Individual Specialization in the Hunting-wasp *Trypoxylon* (*Trypargilum*) *agamemnon* Richards (Hymenoptera: Crabronidae)

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Renan B. Pitilin, Márcio S. Araújo, and Maria L.T. Buschini (2012) Individual specialization in the hunting-wasp *Trypoxylon* (*Trypargilum*) *agamemnon* Richards (Hymenoptera: Crabronidae). *Zoological Studies* **51**(5): 655-662. Individuals of a population may differ with respect to resource use. This among-individual variation in resource utilization is called 'individual specialization' and may substantially impact the ecological and evolutionary dynamics of a population. The aim of this study was to evaluate whether females of 1 population of the hunting-wasp *Trypoxylon agamemnon* differed in their preferences for spider size and/or taxa. To observe the behavior of wasps, trap-nests were installed in an araucaria forest fragment in the Parque Municipal das Araucárias, Guarapuava (PR), southern Brazil. The indices within-individual component (WIC)/total niche width of a population (TNW) and average of values of the proportional similarity index (IS) were used to measure the degree of individual specialization. We found evidence of strong, significant individual specialization in *T. agamemnon* in terms of both prey size (WIC/TNW = 0.43) and taxa (IS = 0.45). We hypothesized that individual specialization in this species resulted from cognitive tradeoffs that limit individuals to exploring a small subset of available resources. http://zoolstud.sinica.edu.tw/Journals/51.5/655.pdf

Key words: Anyphaenidae, Apoidea, Cognitive tradeoffs, Intra-population variation, Niche variation.

Individuals within a population may differ with respect to resource use due to differences in the microhabitats they inhabit (Durell 2000), or in some cases due to their sex or age (Slatkin 1984, Polis 1984). However, individuals of the same age or sex which inhabiting the same place may also use different resources. For example, individuals within natural populations of the marine snail *Nucella emarginata* Deshayes specialize on different food resources, even when they share the same rocky shore and are exposed to the same types of prey (West 1986).

The variation in resource utilization that cannot be explained by sex or age is called 'individual specialization' and can have important ecological and evolutionary implications (Bolnick et al. 2003, Araújo et al. 2011). First, among-individual niche variation can affect individuals' interactions with competitors and/or parasites (Johnson et al. 2009, Duffy 2010). For example, in populations of *Daphnia dentifera*, individuals that stay in the hypolimnion suffer competition interference from *D. pulicaria*, whereas individuals of *D. dentifera* that perform daily vertical migrations do not suffer from such competition (Duffy 2010). Recent theoretical models show that incorporating individual variations in ecological parameters (e.g., attack rates of a predator and competitive interference) can dramatically alter the dynamics of populations and communities (Bolnick et al. 2011). Therefore, to the extent that individual specialization in habitat or resource use provides a

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mechanism for variation in ecological interactions, it is expected to impact ecological dynamics. Second, when there is individual specialization, interactions become frequency dependent (Roughgarden 1972, Taper and Case 1985), which may generate stable disruptive selection (Wilson and Turelli 1986, Bolnick 2004) and speciation (Dieckman and Doebeli 1999).

Individual specialization has been documented in almost 200 species (Araújo et al. 2011), indicating that it is a widespread phenomenon. However, most studies so far have only been able to document the presence of individual specialization, whereas in order to be able to identify the ecological mechanisms that generate and maintain it in natural populations, we should be able to quantitatively measure the degree of individual specialization. For example, experimental enclosures placed in a natural lake containing higher densities of the threespined stickleback, *Gasterosteus aculeatus*, showed higher degrees of individual specialization after 2 wk, indicating that higher levels of intraspecific competition favor individual specialization (Svanbäck and Bolnick 2007).

One of the main difficulties in quantifying individual specialization in natural populations is obtaining repeated observations of the same individuals over time in order to determine the temporal consistency of individual preferences (Araújo et al. 2011). Because of their solitary lifestyle and nesting behavior (Lin and Michener 1972), hunting-wasps of the genus *Trypoxylon* Laitrelle offer a suitable model for investigating this phenomenon in natural populations. In the genus *Trypoxylon*, some species build nests of mud, while others have a habit of nesting in preexisting cavities (Fig. 1) (Evans 1966, Krombein 1967, Evans and West-Eberhard 1970, Coville 1982). These wasps capture many spider species, and according to Buschini et al. (2008), a single species of *Trypoxylon* can capture more than 50 species of spiders. All species of the subgenus *Trypargilum* provision the cells that compose nests with paralyzed spiders (Coville and Coville 1980) (Fig. 2). Thus, nests provide individual records of long-term foraging behavior. A few recent studies suggested that females within populations of hunting wasps of the genus *Trypoxylon* may show different preferences for prey. For example, Coville and Coville (1980) observed that a nest founded by 1 female of *Trypoxylon tenoctitlan* Richards had spiders of the family Araneidae, whereas a nest belonging to another female had only jumping spiders (of the Salticidae) in it. Coville (1987) suggested that these between-individual differences in prey preferences in this species might be due to the fact that females were

Fig. 1. Female of *T. agamemnon* arriving at a trap-nest carrying a spider, while the male is inside the nest. The ruler is in centimeters.

hunting in different areas, or exploring different aggregations of spiders, or becoming conditioned to certain taxa. Additionally, Araújo and Gonzaga (2007) observed that in a population of *T. albonigrum* Richards exploiting 6 spider genera (of the Araneidae), individual females preferentially hunted a single genus.

We still do not know; however, how wide-spread this phenomenon is among hunting-wasps. In order to determine the prevalence and, most important, the degree of individual specialization in hunting-wasps of the genus *Trypoxylon* in particular and hunting wasps in general, we tested for the presence of individual specialization and measured its degree in a population of *T. agamemnon* Richards. This wasp is endemic to araucaria forests of southern Brazil (Buschini and Fajardo 2010) and mainly hunts spiders of the family Anyphaenidae (Buschini et al. 2010a).

MATERIALS AND METHODS

Study area

This study was carried out at the Parque Municipal das Araucárias, in the municipality of Guarapuava, state of Paraná, southern Brazil (25°23'S, 51°27'W) at an elevation of 1120 m. This area is characterized by a wet, cool season, and during the warmest months, the average temperature is < 22°C. Hoarfrosts are common and severe in this region. The landscape of Guarapuava is mainly composed of araucaria forest with mainly *Araucaria angustifolia* and grasslands (Veloso et al. 1991). However,

the grasslands have suffered high anthropic interference, and the araucaria forest has been reduced to approximately 5% of its original size due to agriculture and tree felling. The total area of the Parque Municipal das Araucarias is 104 ha and is comprised of araucaria forest (43 ha), grasslands (6.8 ha), swamps (11.1 ha), riparian forest (10.1 ha), and altered areas (33 ha).

Sampling program and capture of spiders

Wasp nests were obtained using trap-nests made of blocks of wood (25 × 20 × 120 mm), drilled longitudinally to a depth of 80 mm with apertures of 5.0, 7.0, 10.0, and 13.0 mm in diameter. These nests were grouped in a larger block of 16 trap-nests, with four for each opening diameter. Following Buschini et al. (2008), each block was placed 1.5 m above the ground. Twenty-one blocks were used totaling 336 trap-nests. These traps were randomly installed in the araucaria forest, because Buschini and Fajardo (2010) observed that this wasp nests only in this environment.

All females of *Trypoxylon agamemnon* which were beginning to build a nest were marked with a combination of colors and numbers of nontoxic ceramic paint on the thorax. This made it possible to identify all of the nests built by each female and thus identify the species of spiders that each one collected. Wasps were monitored daily from Sept. 2008 to Apr. 2009. When each nest was completed, it was transported to the laboratory where the eggs and newly hatched wasps were killed. The spiders in each nest were individually weighed (fresh weight), subsequently stored in
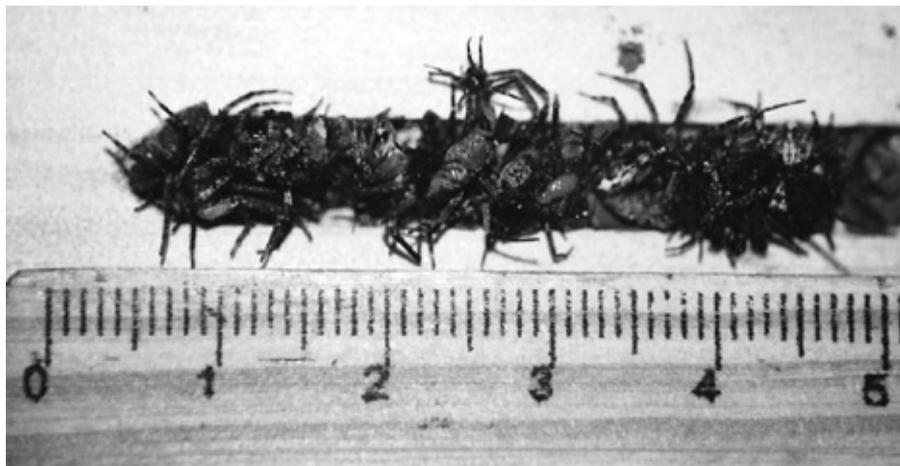

Fig. 2. A trap-nest of *T. agamemnon* with many paralyzed spiders of the family Anyphaenidae. The ruler is in centimeters.

70% alcohol, and sent to the Instituto Butantan (SP, Brazil) for identification.

Data analysis

As individuals may specialize in different sizes or taxa of prey, we measured the degree of individual specialization on both prey mass and taxon.

Prey size

To measure the degree of individual specialization on prey size, we used Roughgarden's (1974) within-individual component (WIC)/total niche width of the population (TNW) index of individual specialization for continuous data. According to this index, the total variance of resources corresponds to the TNW and can be divided into 2 components: the WIC and the BIC (between-individual component). The WIC is the average variance of prey sizes used by each individual (x_j / i) measures the average individual niche width. Variation between individuals is measured by the BIC, which is the variance among individuals' mean prey sizes ($E(x_j$ / $i)$:

TNW = Var(x_{ij});
WIC = E[Var(x_j / i)]; and BIC = Var[$E(x_j$ / $i)$].

Traditionally, the degree of diet variation is described by calculating the proportion of the total niche variation ascribed to individual niche widths (WIC/TNW). The higher the value of WIC is relative to TNW, the more similar individuals are, and vice versa. Therefore, WIC/TNW varies from 0 (maximum individual specialization) to 1 (no individual specialization).

If individuals specialize on prey taxa that differ in size (e.g., taxon A is much larger than taxon B), individual specialization on prey size may simply be a byproduct of specialization on taxa. However, if prey taxa are similar-sized but evidence of individual specialization on prey size is still apparent, this means that individuals are actually specializing on different portions of the prey size spectrum regardless of the prey taxa. To discern between these scenarios, we compared prey sizes of the main prey taxa consumed by *T. agamemnon* with an analysis of variance (ANOVA) on the ln-transformed dry masses of the spiders. The ANOVA was performed in the R environment (R Development Core Team 2009).

Prey taxa

To measure the degree of individual specialization on prey taxa, we adapted Schoener's (1968) proportional similarity index, PS, to measure individual specialization, which measures the overlap between an individual i's diet and the population diet (Bolnick et al. 2002):

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j|;$$

where PS_i is the overlap between individual i's niche and the population niche, p_{ij} is the proportion of prey category j in individual i's diet, and q_j is the proportion of the jth resource category in the population niche. For individual i that specializes on a single prey category, j, its PS_i will take on q_j, whereas for individuals that consume prey in direct proportion to the population as a whole, PS_i will equal 1. PS_i values of all individuals in a population can be calculated and summarized as a population-wide measure of individual specialization, which is the average of PS_i values, IS (Bolnick et al. 2002). IS varies from 1 (no individual specialization) to lower values (increasing individual specialization). The calculation of all indices was performed in IndSpec1.0, a program to calculate indices of individual specialization (Bolnick et al. 2002).

We estimated the probability that our empirically observed measures could occur via random sampling from a single diet distribution shared by all individuals. IndSpec1.0 uses a nonparametric Monte Carlo procedure to generate replicate null diet matrices drawn from the population distribution to test the significance of WIC/TNW and IS (Bolnick et al. 2002). Briefly, the number of prey items consumed by each individual in the empirical sample, n_i, is a fixed parameter. In each run of simulations, each individual is allowed to randomly draw n_i items from the population diet proportions by multinomial sampling, after which the indices are calculated. We used 10^4 replicates in Monte Carlo bootstrap simulations to obtain p values for these indices.

RESULTS

Twenty-one females of *T. agamemnon* were marked. Altogether they built 42 nests and hunted 906 spiders. The average ± standard deviation

(S.D.) number of spiders per female was 43.14 ± 34.35. They were followed for an average of 22.0 ± 14.55 d throughout the period of foraging and collecting spiders.

All spiders captured by females belonged to the family Anyphaenidae. Most spiders were young (87%), which made it impossible to identify them beyond the family level. At the family level, all wasps had identical prey preferences and therefore no individual specialization. Among spiders that could be identified to genus or species level, we found 12 species and 4 genera. *Teudis* Cambridge was the most common genus, followed by *Sanogasta* Mello-Leitão and *Aysha* Keyserling (Fig. 3).

We found evidence of strong individual specialization in both the size and taxa of prey. Our measure of individual specialization on the prey mass data indicated that nearly 57% of the variance in the mass of spiders consumed by the population could be accounted for by variations between individual wasps (WIC/TNW = 0.4327; $p < 0.001$). Additionally, the prey preferences of each female wasp overlapped on average by only 45% with those of the population as a whole (IS = 0.45; $p < 0.001$). It is worth noting that these measures significantly differed from the null expectation of random sampling from a common resource pool, as indicated by the simulations. Finally, prey mass did not differ among the 3 most abundant genera found in the nests (ANOVA; $F_{2,84} = 1.874$, $p = 0.1599$), indicating that individual specialization on prey size was not merely a byproduct of specialization on prey taxa and vice-versa.

DISCUSSION

Our results indicate that *Trypoxylon agamemnon* is a hunting-wasp that specializes on the spider family Anyphaenidae, confirming a common trend in this family of wasps (Crabronidae), and hunting-wasp species in general are usually specialized on 1 or 2 spider families (Gonzaga and Vasconcellos-Neto 2005, Buschini et al. 2008 2010a b). On the other hand, at the prey species level, *T. agamemnon* may be considered an ecological generalist as it consumes 12 different species of spiders. Our study shows that contrary to the null expectation that individuals feed opportunistically from a common pool of resources, individual females showed strikingly distinct preferences for different prey sizes and taxa, using only a small portion of the resources used by the population as a whole. Approximately 57% of the total variation in prey mass was due to variations between individuals, and on average, preferences of females for spider genera were only 45% similar to the population as a whole. This represents an example of strong individual specialization. This is the 2nd example we have documented of individual specialization in the genus *Trypoxylon*, suggesting that this might be a common feature of this genus and of hunting-wasps in general.

We acknowledge that our conclusions are limited by the fact that we were only able to identify 13% of the spiders found in the surveyed nests. We would like to note; however, that it is very unlikely that we overestimated the strength of individual specialization because of this problem.
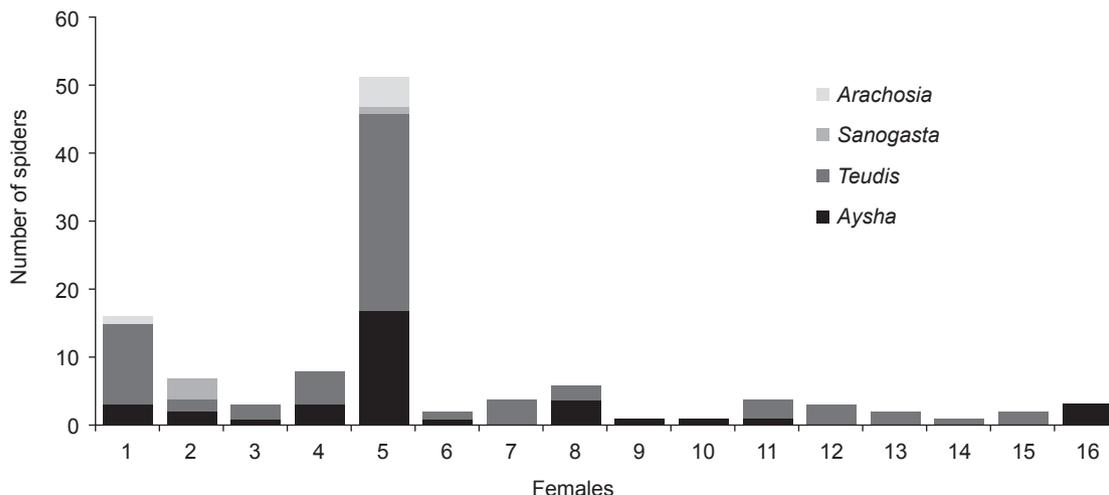

Fig. 3. Composition of prey items of females of *T. agamemnon*.

In fact, subsampling the population niche should bias estimates of individual specialization toward a weaker degree. As an illustration, assume that wasps utilized only 2 spider genera, A and B, and that A is much easier to identify than B. As a consequence, we were only able to identify spiders from genus A, but not those from genus B. We would conclude that all wasps hunt spiders of A, potentially missing individual prey preferences in which some wasps preferentially hunt A while others hunt B. In spite of the fact that we were able to identify a relatively small subset of the prey consumed by wasps, we still observed strong individual specialization.

A recent study on how the availability of prey and individual specialization for both prey taxa and size, shape niche variations across generations in the grasshopper-hunting digger wasp Stizus (Klug) (Crabronidae) was carried out by Santoro et al. (2011). They found strong individual specialization in the 2 generations, both in prey size and taxa. They also found that the relationship between this strong individual specialization and niche width variation differed when considering prey size or taxa, evidencing 2 distinct mechanisms of niche variation. According to them, changes in environmental prey availability and the environmental distribution of prey sizes interact with individual-based complex behavior, strongly influencing mechanisms of niche variation.

At a proximate level, individual specialization is usually associated with cognitive, biomechanical, and physiological constraints that arise from functional tradeoffs, where an individual who is efficient in the use of a resource type is necessarily inefficient in the use of another (Werner et al. 1983, Persson 1985, Lewis 1986, Afik and Karasov 1995, Robinson 2000). Tradeoffs are known to occur in many aspects of foraging, including the recognition, capture, and digestion of prey. Individuals that vary in phenotype and experience and as a consequence, in their skills toward different prey, will rank prey differently, and their diets will consequently differ (Bolnick et al. 2003).

In the case of hunting-wasps, individual specialization is possibly a result of cognitive tradeoffs associated with prey hunting (Araújo and Gonzaga 2007). Spiders show various mechanisms against predation which include web structures, different types of decorations on the web, the presence and types of shelters, and behavioral and morphological differences, that may require learning by the wasps and therefore determine which species are located and captured

(Eberhard 1970, Gonzaga and Vasconsellos-Neto 2005, Punzo 2005, Araújo and Gonzaga 2007). To the extent that learning is an important step in hunting, individuals may become specialized as they learn how to detect, capture, and handle certain prey. In support of this hypothesis, in the hunting-wasp *Pepsis mildei* Stal (Pompilidae), foraging efficiency increases with repeated encounters with prey (Punzo 2005). In the studied population, *T. agamemnon* consumed spiders of the family Anyphaenidae, which have a hunter wandering habit and do not build webs; they live in constant contact with the vegetation and use the surfaces of plants for foraging, shelter, and reproduction (Uetz et al. 1999). There are no data on the defensive behavior of these spiders, but given the great diversity of genera and species in this family, it is likely that they show a variety of defensive behaviors that potentially require different hunting techniques by the wasps. Albeit speculative at this point, our suggestion offers a hypothesis that could be tested with experimental approaches that demonstrate increased efficiency with experience in *T. agamemnon*. This could be measured in the field by defining some proxy for feeding efficiency (e.g., the average time to provision 1 chamber) and testing it against a measure of the degree of specialization of individuals (e.g., PS_i).

Individual specialization in *T. agamemnon* may have important implications for the reproductive success of individuals (and ultimately their fitness). Wasps in the genus *Trypoxylon* lay 1 egg in each nest chamber and must provision each chamber with several spiders (Gonzaga and Vasconcelos-Neto 2005, Buschini and Wolff 2006, Buschini et al. 2006, Buschini and Fajardo 2010). Thus, if as hypothesized, individual specialization imparts increased foraging efficiency, individual specialists should increase their fecundity by provisioning a greater numbers of nests per unit time. Moreover, nests of this genus are heavily parasitized by parasitoid flies (of the Bombyliidae, Sarcophagidae, Dolichopodidae, and Phoridae) and wasps (of the Chrysididae, Ichneumonidae, and Braconidae). Mortality rates of immatures due to parasitoids may be around 26% in *T. agamemno*n (Buschini and Fajardo 2010), 14% in *T. lactitarse* Saussure (Buschini et al. 2006), and 65% in *T. opacum* Brèthes (Buschini and Wolf 2006). Parasitoids attack nests by entering open chambers that are being provisioned by female wasps before being sealed with mud. By increasing their foraging efficiency, wasps would be

able to finish provisioning any nest chamber faster; therefore, reduce attack rates by parasitoids.

In the present study, we provide the 2nd example of individual specialization in wasps of the genus *Trypoxylon* and hunting-wasps in general. This finding suggests that this phenomenon may be a common feature of this group of insects, which remains to be investigated. Finally, the example documented here adds to the growing list of instances of individual specialization, indicating that it is a widespread phenomenon in natural populations.

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