

Graduate-Meeting of the Specialized Section 'Ecology'  
of the German Zoological Society

“The ecology of specialized individuals in populations:  
prerequisites – constraints – development – relevance”

Rees-Grietherbusch, Germany, 7.-9.3.2008

Thursday, 6.3.2008 Arrival, get together in the evening

Friday, 7.3.2008

- 9:00 Plenary talk Dan Bolnick: “Yes, we are all individuals!”: Patterns and consequences of individual specialization
- 10:00 Jost Borchering: Causes and consequences of individual diet specialization
- **10:40 Coffee break**
- 11:10 Lisa Heermann: Consequences of diet specialization within the early life stages of Eurasian perch
- 11:50 Jari Syväranta: Stable isotopes indicate changes in feeding niche widths of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) after competitive release
- **12:30 Lunch**
- 14:00 Plenary talk Richard Svanbäck: Intraspecific competition drives increased resource use diversity in fish populations
- 15:00 Diana Schleuter: Individual foraging strategies in percids: No fitness advantage for bold individuals in a complex environment
- 15:40 Torsten Schulze: From gill net catches to individual predator perception?
- **16:20 Coffee break**
- 16:40 Caroline Peyer: Niche width collapse in a resilient top predator following ecosystem fragmentation
- 17:20 Ulrike König: Variation in prey selection of perch is affected by food density and experience
- **18:00 End first day**
- 19:00 Dinner and come together

Saturday, 8.3.2008

- 9:00 Marcio Araujo: Network theory as a useful tool in investigating individual specialization in natural populations
- 9:40 Alexander Kobler: Distinct behavioural types in freshwater fish populations: a field study in pike (*Esox lucius*) and a project in European bullhead (*Cottus perifretum*)
- 10:20 Anna Siwertsson: Incipient ecological speciation in subarctic whitefish populations – a starting project
- **11:00 Coffee break**
- 11:20 Workshop on “The ecology of specialized individuals in populations” with extended discussions on special topics, how to do, what to sample to answer certain questions, statistics, what to conclude etc.
- **12:30 Lunch**
- 14:00 Continuation workshop
- 16:00 Excursion with boat tour, Diersforter Waldsee
- **18:40 End second day**
- 19:00 Dinner and come together

Sunday, 9.3.2008

- 9:00 Final discussion with future prospectus
- 11:00 End of Graduate Meeting

List of participants (due to 23.2.2008)

1. Marcio Araujo, Brazil
2. Hartmut Arndt, Germany
3. Pia Bartels, Sweden
4. Peter Beeck, Germany
5. Dan Bolnick, USA
6. Jost Borchertding, Germany
7. Lisa Heermann, Germany
8. Martina Heynen, Germany
9. Alexander Kobler, Germany, Belgium
10. Ulrike König, Germany
11. Mar Monsonis, Germany
12. Caroline Peyer, USA
13. Diana Schleuter, Germany, France
14. Torsten Schulze, Germany
15. Anna Siwertsson, Norway
16. Richard Svanbäck, Sweden
17. Jari Syväranta, Finland
18. Jennifer Wey, Germany
19. Christine Willen, Germany

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- Deutsche Zoologische Gesellschaft e.V.
- Freunde und Förderer der Außenstelle Grietherbusch und Forschungsstation des Zoologischen Instituts der Universität zu Köln e.V.

## Abstract list

Author:

Daniel I. Bolnick

Affiliation:

Section of Integrative Biology

University of Texas at Austin, USA

Title:

“Yes, we are all individuals!”: Patterns and consequences of individual specialization

Abstract:

Traditionally, ecologists have tended to treat species as ecologically homogenous units, for example representing a species as a single node in a food web network. However, there are many examples of apparently generalized species that are composed of ecologically heterogeneous but relatively specialized individuals. In this talk, I provide a review of the concept of individual specialization, distinguishing between various forms of within-population niche variation and providing a few case studies illustrating different mechanisms of individual specialization. I then show why individual specialization needs to be considered to understand the ecology and evolution of species and communities. Diet variation among individuals permits frequency-dependent interactions that can drive evolutionary diversification. I illustrate this point with studies of disruptive selection in threespine stickleback. Variation can also serve as a basis for assortative mating and reproductive isolation. I illustrate this by showing that stickleback mate assortatively by diet, even within apparently panmictic populations. Finally, diet variation may influence ecological dynamics. This is illustrated by an experiment using laboratory populations of *Tribolium*, in which ecologically heterogeneous populations showed more stable population dynamics over 12 generations. Finally, I close by considering important future directions and open questions in research on individual specialization.

Author:  
Richard Svanbäck

Affiliation:  
Department of Ecology and Evolution, Limnology  
Uppsala University, Sweden

Title:  
Intraspecific competition drives increased resource use diversity in fish populations

Abstract:

Resource competition is thought to play a major role in driving evolutionary diversification. For instance, in ecological character displacement, coexisting species evolve to use different resources, reducing the effects of interspecific competition. It is thought that a similar diversifying effect might occur in response to competition among members of a single species. Individuals may mitigate the effects of intraspecific competition by switching to use alternative resources not used by conspecific competitors. This diversification is the driving force in some models of sympatric speciation, but has not been demonstrated in natural populations. Here, I will present data from a fluctuating natural population (Eurasian perch) and experimental (threespine stickleback) evidence confirming that competition drives ecological diversification within natural populations. Increased population density in both perch and stickleback led to reduced prey availability, causing individuals to add alternative prey to their diet. In stickleback, competition also increased the diet–morphology correlations, so that the frequency-dependent interactions were stronger in high competition. These results not only confirm that resource competition promotes niche variation within populations, but also show that this increased diversity can arise via behavioural plasticity alone, without the evolutionary changes commonly assumed by theory.

Author:  
Marcio Araujo

Affiliation:  
Departamento de Parasitologia  
Instituto de Biologia  
Universidade Estadual de Campinas, Brasil

Title:  
Network theory as a useful tool in investigating individual specialization in natural populations

Abstract:

Natural populations can be composed of ecologically heterogeneous individuals, so that generalist populations exploiting a wide variety of resources may actually be composed of specialized individuals whose niches are only subsets of the population niche. This individual specialization has been documented in a broad range of animal taxa, but most studies so far have been able to just reject the null hypothesis that individuals sample randomly from a common resource pool. In order to better understand the ecological forces that generate and maintain individual specialization in natural populations, quantitative approaches that describe how individuals share resources within the population are necessary. In this talk, I will demonstrate that network theory can provide valuable insights on how individuals within a population partition resources. First, we developed an index that measures to what extent populations are organized into discrete diet clusters. We applied this method to diet data of the threespine stickleback showing that morphologically divergent individuals specialize on different resources, forming discrete diet clusters. Second, we showed that in two populations of a Neotropical marsupial, the diets of some individuals are not only subsets of the population diet, but also predictable subsets of other, more generalist individuals' diets, a pattern known in the network literature as nestedness. We discuss these patterns in light of a recent model of optimal foraging in which phenotypically variable individuals have different rank preferences for prey or vary in their willingness to add lower-ranked prey to their diets. These are previously undocumented patterns of intra-population diet variation that can have profound implications on how ecologists model competitive interactions in natural populations.

Authors:

Jost Borcharding, Peter Beeck and Werner R. Scharf

Affiliation:

Zoological Institute, University of Cologne

General Ecology and Limnology

Rees-Grietherbusch, Germany

Title:

Causes and consequences of individual diet specialization

Abstract:

Individual specialization is increasingly documented in a broad range of animal taxa. Starting as a homogenous population, parts of a population begin to exploit new resources, thus not only extending the population niche but also enhancing further morphological and ecological diversification. Individual specialization may be related to a variety of environmental factors (e.g. temperature, food abundance) that are combined with population constraints (e.g. density, intra- and inter-specific competition) and may be further modified when ontogenetic niche shifts occur. It is important to know when, why and to what extent diversification starts within a homogenous population, and what are the consequences of this specialization process, to better understand population and community dynamics. In the first weeks after hatching Eurasian perch live in the pelagic area where zooplankton is the major food resource. With a certain size perch started their first ontogenetic niche shift to the littoral where new resources become available. One remarkable possibility of individual specialization is predation on fish larvae, a process that causes size divergence up to the development of a bimodal length frequency distribution that may even start intra-cohort cannibalism. Size divergence within the population was clearly related to the occurrence of appropriate sizes of this alternative food resource in a small time window, further modified by densities of predator and prey. These investigations not only give first hints on mechanistic relationships in such processes of individual specialization but also allow a better understanding of population dynamic of perch in different environments.

Authors:

Lisa Heermann, Werner R. Scharf, Jost Borcharding

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General Ecology and Limnology

Rees-Grietherbusch, Germany

Title:

Consequences of diet specialization within the early life stages of Eurasian perch

Abstract:

Within-population variation is assumed as a key requirement for frequency-dependent interactions that may influence the population dynamics and ecological interactions of species. Individual specialisation within one population was recently found for many species and was attributed to e.g. morphology, different habitat use, the use of habitat specific resources, the density of predatory species or competitive inter- and intra-population dynamics. Due to this variety of influencing factors, the mechanisms behind the processes of individual specialization are often hardly to identify in the field. In our case study we aimed on constraints that trigger the onset of individual specialization in juveniles of Eurasian perch. Therefore we stocked four experimental ponds with either adult perch or adult perch and bream, concentrating on the processes of individual specialization of perch after hatching and its consequences for the population. During the first weeks of life, the offspring of perch faced a rapidly decreasing zooplankton resource that formed the limiting factor. Under this competitive pressure a part of the population switched to macrozoobenthos or even preyed on bream larvae much earlier than previously reported, while the majority had to feed on low-grade resources. The alternative strategy of early piscivory in the ponds leads to enormous size differences and later on to intra-cohort cannibalism that further increased the niche breadth. Thus, initiated by decreasing availability of “normal” resources, parts of the population developed to diet specialists, enhancing intra-population differences in morphology, activity and behaviour.

Authors:

Kobler, Alexander<sup>1</sup>; Klefoth, Thomas<sup>2</sup>; Mehner, Thomas<sup>2</sup>; Eens, Marcel<sup>1</sup>; Arlinghaus, Robert<sup>2,3</sup>

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<sup>3</sup> Humboldt-University of Berlin, Faculty of Agriculture and Horticulture, Institute of Animal Sciences, Invalidenstrasse 42, 10115 Berlin, Germany

Title:

Distinct behavioural types in freshwater fish populations: a field study in pike (*Esox lucius*) and a project in European bullhead (*Cottus perifretum*)

Abstract:

There is an increasing interest in the causes and consequences of intrapopulation variation in fish behaviour and its importance for population dynamics. Information from the field about different specialisation or behavioural types in fish is limited and there is a growing demand for new insights to better understand the function of an individual within a population. First, we present results of a lentic pike (*Esox lucius*) population and second a future project in bullhead (*Cottus perifretum*). The aim of the first study was to test the assumption brought forward by previous research that pike populations are composed by clusters of individuals exhibiting distinct behavioural types. In a small lake (25 ha), 17 radio-tagged pike were tracked weekly for 24 hours with tracking intervals of three hours from June to September 2005. The percentage habitat use and the movement at day and night were used to identify distinct behavioural types inside the population by hierarchical cluster analysis. Three types were identified and described as habitat generalists (N=8), weed specialists (N=4) and reed specialists (N=5). It was concluded that lentic pike populations are indeed composed of different behavioural types which is probably a mechanism of maximising the fitness of the individual. Second, until recent years European bullhead was thought to be strictly sedentary and its migratory movements were considered of limited importance. But there is growing evidence that populations consist of both sedentary and mobile individuals. The aim of this project is to close gaps in the knowledge of bullhead behaviour, identify differences in movement behaviour and relate individual movements to size, sex, morphology, metabolism, and genetics of the animal. Additionally, we consider fitness variables for differentiation of the population and try to link individual behaviour in the field with other behavioural traits in aquaria. Field data will be weekly collected using PIT tag telemetry with a mobile antenna and permanently with PIT tag stations recording movements at specific sites. Abiotic and biotic parameters will be recorded to interpret influences on movement behaviour and home range size of the population. The general goal of this study is to define determinations of individual movement behaviour in a benthic fish species.

Authors:

Ulrike König, Jost Borchering

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General Ecology and Limnology

Rees-Grietherbusch, Germany

Title:

Variation in prey selection of perch is affected by food density and experience

Abstract:

Instead of treating conspecific individuals as ecologically equivalent, studies of resource use and population dynamics increasingly focus on individual specialisation and its impact on ecological mechanisms. Experiences with certain food resources as well as food density may affect foraging behaviour and food selectivity, thus the first steps in the process of individual specialization. To test this assumption, we fed young-of-the-year perch for 8 weeks either with zooplankton or cyprinid fish larvae, resulting in significantly different morphotypes. In the following behavioural experiments, both groups of trained perch as well as a control group from the field had the opportunity to select their food from a mixture of zooplankton and an alternative food resource. In contrast to the always stable zooplankton concentration, the alternative food resource was offered to individual perch in consecutive rounds with three levels (energetically equivalent, half and double of the zooplankton). In addition to the tests with fish as the alternative food resource, benthic Mysidacea were offered as a novel food resource to all experimental groups. With increasing availability of the alternative food resource, the energy intake also increased for all experimental groups. Independently from their experience, all perch selected active swimming fish to a higher extent than benthic mysids. Prey fish density had no effect on trained perch that always positively selected this alternative food resource. In contrast, untrained perch from the field did not positively select on the alternative food resource fish and even negatively selected mysids at lower prey densities. However, untrained perch significantly increased their selection on both food resources at the highest prey density. These results give evidence that the density of an alternative and more profitable food resource as well as the experience of organisms during preceding periods enhance the initiation of the process of individual specialization.

Author:

Caroline M. Peyer, Craig Layman

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Marine Sciences Program, Department of Biological Sciences, Florida International University  
North Miami, USA

Title:

Niche width collapse in a resilient top predator following ecosystem fragmentation

Abstract:

Much research has focused on identifying species that are susceptible to extinction following ecosystem fragmentation, yet even those species that persist in fragmented habitats may have fundamentally different ecological roles than conspecifics in unimpacted areas. Shifts in trophic role induced by fragmentation, especially of abundant top predators, could have transcendent impacts on food web architecture and stability, as well as ecosystem function. Here we use a novel measure of trophic niche width, based on stable isotope ratios, to assess effects of aquatic ecosystem fragmentation on trophic ecology of a resilient, dominant, top predator. We demonstrate collapse in trophic niche width of the predator in fragmented systems, a phenomenon related to significant reductions in diversity of potential prey taxa. Collapsed niche width reflects a homogenization of energy flow pathways to top predators, likely serving to destabilize remnant food webs and render apparently resilient top predators more susceptible to extinction through time.

Authors:

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Title:

Individual foraging strategies in percids: No fitness advantage for bold individuals in a complex environment

Abstract:

In this study we investigated individual differences in the foraging behaviour, growth and predation risk of the two percid fish species Eurasian perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* (L.)). We hereby especially focussed on the shyness and boldness of the individuals and their corresponding fitness.

In outdoor mesocosms we conducted feeding experiments using PIT-technology. Additionally to the limited, naturally occurring food we provided living chironomid larvae three times a day in one of four feeding stations. The time of feeding and the feeding station, in which the food was provided, were randomly assigned. To use this additional food source, the PIT-tagged fish had to enter the feeding stations through a tunnel like passage, which was featured with a PIT-antenna. During the experiments the time and date of the passage through the antenna and the number of the corresponding fish were continuously logged. As bold we defined the individuals that were most successful in finding the food, as shy the individuals that were least successful. Others were regarded as intermediate.

We found strong individual differences in foraging behaviour in both species. The degree of boldness strongly correlated with activity, the time needed to find the food, and the time the individuals spent in the feeding station. However, we could not find better overall performances for bold individuals: in ruffe the degree of boldness did not correlate with growth and in perch we rather found better growth for shy individuals. Additionally, we found evidence in perch that predation risk was higher for bold individuals, if pike was used as a predator.

Authors:  
Torsten Schulze

Affiliation:  
Dresden University of Technology  
Institute of Hydrobiology, Germany

Title:  
From gill net catches to individual predator perception?

Abstract:

The fate of an individual to be captured or not by a predator depends on the ability to correctly estimate its individual risk. This becomes important if available resources are scarce and foraging habitats providing required food are threatened by predators. In fish, it has been shown for roach that cohorts react precisely to the specific threat of predators by adjusting their habitat use and activity patterns. So, small roach performs characteristic daily habitat shifts to avoid pelagic predators during day by staying in the littoral zone and migrating to the pelagic zone during night to forage on zooplankton. Growing up, this behaviour alters towards a rather pelagic habitat use even during day, but avoiding the vicinity of larger predators. From gill net catches of roach indicating the habitat use during day and night it seems that subpopulations of roach have different perceptions of their risk being predated by their predators and therefore differ in the habitat (resources) they use. During the workshop I'd like to discuss the possibilities and limitation to use these gill net data to be used in an individual based model (IBM) to simulate the perceived predation risk of medium sized roach and its resulting habitat use and activity patterns.

Authors:

Anna Siwertsson, Rune Knudsen, Per-Arne Amundsen

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Department of Aquatic Biology  
Norwegian College of Fishery Science  
University of Tromsø, Norway

Title:

Incipient ecological speciation in subarctic whitefish populations – a starting project

Abstract:

Ecological speciation is the process where isolating mechanisms develop between populations due to ecologically-based divergent selection. One suggested important step in the speciation process is the trophic specialization of individuals. In this project we will explore mechanisms promoting divergent selection leading to polymorphism and possibly speciation in subarctic whitefish populations. Postglacial lakes in northern Norway provide excellent cases for studying incipient processes in ecological speciation as they are young in evolutionary time (<12000 years), replicated over a large area as discrete but variable entities and frequently inhabited by allopatric or sympatric whitefish morphs. Whitefish is a highly polymorphic species with demonstrated differences in morphology, trophic ecology, life history and genetic identity. The morphs are easily separated by the number of gill-rakers, a heritable morphological trait with long traditional use. Until now we have discovered four different patterns of gill raker distributions within three different watercourses, possibly representing different stages in an ecological speciation process. To reveal both extrinsic and intrinsic factors that may influence the development of divergence, polymorphism and ecological speciation in whitefish, we will use a multidisciplinary approach including ecological, molecular and morphometric methods in a large cluster of postglacial lakes.

Author:  
Jari Syväranta

Affiliation:  
Department of Biological and Environmental Science,  
University of Jyväskylä, Finland

Title:  
Stable isotopes indicate changes in feeding niche widths of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) after competitive release

Abstract:

Stable isotope analyses of carbon and nitrogen ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) were used to characterise possible impacts of a biomanipulation on a freshwater lake recovering from severe eutrophication. Results are presented on an empirical test of a recent proposal that feeding niche widths might be detected by variation in stable isotope values. Biomanipulation, by means of mass fish removals, was started in spring 2004 and continued until 2006. A considerable amount of fish was removed from the lake, potentially creating more available niche space and resources for the remaining fish. Stable isotope ratios of carbon and nitrogen from two key fish species, perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) were analysed from fish caught in 2003-2006. Variances in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values first increased significantly in both fish populations, indicating a wider food spectrum and expanded feeding niche width following competitive release. Greater changes were observed in the perch population than for roach. In 2006 the perch population abruptly changed its diet so that most individuals were primarily consuming the abundant young-of-the-year (YOY) fish, which was reflected as significantly reduced variances in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. In addition to isotope variances, a more thorough evaluation of niche widths of these two fish populations is made by combining stable isotope results with two dimensional home-range analyses. In conclusion, stable isotope values can indeed reflect changes in feeding niche width and offers a promising way to study such general ecological concepts.