6. General Discussion:

This thesis addressed the question of how stability in natural ecosystems is driven by interaction strengths, which are constrained by allometry and environmental temperature. The body mass and temperature dependency of ingestion rates were investigated with the model organisms ground-beetles and wolf-spiders (Chapters 3.1. & 3.2.). Ingestion is classically assumed to follow the metabolic dependencies of the predators (Peters 1983; Brown et al. 2004). For this reason, feeding is expected to follow a 3/4 power law with increasing predator mass (Peters 1983; Brown et al. 2004). However, the results investigated in Chapter 3.1. showed that feeding on a prey of a specific size class leads to a hump-shaped curve with increasing predator-prey body-mass ratio (Chapter 3.1.). This result suggests that the strongest interactions occur when the predator has an intermediate "optimal" body-mass ratio to its prey. Additionally, it contrasts earlier assumptions which stated that the interaction strength increases with increasing body mass of the predator (e.g. Peters 1983; Carbone et al. 1999). However, it is noteworthy that the analyses made in chapter 3.1. were not replicated at different prey densities, even though feeding interactions are known to follow saturating functions with increasing prey density (functional responses (Holling 1959a, b; Real 1977, 1979; Koen-Alonso 2007); see Chapter 2.3.).

The functional response is a mechanistic model that offers insights into the different parameters (handling time and attack rate) influencing the feeding of a predator on its prey. Using the framework of the functional response, we unraveled the mechanistic basis behind the hump-shaped ingestion rates as observed in chapter 3.1.. The allometric slope of the maximum ingestion rates (see Chapter 2.3. for a detailed explanation) followed the predictions of the Metabolic Theory of Ecology by yielding a value of approximately 3/4. The hump-shaped curve, observed in Chapter 3.1. was caused by a decreasing attack rate of the predators on the prey. This decrease in attack rates can be explained by higher efficiency of escape for very small prey or size-dependent refuges (Aljetlawi et al. 2004; Brose in press). These results are in line with studies from other ecosystem types such as for pelagic marine crustaceans (Aljetlawi et al. 2004), freshwater fishes (Wahlström et al. 2000), and freshwater insects (Spitze 1985). In addition to the hump-shaped function, we found that the functional response curve shifts from a hyperbolic type II functional response to a sigmoidal type III functional, which we found to have an extremely stabilizing effect on food-web dynamics and persistence (Chapter 5.1.)

In addition to the laboratory experiments in chapters 3.1. & 3.2., the influences of allometry on population and food-web stability were inspected. In Chapter 3.3., we investigated the theoretically possible body-mass ratios that lead to persistent tri-trophic food web motifs (Fig 3.3.2). In natural food webs, over 97% of all existing tri-trophic food chains have a body-mass distribution that falls into our predicted range of possibilities. Moreover, the distribution of those species in the food web is not random but follows allometric degree distributions. These findings contribute to prior studies, which suggested that an order in the body-mass structure (larger species feed on smaller species) causes stability in real ecosystems (Elton 1926; Brose et al. 2006b).

Extending this approach and adding hump-shaped dependencies of attack rates (Chapter 3.2.) into the model, we investigated the influence of body mass on the long standing theoretical problem that omnivory motifs are generally unstable (Holt & Polis 1997; Vandermeer 2006). The hump-shaped curve of interaction strength with increasing body-mass ratio yielded stable omnivory motifs at high body-mass ratios (Chapter 3.4.), whereas omnivory motifs that were outside that range were extrinsically stabilized by the surrounding food-web structure. Furthermore, we tested if these hump-shaped feeding interactions were not only a laboratory artefact (i.e. predators would not hunt on prey which are not worth it) by developing a multi-species functional-response statistic that was applicably to gut-content analyses of the best resolved food web to date, Broadstone Stream (Woodward et al. 2005). Corroborating the laboratory findings, we found also hump-shaped feeding interactions in this "real" empirical food web data. These results suggest that omnivory is common in most food webs because the feeding interactions and the allometric degree distribution automatically lead to stability in natural food webs.

Metabolic and feeding rates are determined by intrinsic body-mass effects as well as by environmental influences such as temperature. Knowledge of these dependencies is crucial to understand the effects of global warming on ecological communities (Abrahams et al. 2007). Because interaction strength depends on the metabolism of animals, it should scale with the same slope as metabolism, otherwise predators would loose the ability to satisfy their metabolic demands. Interestingly, warming increases ingestion less than metabolism (Chapter 4.1.). This leads to decreased population cycles (increased stability). However, if the ingestion decreases below a critical threshold of metabolic demands, it would lead to extinction due to starvation. This phenomenon was already recognized in microcosms with unicells and bacteria (Petchey et al. 1999), but a mechanistic insight was not possible without exact knowledge of the temperature dependence of simple feeding interactions. Additionally, caused by the same foraging patterns, food web structure may change with environmental warming that could lead (1) to a compensation by consumption on more prey species, and (2) to an additional negative effect by a reduced number of prey items (Chapter 4.2.). However, an empirical test of both hypothesis is not yet possible because neither the food web structure nor the ingestion rates have yet been explored in real food webs on a temperature gradient.

In conclusion, the results of my doctoral thesis show that precise knowledge of interaction strength is crucial to understand the stability of real ecosystems. Especially, in a changing environment forecasting models may not be plausible as long as the basic components are not explored. As reported in this thesis, investigating interaction strength in the laboratory is a good approach to parameterise food web models and gain general insights (Chapter 3.4.). However, the knowledge of temperature effects on stability is only theoretical, while a general scaling on interaction strength with temperature is still lacking. In my opinion, filling this gap by gaining basic knowledge is crucial to create a fundamental theoretical basis, enabling us to understand the problems humanity will be facing in the next century.

7. Bibliography

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Zhang, Y., Zhang, Z., Lin, J.Z. & Liu, Q.Y. (1998) Predation of *Amblyseius longispinosus* (Acari: Phytoseiidae) on *Aponychus corpuzae* (Acari: Tetranychidae). *Systematic and Applied Acarology*, **3**, 53-58.

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8. Appendix

8.1. Curriculum vitae

Personalities

Name:	Björn Christian Rall
Address:	Goethestr. 42, Darmstadt
Date of Birth:	01/05/1979 in Bensheim, Germany

Scientific Career

1985-1989:	elementary school; Grundschule Kirchbergschule (Bensheim);
1989-1998:	Grammar school: Goethe Gymnasium (Bensheim);
1998:	Abitur (University entrance diploma);
1998-1999:	Material Sciences; Chemistry and Geological Sciences (teacher); both University of Technology, Darmstadt;
1999-2005:	Biological Sciences, University of Technology, Darmstadt;
2005:	Diploma Degree in Biological sciences;
since April / 2006:	Doctoral-Thesis in Ecology on the topic “Allometry, temperature and the stability of food webs” at the University of Technology, Darmstadt;

Further Education

2005:	SENSE PhD course “Community Ecology”

Lectures

2009:	Internal working group lecture on the operating system **Ubuntu Linux**
2008:	Internal working group lecture in the statistical software **R**

Supervisions and Co-Supervisions

2009: Binzer, Amrei: *The strength of trophic cascades in model communities.* (Diploma Thesis)

2008: Schwarzmüller, Florian: *"Trophic-whales" dampen enrichment effects in a tri-trophic food-chain, a body-size dependent effect.* (Forschungspraktikum)

2008: Ott, David: *Size dependent functional responses of epigeic wolf-spiders*. (Forschungspraktikum)

2007-2008: Hibbeln, Simone: *Temperatureffekte auf Räuber-Beute Systeme* (Staatsexamen)

2007: Kalinkat, Gregor: *Consumption preferences of epigeic spiders driven by prey body mass*. (Dipoma Thesis)

2007: Scheider, Florian D.: *Body-mass ratio dependent consumption rate in a tri-trophic food chain and the effect of omnivory*. (Forschungspraktikum)

Memberships

since 2007: Gesellschaft für Ökologie

since 2007: Ecological Society of America

Reviewer for the journals

Journal of Animal Ecology; Oikos; Limnology & Oceanography

8.2. List of publications and talks

a) Articles

Peer reviewed articles

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Petchey, O.L., Brose, U. & **Rall, B.C.** Predicting the effects of temperature on food web connectance. *submitted.*

Vucic-Pestic, O., Birkhofer, K., **Rall, B.C.**, Scheu, S. & Brose, U. Habitat structure and prey aggregation determine the functional response in a soil predator-prey interaction. *submitted*.

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Rall, B.C., Binzer, A., Kefi, S., Schneider, F.D., Woodward, G. & Brose, U. The omnivory conundrum: allometry balances weak and strong interactions in complex food webs. *in prep.*

Rall, B.C., Kalinkat, G., Vucic-Pestic, O. & Brose, U. Taxonomic versus allometric constraints on non-linear interaction strengths. *in prep.*

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b) Posters and Talks

Jousset, A., **Rall, B.C.**, Kalinkat, G., Scheu, S., Brose, U. (2009) Extracellular toxin production by soil bacteria cause a shift from a type III to type IV functional response by microfaunal predators - Oral presentation at the 39th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland

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8.3. Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation selbständig und nur mit den angegebenen Hilfsmitteln angefertigt habe.

Darmstadt, den 16. Dezember 2009

Björn C. Rall

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