size) per day (Churchfield 1982). Together with declining temperatures and occasional phases of overnight frost, shrews may cause a severe reduction of insect density and thus cause additional nutritional stress in lactating bank vole mothers. (3) Because bank voles could not reduce their home ranges under bad environmental conditions in autumn, chances for acts of interference (e.g. aggressive encounters) were enhanced compared to the summer scenario. Due to this loss of time and energy, bank vole mothers could allocate a smaller proportion of time to foraging, an effect that can reduce survival rates and reproductive success of individuals (Laundre et al. 2001).

Seasonal effects

Independent of the shrew presence we found reduced activity times outside the nest in autumn compared to the voles´ activity patterns in summer. The long bouts of inactivity in the nest can be interpreted as an attempt to maintain nest and pup temperature above a minimum threshold. Temperatures in nests without an adult drop rapidly (0.1°C / min, see material and methods) if ambient temperatures are low (Wolff and Bateman 1978). This allocation of time is followed by a reduced time budget for foraging activities. Consequently, offspring condition is worse in autumn than in summer.

Conclusion

Our experiment shows that voles in coexistence with shrews altered their spatial and temporal behaviour throughout the breeding season in summer in order to avoid detrimental effects due direct interference. By adjusting activity patterns and home range sizes (e.g. staying close to nest in shrew presence), bank vole mothers can maintain their inclusive fitness by protecting their nestlings from nest predation.

In autumn, both, voles and shrews face diminishing food resources and start to compete for common invertebrate food. While vole mothers have to compensate exploitation (by maintaining big home ranges) and low temperatures (by nest warming), shrews might take the chance to spice up their diet by consuming vole pups.

Our study provides evidence that the transition between the interaction types (e.g. from interference to exploitation competition) can be caused by seasonal constraints, but as well, that all types of interaction can occur simultaneously and alter the behaviour and fitness of coexisting species.

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Recapitulatory results, discussion and conclusion

Results

In my experiments, common and bank voles (*Microtus arvalis* and *Myodes glareolus*) showed adaptive behavior within the provided set-ups. Their behavioral plasticity allowed them to deal with the artificial arenas, unfamiliar environments and novel food sources and thus made them ideal experimental foragers in the various tasks given to them. Common voles immediately used strategies to cope with homogeneously distributed risk. When there was no chance to change between habitats of different risk or to avoid risky timeframes, they changed their pattern of exploitation of the sources provided in their environment and adjusted their time management accordingly. Instead of maximizing their intake by sampling many sources and exploiting them with little investment of time and energy, they switched to a risk minimizing behavior: they reduced travelling between stations but exploited few stations to a deeper level, thus investing more time and energy at these stations. This concentration of effort resulted in a reduced efficiency because animals accepted lower returns as trade against risky travelling events (Eccard and Liesenjohann 2008). Their strategies contained distinct predator specific answers. For example, the addition of weasel odor to homogeneously distributed simulated avian predation risk caused an additive (but not emergent) reduction of food intake and number of visited food patches (Liesenjohann and Eccard 2008). Additionally, they adapted their temporal patterns to the two types of risk: The amount of travelling in the landscapes was reduced in scenarios with high avian predation risk, whereas treatment combinations of high avian and high mammalian risk produced changes in temporal activity patterns. Additionally, the voles' intake and use of foraging stations depended on previous treatment conditions. According to the relative quality of the previous experience (higher or lower risk than the actual treatment), animals followed strategies of compensatory feeding and, depending on the actual treatment, performed a smaller or a higher number of activity bouts, according to an interaction of the two factors of avian and mammalian predation risk.

In experiments where male and female common voles were tested simultaneously, the two sexes followed different foraging strategies. Males resumed activity earlier than females and were more active in terms of changes between foraging stations than females. On the other hand, both sexes were not affected in their total time spend active by any treatment. Yet, both sexes changed their activity patterns and performed more and shorter periods of activity when any risk condition was high. They additionally reduced their intake in high risk scenarios, resulting in a reduced efficiency while active.

Bank voles (*Myodes glareolus*) showed adaptations to the presence of a potential nest predator (the common shrew, *Sorex araneus*) and followed different strategies in different seasons. The intake and the giving-up densities (GUDs) of the trays depended on an interaction of the two factors: In summer (with high natural food provisioning) foraging stations were used less in shrew presence, in late autumn (with low resource levels) foraging stations were used more often when shrews were present. As in the indoor experiments, a concentration of effort could be calculated in shrew presence, thus a higher amount of food was taken from a lower number of food patches under the threat of a nest predator.

Additionally, vole mothers avoided foraging in the trays near the nest when shrews where present.

The presence of shrews had an effect on offspring survival in autumn, reducing successful recruitment, whereas in summer, with high resource provisioning for both species, there was no effect of shrews on the number of offspring. But, in summer there was an effect of shrews on the homerange of the bankvole mothers. The mothers significantly reduced their homerange in shrew presence, and shrew presence provoked higher levels of activity in summer and autumn.

Discussion and Conclusion

All animals are adapted to the environmental conditions of the habitat they chose to live in. It was the aim of this PhD-project, to show which behavioral strategies are expressed as mechanisms to cope with the constraints which contribute to the natural selection pressure acting on individuals. I was able to show that wild-caught voles have strategic answers to homogeneously distributed risk. Thus it can be argued that prey animals merely have the chance to actively choose between safer and riskier patches or habitats (as stated in earlier studies (Gilliam and Fraser 1987, Hugie and Grand 2003), but have to deal with an overall level of homogeneous risk, which is perceived by tactile, olfactory or acoustic cues. This line of arguments does not necessarily need the assumptions of the optimal foraging theory. Animals do not have to know the quality (e.g., in terms of food provisioning and risk levels of all possible habitats), but they can adapt their behavior to the actual circumstances. Deriving risk uniform levels from cues and adjusting activity levels to the perceived risk is an option to deal with predators of the same size or with unforeseeable attack rates. Thus offering two different habitats, deliberately made heterogeneous in their risk, and letting individuals choose between these (Kotler and Blaustein 1995, Jacob and Brown 2000), might not reflect natural conditions. I was able to show that as long as there are no safe places or times, it is best to reduce activity and behave as inconspicuous as possible as long as the costs of missed opportunities do not exceed the benefits of a higher survival probability. These costs apparently grow faster for males than for females, especially in times of inactivity. Sexual selection favors active males that defend their territory and mate with multiple females in polygynous and promiscuous species. This is supported by strong predatory pressure on the most active groups of rodents (young males, sexually active or dispersers) leading to extremely female-biased operative sex ratios in natural populations (Niethammer 1982).

Other groups of animals, those with parental duties such as nest guarding, for example, have to deal with the actual risk in their habitat as well. As long as they do not want to leave their offspring to predators, they have to cope with any threat (shown for birds and fish by Winkelman 1996, Kreisinger and Albrecht 2008, Morat et al. 2008). Bank vole mothers, confronted with a nest predator that posed no actual threat to themselves, adjusted their behavior as if an actual predator was present. They reduced travelling and concentrated their effort in the presence of shrews, independent of the different nutritional provisioning of food by varying resource levels due to the different seasons. Additionally, they exhibited nest-guarding strategies by not foraging in the vicinity of the nest site in order to reduce conspicuous scent marks. This has been shown for lemmings only (Boonstra et al. 1996), but seems to be a sensible strategy, for olfactory marks are known to be reliable cues for predators (Kats and Dill 1998). The repetition of the experiment in summer and autumn showed that changing environmental constraints can have a severe impact on results of outdoor studies. In our case, changing resource levels changed the type of interaction between the two species. In summer, food provisioning for both species was good, resulting in a mere interference avoidance relationship, while in autumn the foraging stations gained worth for the bank vole, while the bank vole offspring gained worth as a source for the shrews. Thus, which type of interaction is measured (either the concurrence for insect food or a predator-prey relationship between shrews and vole pups), can be a question of the alternative food supply and environmental conditions. For it is hard to disentangle the types of interaction anyway (Scharf et al. 2008) and hard to observe them under natural conditions, few studies on this topic exist so far. Attempts are made to explain species coexistence when food provisioning is sufficient (Hoset and Steen 2007), but changes of interactions are poorly documented. Again, our findings can have impact on the interpretation of studies conducted under laboratory conditions. Results can depend on the actual community structure from which the tested animals are taken and thus have to be interpreted accordingly.

This thesis proves that it is important to identify the environment in which the investigated species lives and to adjust the assumptions to the attributes of the habitat (homogeneous or heterogeneous?) and the predators an animal is exposed to (avian or mammalian, same sized or not, assessable via cues or not?). Additional factors like season or community structure can cause severe effects and should be estimated and considered accordingly.

I was able to show that it is important to analyze decision making and optimality models on an individual level, and when that is not possible (maybe because of the constraints of field work), groups of animals should be classified by using the least common denominator that can be identified (such as sex, age, origin or kinship). This will control for the effects of the sex or stage of life history or the individual´s reproductive and nutritional status on decision making and will narrow the wide behavioral variability associated with the complex term of optimality.

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Zusammenfassung der Ergebnisse, Diskussion und Fazit

Ergebnisse

Die räumlichen und zeitlichen Anpassungen an Risikohomogenität wurden ohne Verzögerung umgesetzt. Hierbei zeigte sich, dass eine generelle Strategie, unabhängig vom Prädationstyp, darin besteht, Laufwege zu vermeiden und dafür eine ineffiziente Ressourcenausbeutung in Kauf zu nehmen. Zusätzlich wurde versucht, gefährliche Zeitfenster auszusitzen, was zu Aktivitätsverlagerungen und Aufholstrategien hin zu Zeiträumen führte, die als sicherer empfunden wurden.

Es konnte gezeigt werden, dass diese Effekte durch bestimmte Prädationstypen noch verstärkt werden. So wird zum Beispiel bei fehlender Deckung (als Indikator für hohes Prädationsrisiko durch Raubvögel) Bewegung soweit irgend möglich vermieden. Bei frischen Duftmarken von Bodenprädatoren wird zusätzlich noch die Futteraufnahme stärker verzögert, um die Phasen des hohen Risikos auszusitzen. Simultan auftretende, unterschiedliche Prädationstypen verursachten also, den vorhandenen Modellen entsprechend (Sih et al. 1998, Morosinotto et al. 2009), additive Effekte auf verschiedenen räumlichen und zeitlichen Ebenen.

Im zweiten Versuch wurde nachgewiesen, dass diese Muster für Männchen und Weibchen leicht unterschiedlich sind: Nach gefährlichen Vorkommnissen nehmen Männchen eher wieder ihre Aktivität auf und behalten ein relativ zu den Weibchen erhöhtes Aktivitätspensum. Hierbei weisen Männchen eine erhöhte Wechselfrequenz zwischen Futterstellen auf, während Weibchen länger an einer einmal gefundenen Futterquelle verweilen. Dies führt dazu, dass beide Geschlechter die gleiche Zeit aktiv sind und die gleiche Menge an Futter aufnehmen, dies jedoch durch unterschiedliche Aktivitätsmuster erreicht wird.

Im dritten Versuch zeigt sich, dass Weibchen, die einem indirekten Prädationsrisiko wie zum Beispiel der Nestprädation ausgesetzt werden, mit Mustern reagieren, die ähnlich denen sind, die sie zeigen wenn sie selber einer Gefahr ausgesetzt sind. Sie konzentrieren jedoch ihre Aktivitäten entweder auf einen kleinen Raum um ihr Nest, wenn dies eine effiziente Nestverteidigung verspricht oder sie vermeiden die Futtersuche in der Nähe des Nestes. Zusätzlich verkleinern sie ihren Aktionsradius (home-range) und verringern ihre Gesamtpräsenz außerhalb des Nestes wenn ein Nestprädator präsent ist. Diese gezeigten Strategien sind jedoch nur bei ausreichender Ressourcenversorgung möglich. Eine Wiederholung diese Versuches mit einer schlechten Nahrungsversorgung zeigte, das die Weibchen ihre eigene Grundversorgung durch erhöhte Aktivität (es waren größere homeranges nötig um Nahrung zu suchen) sichern mussten, was zu geringeren Überlebensraten der Jungen führte.

Diskussion

Alle getesteten Tiere stellten sich mühelos auf die vorgegebenen Versuchsbedingungen ein und adaptierten ihre Strategien relativ zeitnah. Dies deutet darauf hin, dass ihr evolutionärer Anpassungsprozess in Szenarien stattfindet, die den von uns simulierten Bedingungen ähnlich sind. Somit stehen den Tieren plastische Verhaltensweisen zur Verfügung, die es ihnen erlauben, sich auf die vorgegebene homogene Risikoverteilung durch verschiedene Prädatoren einzustellen.

Diese Adaptationen erfolgten auf verschiedenen Ebenen: einerseits auf einer zeitlichen Ebene (Verschieben von Aktivitätszeit, Verlängern und Verkürzen von Aktivitätsphasen). Dies bestätigt, dass die Tiere in der Lage sind, ihr Zeitbudget entsprechend dem empfundenen Risiko und Prädationstypes einzuteilen und somit auch die Rhythmik ihres Prädators einzuschätzen (Ferrari and Chivers 2010, Lima and Bednekoff 1999). Dafür benötigen sie kein Wissen über Futterquellen und Gefahrenpotential aller in Frage kommenden Habitate wie bisher vorausgesetzt (Charnov 1976, Cezilly and Benhamou 1996, Klaassen et al. 2007) sondern reagieren vielmehr ausschließlich auf den Ist-Zustand und die Änderungen ihres Umfeldes (Bayesien foraging: Olsson and Holmgren 1998, Olsson and Holmgren 1999, Green 2006, van Gils 2010). Diese Vereinfachung hilft den Tieren ebenfalls, mit schwer vorhersehbaren Prädatoren umzugehen: Die Gefahr durch Luftprädatoren wird nicht, wie häufig angenommen (und für Vögel oder Krabben auch nachgewiesen (Fernandez-Juricic et al. 2004, Hemmi 2005)) direkt vom Erscheinen eines Raubvogels abgeleitet, sondern über die indirekte Abschätzung des Gesamtrisikolevels, z.B. über die vorhandene Bodendeckung (Fanson 2010). Hierbei entstehen deckungsabhängige Bewegungsmuster, die einen hohen Level an Sicherheit bieten und für die ein Tier sich nicht einer direkten Prädation aussetzen muss um den Gefährdungsgrad einzuschätzen.

Zusätzlich wurden prädator-spezifische Reaktionen gezeigt, die belegen, dass die Tiere sich auf den vorhandenen Prädationstyp, auf simultan auftretende Prädatoren und auf homogene Verteilung von Risiko anhand von indirekten Anhaltspunkten einstellen können. Die Verringerung von Bewegungsaktivität zum Beispiel bietet keine Sicherheit vor der Prädation durch Mauswiesel, die den Mäusen in alle Gänge und Höhlen folgen können (Sundell and Ylönen 2004), sie reduziert aber die Sichtbarkeit für Luftprädatoren. Jedoch kann die Verschiebung von Aktivität sinnvoll sein, wenn ein Bodenprädator anhand seiner Markierungen und seine Duftes bemerkt wurde (Fanson 2010). Hier ist eine Abschätzung des Alters der olfaktorischen Signale möglich und es kann entsprechend zeitlich reagiert werden (z.B. durch ein Verlängern der inaktiven Phasen wird versucht, akut erkannte Gefahren auszusitzen („risk-allocation-hypothesis“, Lima and Bednekoff 1999)). Auf der anderen Seite ist eine Verschiebung von Aktivität in andere Tageszeiten kein Schutz vor Luftprädation, denn es gibt zu jeder Tages- und Nachtzeit einen auf Mäuse spezialisierten Luftprädator (Niethammer and Krapp 1982). Es konnte also nachgewiesen werden, dass auf das simultane Auftreten von mehreren Prädationstypen sowohl mit zeitlichen als auch mit räumlichen Strategien individuell reagiert werden kann, jeweils in Kombinationen, die das minimale Risiko zur Folge haben.

In den Versuchen zeigten Männchen und Weibchen unterschiedliche Futtersuchstrategien und Aktivitätsmuster. Dies erklärt sich vor allem dadurch, das Männchen mit der Futtersuche alternative Aktivitäten verknüpfen und sich somit länger und sichtbarer einem Risiko aussetzen. Dies kann die 3-4 fachen Mortalitätsraten der Männchen in natürlichen Habitaten erklären (Niethammer and Krapp 1982) und kann als Ergebnis der starken intraspezifischen Konkurrenz um Paarungspartner in polygynen, multivoltinen Spezies gesehen werden (Kraus et al. 2008). Die Kosten für verpasste Alternativen während einer inaktiven Phase sind also für Männchen höher als für Weibchen. Die hier evolvierten Sozialsysteme, bei denen ein Männchenrevier das mehrerer Weibchen abdeckt, erfordern riskantes und zeitaufwendiges Territorialverhalten, um einen hohen Reproduktionserfolg zu erhalten (Ostfeld 1990), dies schlägt sich auch in den Mustern der Nahrungssuche wieder. Im Gegensatz zu bisherigen Studien ist es also sehr wichtig, das Geschlecht als Faktor mit zu analysieren und zu berücksichtigen, in welchen Sozialsystemen die Tiere sich bewegen. Diese Faktoren können, wenn nur eine Population in ihrer Gesamtheit untersucht wird, einen erheblichen Teil der Varianz ausmachen.

Auch das indirekte Risiko, zum Beispiel durch einen Nestprädator, hat Änderungen der Nahrungssuchstrategien von Feldmäusen auf zeitlicher und räumlicher Ebene zur Folge. Laktierende Weibchen vermeiden zum Beispiel zu viel Aufenthalt in direkter Nestnähe, um potentielle Prädatoren nicht durch olfaktorische, akustische oder optische (Falken und Bussarde sind in der Lage, die ultravioletten Reflexionen von Säugetierurin zu sehen) Signale zum Nest zu locken. Ähnliches ist bisher nur von Lemmingen (*Dicrostonyx groenlandicus*) bekannt, die im Sommer keinerlei Duftmarken in der Nähe ihrer Höhlen hinterlassen (Boonstra et al. 1996). Dieses Verhalten zeigt, dass die untersuchten Wühlmäuse plastische Verhaltensmuster haben, die sie der Situation und dem Prädatortyp anpassen können, auch wenn die Gefahr nicht für sie selbst, sondern für ihre Nachkommen besteht. Sie sind in der Lage zu erkennen ob ein Prädator ein Risiko für sie selbst darstellt oder nur für ihre Nachkommen, und adaptieren ihre Verhaltensmuster entsprechend. Hierbei scheint auch das Alter und die Zahl der Jungen und somit ihre Verwundbarkeit eine Rolle zu spielen, Studien zeigten, das große Würfe stärker aktiv verteidigt werden als kleine, und junge Nachkommen stärker als schon ältere (vor allem bei dem Auftreten infantizidaler Männchen (Koskela et al. 2000). Dies bestätigt, dass auch der Status (z.B. trächtig, laktierend, Alter des Wurfes) als Faktor in weiteren Studien analysiert werden sollte, er hat einen Einfluss auf die Einschätzung von Optionen und kann damit ebenfalls gefundene Muster der Aktivität und Futtersuche erklären. Dieser Versuch zeigt außerdem, dass abiotische Faktoren wie die Ressourcenverfügbarkeit einen starken Einfluss auf die Interaktionen zwischen verschiedenen Arten haben können. Damit muss überlegt werden, inwieweit sich Verhaltensstudien im Labor mit isolierten Individuen auf natürliche, dynamische Systeme und Artengemeinschaften übertragen lassen. Hierfür sind weitere, vergleichende Studien unter natürlichen und künstlichen Bedingungen nötig, in denen die abiotischen, saisonalen Vorgaben (zum Beispiel Temperatur und Nahrungsverfügbarkeit) berücksichtig werden.

Fazit

Mit der vorliegenden Arbeit konnte gezeigt werden, dass Tiere, auch ohne eine Wahl an unterschiedlichen Habitaten, Optimierungsstrategien zeigen und in der Lage sind, geeignete, risikominimierende Verhaltensmuster als Adaptation abzurufen. Vor allem die vorher noch nicht untersuchten Anpassungen an homogen verteiltes Risiko (z.B. an das schwer einschätzbare Risiko von Räubvögeln, das nur indirekt über den Deckungsgrad des Bodens abgeschätzt werden kann) spiegelten sich in effizienten Nahrungssuchstrategien wider. Es konnte auch der starke Einfluss des Geschlechts auf Nahrungssuchstrategien und Allokationsmuster nachgewiesen werden. Obwohl geschlechtsspezifische Verhaltensmuster aus vielen Themenkomplexen bekannt sind (z.B. geschlechtsabhängige Investition in den Nachwuchs oder geschlechtsabhängige Mortalitätsraten), wurde der Einfluss auf Futtersuchstrategien bisher nicht untersucht. Und das, obwohl der selektive Druck auf die Optimierung der Futtersuche enorm sein muss. Mit der Futtersuche ist das Überleben, und damit auch der reproduktive Erfolg, direkt verbunden. In der vorliegenden Arbeit wurde ebenfalls nachgewiesen, dass mit elterlichen Pflichten Änderungen im Bereich der Futtersuche und der Effizienz von Bewegungsmustern verbunden sind. Laktierende Weibchen sind in der Lage, eine Risikoabschätzung für sich selbst und für den Nachwuchs vorzunehmen und damit nicht nur ihre eigenen Überlebenschancen zu maximieren, sondern auch die eigenen Jungen effektiv zu schützen und zu versorgen.

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Appendix : Short notes on the experimental animals

Small mammals, especially rodents, provide an excellent model species to study adaptive strategies for answers to questions about direct and indirect predation risk. They are prey to a wide range of species, forming the basis of food chains as well for avian (Millon et al. 2008, Millon and Bretagnolle 2008) as for mammalian predators (Hanski et al. 1991, Korpimäki et al. 1991). Thus, adaptations to different types and levels of risk should have been in the focus of selection processes through their evolution.

Rodents breed well under semi-natural outdoor conditions and under laboratory conditions and do not recognize their own pups in the first days (Mappes et al. 1995). Thus for outdoor experiments, a high number of animals can be paired in advance and litter sizes can be fitted to even out energetic differences in mothers with different litter sizes.

Two species of voles were used in my projects, serving as experimental foragers in the in- and outdoor experiments:

1) The common vole, *Microtus arvalis*, was used in indoor and outdoor enclosure tests at the University of Bielefeld as experimental foragers. As they are herbivores, their food sources can be evenly distributed, but can also consist of patchy distributed seeds or seedlings. In preliminary tests, common voles showed good acceptance of artificial foraging stations (food patches) and quickly learned to search for food that was mixed into a medium (e.g., sand). Common voles show multiple periods of activity (activity bouts) per day with main activity phases during dusk and dawn. Their foreseeable rhythm and well studied activity patterns (Gerkema and Vanderleest 1991, Halle and Stenseth 2000) helped in designing experiments that relied on activity and foraging trips (Lehmann and Sommersberg 1980). From their social system as promiscuous, polygynous, multivoltine income breeders (Niethammer et al. 1978), differences in behavioral patterns of males and females could be expected, making them ideal for the study of different assessment of missed opportunity costs. Because of their natural permanent exposure to different types of predators at any time of day or night, behavioral adaptations to both avian and mammalian threats were expected and could be tested. Only wild-caught animals were used in all experiments, to make sure that animals came from a population under the pressure of natural selection.

2) The bank vole, *Myodes glareolus* was used as an experimental forager in the Finnish enclosure experiments. Even though the laboratory breeding, handling, exploring new environments and wearing collars with telemetry transmitters caused them stress, their robustness made it possible to release lactating mothers with 4-5 pups into 2500sqm enclosures. They were also tested for the acceptance of foraging stations and easily learned to exploit artificial sources. Though lactating females had the tendency to store food in their homeboxes in indoor trials, outdoor conditions forced them to explore

sources and immediately consume found food items. The unsocial territoriality of female bank voles (Ziak and Kocian 1996, Koskela et al. 1997) enabled us to release multiple females per enclosure without the problem of intraspecific interference, for example the use of the foraging stations by different animals. Females are known to actively defend their pups against infanticidal males (Koskela et al. 2000), and thus were assumed to be able to adjust their foraging and spacing strategies to the presence of a same sized, potential nest predator, the common shrew (*Sorex araneus*).

Two mammalian species were used as potential predators either by their physical presence or by serving as odour donor:

1) The least weasel (*Mustela nivalis nivalis*) was used in the Bielefeld experiments as donor of cage bedding and thus odour probes to simulate weasel presence. The least weasel is one of the most important predators of small mammals. It is specialized for entering vole burrow-systems and moving within vole runways (Niethammer et al. 1978, King and Moors 1979). Especially the males leave olfactory cues to mark their home ranges, thus adaptation to the scent of weasels as indicator of their presence should be expected in small mammals. We would additionally expect that voles can distinguish between old and new scent marks, for olfactory components are volatile and thus the intensity of an odor probe might be a reliable cue to estimate the actual presence of a predator.

2) The common shrew (*Sorex araneus*) is a highly active insectivore, and needs tremendous amounts of food to satisfy the extremely high and quick metabolism powered by 600 heartbeats per minute. Shrews are known to eat mammal carcasses (Haberl 2002), to prey on vole nestlings (Ruzic 1971, Fulk 1972, Getz et al. 1992), and to be active in multiple activity bouts per hour (Rychlik and Jancewicz 2002, Ochocinska and Taylor 2005). Because they frequently use the burrow systems of voles and the voles react by adjusting their tunnel system to shrew presence (M. Liesenjohann et al. in prep.), we regarded them as a homogeneously distributed threat for vole mothers. As common shrews and bank voles live in the same habitats (Huitu et al. 2004) this species pair was regarded to have most likely evolved adaptations to the presence of each other.

Kurze Zusammenfassung zu den eingesetzten Arten

Microtus arvalis und *Myodes glareolus*

Als experimentelle Futtersucher wurden entweder Rötelmäuse (*Myodes glareolus*) oder Feldmäuse (*Microtus arvalis*) eingesetzt. Kleinsäuger, insbesondere Nagetiere sind ideale Kandidaten für Verhaltensversuche. Sie sind einfach und anspruchslos im Umgang, in hohen Zahlen aus der Natur entnehmbar und leicht im Labor zu züchten. Da sie die Nahrungsgrundlage für ein große Zahl an Prädatoren darstellen, ist ihre Lebensweise und ihr Verhalten Ergebnis einer langen Phase der Koevolution. Vor allem Wildfänge sollten optimal an die vielfältigen Gefahren angepasst sein und adaptive Strategien auf alle Situationen, die das Abschätzen von Gefahren erforderlich machen, zeigen können.

Die polygyne Lebensweise der beiden Arten, bei der die Männchen Territorien ausbilden, die die Habitate mehrerer Weibchen überlagern, lassen Unterschiede in den Nahrungssuchstrategien erwarten. Die durch dieses Sozialsystem erhöhte Aktivität der Männchen führt zu einem verschobenen operationalem Geschlechterverhältnis (durch eine bis zum dreifachen erhöhte Mortalitätsrate der Männchen gegenüber den Weibchen) und damit auch zu hohen alternativen Kosten für die Männchen in inaktiven Phasen (z.B. verpasste Paarungspartner und Verteidigung des Territoriums). Dies lässt erwarten, das Männchen im Gegensatz zu Weibchen, zusätzliche Aktivitäten mit der Nahrungssuche verknüpfen und sich damit ihre Strategien von denen der Weibchen unterscheiden.

Rötelmausweibchen wurden für die Versuche in den Außengehegen gewählt, da sie ebenfalls territorial sind und in der Lage, sich gegen gleichgroße Tiere (wie zum Beispiel Spitzmäuse) zu verteidigen. So wurde sichergestellt, dass die eingesetzten Prädatoren (*Sorex araneus*) keine Bedrohung für ein adultes Tier, wohl aber für Nestlinge, darstellt.

Mustela nivalis und *Sorex araneus*

Streuproben des Mauswiesels (*Mustela nivalis*) wurden in den Arenaversuchen zur Simulation der Gefahr durch einen Bodenprädator benutzt. Das Mauswiesel ist in der Lage, Mäuse in ihre Gänge und Baue zu verfolgen und stellt somit eine permanente Gefahr dar, vor der es keine sicheren Rückzugsorte gibt. Streuproben (bzw. in der Natur Reviermarkierungen und Kot) von Prädatoren sind verlässliche Indikatoren für die Anwesenheit eines Prädators. Durch die volatilen Geruchskomponenten können sie ebenfalls Hinweise geben, wie akut die Gefahr tatsächlich ist.

Die Waldspitzmaus (*Sorex araneus*) wurde als potentieller Nestprädator in den Außengehegeversuchen eingesetzt. Von Spitzmäusen ist bekannt, dass sie in der Lage sind, Mäusenester auszuräubern und das sie die Tunnelsysteme der Wühlmäuse benutzen. Europäische Spitzmäuse sind jedoch nicht in der Lage adulte Wühlmäuse zu überwältigen, so dass die Wühlmäuse sich und ihre Nester aktiv verteidigen können. Da Waldspitzmäuse und Rötelmäuse die gleichen Habitate bewohnen und teilweise die gleiche Nahrungsgrundlage nutzen, kann eine Koevolution der beiden Arten vorausgesetzt werden. Beide Arten sollten in der Lage sein, adaptive Strategien bei Präsenz des Opponenten zu zeigen.

Eine genaue Übersicht über alle Arten findet sich in Niethammer und Krapp, Handbuch der Säugetiere Europas Bände 2/I, 3/II und 5/II, Aula-Verlag, Wiesbaden.

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Red Queen: “Now, here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!'

Lewis Carrol (1865): Alice's Adventures in Wonderland