



# Is different degree of individual specialization in three spider species caused by distinct selection pressures?

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## Abstract

Individual specialization (IS), i.e. the relatively narrower niche of individuals compared to their population, can be caused by the interplay between intrinsic and extrinsic factors. We studied IS on prey type and size in three congeneric euryphagous sympatrically occurring species: *Philodromus albidus*, *Philodromus aureolus*, and *Philodromus cespitum*. We performed prey acceptance experiments in standardized laboratory conditions using adult females. We also studied possible factors affecting IS. As intrinsic factors, we measured aggressiveness toward prey and spider size as the measures of behavioral and morphological differences, respectively. As extrinsic factors, we studied the composition of the guild of actively hunting spiders in the area from where the philodromids were collected. We computed the degree of inter- and intraspecific crowding as a measure of inter- and intraspecific competition, respectively. Then we computed competition coefficients from census data in order to estimate the strength of interspecific competition among three species. There was no IS on prey type in any studied species. In terms of prey size, only *P. albidus* was found to be individually specialized, while there was no IS in the other two species. There was a significant effect of aggressiveness, but no significant effect of body size on IS in *P. albidus*. This species was the least aggressive of the studied species. The philodromids were the dominant actively hunting spiders in the study area. *P. albidus* was exposed to a relatively higher degree of interspecific than intraspecific competition, whereas in the other philodromids the situation was reversed. The presence of interspecific competition between *P. albidus* and the other two species was confirmed by the census data analysis. We documented context-dependent IS in *Philodromus* species. We argue that the higher degree of IS in *P. albidus* was influenced by interference competition mainly from the other two philodromid species. The niches of the other two species were influenced by food limitation, which decreased their IS.

## Zusammenfassung

Individuelle Spezialisierung (IS), d.h., eine im Vergleich zur Population schmalere Nische der Individuen, kann durch das Zusammenspiel von intrinsischen und extrinsischen Faktoren bedingt sein. Wir untersuchten die IS bei drei euryphagen, sympatrisch auftretenden Spinnenarten (*Philodromus albidus*, *P. aureolus* und *P. cespitum*) in Hinblick auf das Beutespektrum und die Größe der Beute. Wir führten Versuche zur Beuteakzeptanz von adulten Weibchen unter standardisierten Laborbedingungen durch. Wir untersuchten außerdem mögliche, die IS beeinflussende Faktoren. Als intrinsische Faktoren maßen wir die Aggressivität gegenüber der Beute und die Körpergröße der Spinnen, um Unterschiede im Verhalten bzw. in der Morphologie anzuzeigen. Als extrinsische Faktoren, untersuchten wir die Zusammensetzung der Gilde der jagenden Spinnen in dem Lebensraum, aus dem

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die Philodromiden stammten. Wir berechneten den Grad der inter- und intraspezifischen Ballung als ein Maß für die inter- bzw. intraspezifische Konkurrenz. Danach berechneten wir Konkurrenzkoeffizienten aus den Zensusdaten, um die Stärke der interspezifischen Konkurrenz zwischen den drei Arten abzuschätzen. Es gab keine IS auf einen bestimmten Beutetyp bei irgendeiner der untersuchten Arten. Individuelle Spezialisierung hinsichtlich der Körpergröße wurde nur bei *P. albidus* gefunden, nicht bei den beiden anderen Arten. Es gab einen signifikanten Effekt der Aggressivität, aber keinen signifikanten Effekt der Körpergröße auf die IS bei *P. albidus*. Diese Art war die am wenigsten aggressive unter den drei Versuchsarten. Die Philodromiden waren die dominanten aktiv jagenden Spinnen im Untersuchungsgebiet. *Philodromus albidus* war in stärkerem Maß interspezifischer als intraspezifischer Konkurrenz ausgesetzt, während sich dies bei den beiden anderen Philodromidenarten umgekehrt verhielt. Das Vorhandensein interspezifischer Konkurrenz zwischen *P. albidus* und den beiden anderen Arten wurde durch eine Analyse der Zensusdaten bestätigt. Wir dokumentierten kontextabhängige IS bei *Philodromus*-Arten. Wir sind der Meinung, dass der höhere Grad von IS bei *P. albidus* durch Interferenz-Konkurrenz, hauptsächlich durch die beiden anderen Philodromidenarten, beeinflusst wurde. Die Nischen der beiden anderen Arten wurden durch limitierte Nahrung beeinflusst, was ihre IS verringerte.

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## Introduction

Individual specialization (IS) (Bolnick et al. 2003) plays a significant role in evolutionary dynamics and ecological interactions within communities (Imura, Toquenaga, & Fujii 2003; Lankau & Strauss 2007; Okuyama 2008; Bolnick et al. 2011; Pruitt & Riechert 2012). IS is a result of the interplay between intrinsic and extrinsic factors (Svanbäck & Bolnick 2005; Agashe & Bolnick 2010). The former include cognitive, morphological and/or physiological trade-offs (Bolnick 2001; Araújo & Gonzaga 2007; Cucherousset et al. 2011). The phenotypic differences among individuals may be based on genetic variation in a population and/or phenotypic plasticity or flexibility (Araújo, Bolnick, & Layman 2011). The trade-offs may cause different individuals to have different rank preferences or use different optimization criteria. Svanbäck and Bolnick (2005) describe three models of how individuals may differ in their resource evaluation: (1) resources have different values for individuals leading to distinct preferences; (2) individuals have similar preferences but differ in their willingness to exploit new resources; (3) individuals have in common the most preferred resource but differ in their evaluation of alternative resources.

The extrinsic factors include resources (types, availability, distribution) and selection pressures (types, intensity), such as intraspecific competition, which extends the population niche because there is a decrease in a preferred resource and the individuals are forced to include alternative resources (Svanbäck & Persson 2004; Svanbäck & Bolnick 2005; Araújo et al. 2011). Population niche expansion may be achieved in two different ways. First, the niches of all individuals extend. Second, the niche widths of individuals remain similar but the individuals turn to different resources (Svanbäck & Persson 2004; Svanbäck & Bolnick 2005; Araújo et al. 2008, 2011). Thus, intraspecific competition may increase or decrease IS; however, the intensity of competition may play a distinct role. Weak and very strong

competition may lead to population homogenization, while medium competition may lead to population heterogenization (Svanbäck & Bolnick 2005).

Interspecific competition may also decrease or increase IS. The result depends on the rank preferences of the competitive species and the resource value (preferred or less valuable) (Bolnick et al. 2010; Araújo et al. 2011). The result may also depend on the mechanism of competition, i.e. interference or exploitation (Bolnick et al. 2010). For example, interference in the form of intraguild predation (IGP) may push part of the population of intraguild prey into habitats where different or less valuable food resources occur. This will lead to niche expansion with population heterogenization and increase in IS of intraguild prey (Bolnick et al. 2010). Whereas, if both competing species have similar prey preferences and competition leads to resource depletion, the individuals may become more opportunistic. This may lead to a decrease in IS due to population homogenization (Bolnick et al. 2010).

Here, we studied the fundamental trophic IS in three closely related sympatric spider species of the genus *Philodromus*, which are abundant in the foliage of shrubs and trees. Philodromids are the dominant species of the spider assemblage in the study area (Michalko & Pekár, in press). They engage in interference competition as they have been found to catch and cannibalize one another. Although the philodromids represent 2% of their overall diet in the field (Michalko 2012), both the adults and juveniles of *Philodromus albidus* are accepted by the adult females of *Philodromus cespitum* readily (in 70% cases on average) in a lab (Michalko, unpublished data). In addition, the chemo-tactile cues of *P. cespitum* elicit an anti-predator behavior in the form of reduced activity in *P. albidus* (Michalko, unpublished data). Therefore, we hypothesized that the main extrinsic factor influencing IS in the *Philodromus* species would be inter- or intraspecific competition. We first estimated the IS of each species using prey acceptance experiments. Then, we measured the

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