

## An ontogenetic shift in habitat use by the Neotropical tarantula *Epebopus murinus* (Araneae, Theraphosidae, Aviculariinae)

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### Summary

We studied the structure and placement of retreats of the tarantula *Epebopus murinus* (Walckenaer, 1837) in the field in French Guiana. We found that early-instar spiderlings construct above-ground silken tubular retreats among low vegetation, and shifted to a fossorial lifestyle when subadult. Discriminant analysis of microhabitat variables associated with each class of retreat demonstrated that each was predicted by different habitat features. The location of above-ground retreats was predicted by the presence of the terrestrial bromeliad *Bromelia* spp., whereas leaf-litter predicted the placement of the burrows. This is one of the few examples of an ontogenetic habitat shift (OHS) in a spider. OHS has been suggested to fulfill an ecological function by reducing cannibalism and intraspecific competition. *Epebopus* is a fossorial tarantula genus in an otherwise arboreal subfamily. Because of this we suggest that the fossorial lifestyle of subadult/adult *E. murinus* has evolved secondarily, with the arboreal habit of the early instars reflecting the ancestral habit. This would be a case where phylogeny, and not ecology, explains OHS.

### Introduction

Spiders have proven to be a very useful research taxon with which to study habitat selection and its consequences (e.g. Wise, 1993). One of the main reasons is that many spider species are sedentary, making habitat choice unambiguous. Web-building spiders have been the focus of habitat selection studies because the web itself is a foraging mechanism, making site choice a significant investment (Riechert, 1974, 1976; Hodge, 1987a, b).

Despite the extensive literature documenting the ecology of habitat selection and its consequences for araneo-

morph spiders, the body of literature on mygalomorph ecology is small (e.g. Stradling, 1994). Coyle (1986) provides an excellent review of the literature on prey capture by liphistiomorphs and mygalomorphs. He notes that mygalomorph spiders are sedentary, and foraging behaviour generally consists of sitting by the entrance of the retreat at night, waiting for prey to come within striking range. Despite the availability of Coyle's (1986) synthesis, Foelix (1996: 165) reiterates the common misconception that mygalomorphs are vagrant: "... which merely move about until they come across potential prey". Far from being vagrant, the vast majority of mygalomorphs are sedentary to the point of being functionally sessile.

Diverse animal taxa have been observed to exhibit an ontogenetic habitat shift, in which different age/size classes selectively utilise different microhabitats (reviewed in Werner & Gilliam, 1984). Ontogenetic habitat shifts (hereafter referred to as OHS) have been suggested to reduce size-dependent predation, cannibalism and intraspecific competition and are particularly well documented in fish (Werner & Gilliam, 1984, Werner & Hall, 1988). Previous research into habitat use in spiders has found evidence of spatial and temporal OHS, e.g. the OHS exhibited by the wolf spiders *Rabidosa (Lycosa) santrita* (Chamberlin & Ivie, 1942) (Kronk & Riechert, 1979) and *Pardosa (Lycosa) lugubris* (Walckenaer, 1802) (Edgar, 1971) as well as the web-placement shift in colonies of the orb-weaver *Metepeira incrassata* F. O. P.-Cambridge, 1903 (Rayor & Uetz, 1993).

This study describes an apparent case of OHS in the Neotropical tarantula *Epebopus murinus* (Walckenaer, 1837). The tarantula genus *Epebopus* Simon, 1892 is a fossorial member of the otherwise arboreal subfamily Aviculariinae (Lucas *et al.*, 1991, 1992). Members of this genus bear urticating hairs on the apical prolateral surface of the palpal femora as opposed to the dorsal surface of the abdomen as in all other urticating hair-bearing theraphosid spiders (Marshall & Uetz, 1990). In the field in French Guiana we discovered that early-instar spiderlings build tubular, silken retreats off the ground among vegetation in contrast to the distinctive burrows that older juveniles and adult females build in the soil. The aim of this study was to quantify retreat-site variables for a population of *E. murinus*.

## Material and methods

We conducted our studies at Emerald Jungle Village, a private biological preserve in Montsinery, French Guiana ( $4^{\circ}47'05.50''\text{N}$ ,  $52^{\circ}24'45.05''\text{W}$ ). These data were collected during March 1999. The forest at Emerald Jungle Village is a 3.0 ha patch of gallery forest in a wet savannah landscape. The terrain is low-lying and drained in part by a system of canals (remnants of earlier land-use practices). In this forest fragment we also observed the tarantula species *Epehebopus rufescens* West & Marshall, 2000, *Tapinauchenius plumipes* (C. L. Koch, 1842), *T. gigas* Caporiacco, 1954, *Avicularia* spp., *Hemiercus* spp. and *Holothele* spp.

For the present study we located active above-ground and fossorial retreats of *E. murinus* within the 3.0 ha forest. At each retreat site we recorded microhabitat variables and retreat characteristics. The above-ground retreats consisted of a silken tube constructed within a whorl of leaves or a crevice in standing dead or living vegetation. These tubes were entirely above ground, and could be surprisingly long, depending on the volume of the space used. The fossorial retreats were vertically-oriented 'J'-shaped burrows with an enlarged terminal chamber, embellished at the entrance with a wide funnel constructed of silk and debris.



Plate 1: Early-instar *Ephebopus murinus* on leaf of *Bromelia alta*. Scale bar = approximately 10.0 mm.

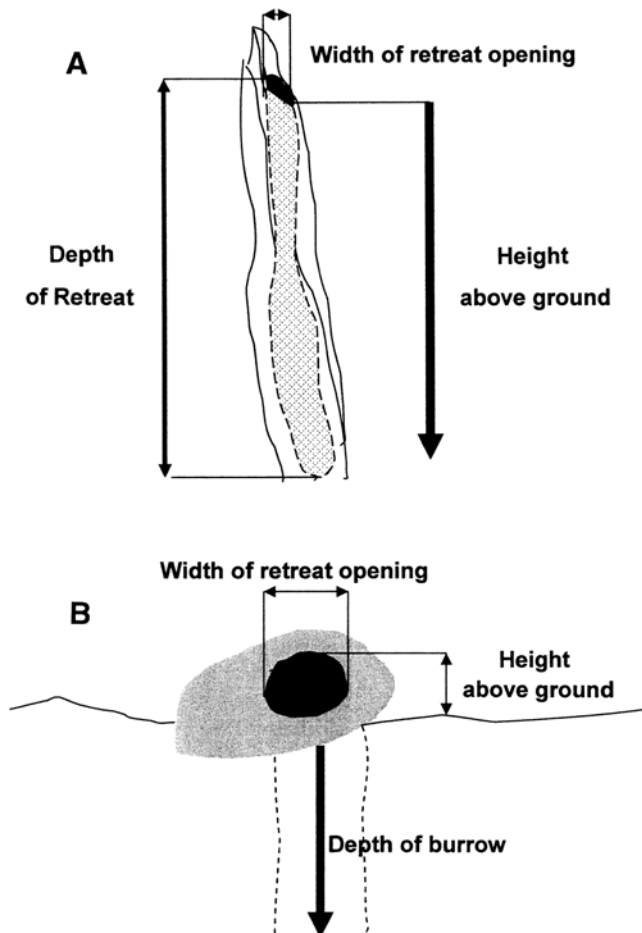


Fig. 1: **A** Diagram of structure of a retreat of an early-instar *E. murinus* in central whorl of leaves of *B. alta*, showing measurements taken. **B** Diagram of a burrow of adult *E. murinus*, showing measurements taken.

**Habitat use:** We quantified the microhabitat features around each retreat site using two, 1 m line transects, running at right angles to each other centred on the retreat mouth and oriented N–S & E–W. The presence or absence of habitat features (e.g. substratum type, vegetation) was noted for each 10 cm interval along each transect. For comparison, a second set of data was collected at a point 1 m south and 1 m east of each retreat location as non-retreat sites. The data for both transects (N–S & E–W) for each site were summed, and the values for each point could range from 0 to 20 for each environmental factor (e.g. leaf litter, barren soil, grass, herbaceous vegetation, water). These data were analysed using discriminant analysis (SPSS 14.0, 2005) with variables entered as count data (i.e. integers).

**Retreat architecture:** We recorded descriptive data on the placement and dimensions of the retreats. For the above-ground retreats: substratum, width of opening at the widest point, height off the ground of the retreat opening, and depth of the tube (Fig. 1a). For the fossorial retreats: width of opening at the widest point, height off the ground of the retreat opening, and depth of the burrow (Fig. 1b).

## Results

**Habitat use:** We collected data on 13 above-ground retreats and 13 fossorial retreats, with 25 non-retreat sites for comparison. Despite the proximity of the above-ground retreats and fossorial retreats to one another there was a clear separation of microhabitat use

(Fig. 2). The presence of terrestrial bromeliads (particularly *Bromelia alta* L. B. Smith, 1956) was a significant predictor of above-ground retreats and leaf litter was a significant predictor of fossorial retreats (Wilk's Lambda,  $p=0.011$ ). Based on univariate ANOVA analyses of the data, only the presence of *Bromelia alata* was a significant predictor of above-ground retreats ( $p<0.0001$ ). Of the 13 above-ground retreats studied, 11 were on *Bromelia* spp. plants, 1 was on a *Heliconia* sp., and 1 was on a dead branch.

**Retreat architecture:** Measures of all three variables shared by burrows and above-ground retreats were significantly different. For retreat depth (mean cm  $\pm$  1 sd): above-ground  $42.8 \pm 16.3$ ; fossorial  $27.3 \pm 8.5$  (only 6 fossorial retreat depths measured);  $t=2.15$ ,  $df=16$ ,  $p=0.047$ ; height of retreat opening above ground: above-ground  $58.8 \pm 17$ ; fossorial  $9.15 \pm 2.91$ ;  $t=9.97$ ,  $df=24$ ,  $p \leq 0.0001$ ; retreat mouth width: above-ground  $0.15 \pm 0.05$ , fossorial  $5.19 \pm 1.32$ ;  $t = -13.81$ ,  $df=24$ ,  $p<0.0001$ .

## Discussion

Ontogenetic habitat shifts are predicted to reduce intraspecific competition and the risk of cannibalism by older (and larger) individuals on the smaller age classes in predatory species with size-structured populations (Werner & Gilliam, 1984). One of the best-known examples is Werner & Hall's (1988) study of habitat use in bluegill sunfish (*Lepomis macrochirus* Rafinesque, 1819; Centrarchidae). Sunfish, like spiders, are predators that live in age (size) structured populations and are prone to cannibalism. Werner & Hall found that the smaller age-size classes of bluegill sunfish tend to use the littoral vegetation as cover from predators. In



Plate 2: Adult female *Epehebopus murinus* sitting at entrance to burrow. Scale bar=approximately 10.0 mm.

doing so, they incur a cost of reduced food intake and growth.

Ontogenetic habitat shifts (OHS) have been observed in wolf spiders (Edgar, 1971; Kronk & Riechert, 1979) and an orb-weaver (Rayor & Uetz, 1993). In these examples, the shift in microhabitat use represented the trade-off of foraging success and the risk of predation. Edgar (1971) studied the phenology and seasonal movements of a population of *Pardosa lugubris* at the University of Glasgow Field Station near Loch Lomond. Edgar found that the spiders used different habitats during different life stages. Specifically, adult females with eggs would move to open, sunny habitats during the incubation period (presumably to improve thermoregulation of the eggs). After the spiderlings dispersed, the females would return to wooded areas to feed. Edgar proposed that this spatial separation prevented cannibalism by hungry, ovigerous females. He also noted that the first year and second year juveniles would use different layers of the leaf litter in the forested over-wintering area; also presumably to reduce cannibalism. Kronk & Riechert (1979) studied a population of *Rabidosia santrita* along a stream in the Chiricahua Mountains of south-eastern Arizona. Spiders moved from grassy, riparian habitats to rocky areas near the creek as they matured. The authors noted that the risk of mortality was lower, and foraging success more predictable in the grassy areas and that foraging success for the adult females improved in the stream bed, but exposed the spiders to greater predation risk. Kronk & Riechert (1979) suggested that a trade-off of foraging success against risk of predation drove the OHS. The authors also noted that this spatial segregation might also function to reduce intraspecific competition and cannibalism. Rayor & Uetz (1993) studied the placement of individual *Metepeira incrassata* within large colonies. They discovered that body size (an indicator of age) was correlated with web site placement relative to the core vs. the periphery of the colony. Prey availability for both small and large *M. incrassata* was higher on the periphery of the colony, and so was the risk of predation by sphecid wasps. The spatial segregation arose when the larger spiders dominated the safer core of the colony,

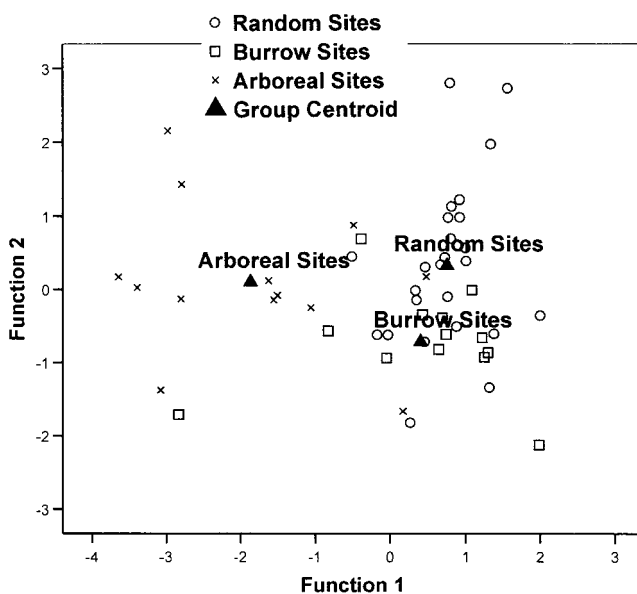


Fig. 2: Graph of standardised canonical coefficients for discriminant analysis of habitat data collected at retreat sites of *E. murinus* burrows and above-ground retreats, with data on non-retreat sites for comparison. Particularly influential factors for function 1 are the presence of terrestrial bromeliads and dead wood, and for function 2 the presence of dead wood, stems and grass.

forgoing foraging success in favour of higher survival rates.

Early-instar *E. murinus* use different microhabitats and exhibit different retreat architecture from late-instar and adult individuals. Based on discriminant analysis of retreat-site habitat, site choice by early-instar *E. murinus* was very different from both the random sites and burrow sites. Not only did habitat use differ, but the height and size of the retreats were significantly different. Retreat diameter is a reflection of body size in *Ephebopus*, but the height above ground represents the very different retreat architecture of early vs. late-instar *E. murinus*. The retreats we observed in the *Bromelia* spp. were always in the central whorl of growing leaves. The spiders would silk the leaves together, constructing a tube. This tube had unique properties as a retreat: the leaves of *Bromelia* spp. are tough and well-armed with marginal spines.

Terrestrial bromeliads have been found to provide shelter for two other spider taxa, a salticid and a theraphosid. Romero *et al.* (2006) studied the relationship between the jumping spider *Psechus chapoda* (Peckham & Peckham, 1894) and the bromeliad *Bromelia balansae* Mez. They discovered that the spiders contributed nutrients to the host plant in the form of frass, exuviae, and prey remains. These inputs resulted in a measurable increase in growth of the plants. The tarantula *Pachistopelma rufonigrum* Pocock, 1901 has been found to use two genera of bromeliad, *Aechmea* and *Hohenbergia* spp., in the Caatinga region of Brazil (Dias & Brescovit, 2003). The authors propose that the dorso-ventral flattening of the body of *P. rufonigrum* is an adaptation to living between the leaves of bromeliads and note they have found them living nowhere else.

Observations made of the four other *Ephebopus* spp. offer a contrast in habitat use and retreat architecture. We have observed all life stages of *E. cyanognathus* West & Marshall, 2000 and *E. uatuman* Lucas *et al.*, 1992. These two species were found to make fossorial retreats in sloping, shaded primary lowland and montane tropical wet forest habitats (*E. uatuman* was observed in the Brazilian Amazon). Retreats consist of a small flared silken entrance raised and supported by surrounding leaf litter that opens into a simple, tubular burrow. Our observations of habitat choice and burrow structure suggest that both *E. cyanognathus* and *E. uatuman* are obligate burrowers that build similar, distinctive retreats. We observed *E. rufescens* in French Guiana and found retreats in such microhabitats as fallen and upright rotting trees, under large rocks, in rock crevices at cave entrances, or up to several metres above ground in natural cavities, moss piles or at the bases of bromeliads found in living or dead trees. In contrast to *E. cyanognathus* and *E. uatuman*, the retreats of *E. rufescens* were not distinctive tubular burrows into the substratum, but generally exploited natural cavities. In many cases the retreats of *E. rufescens* had a silk pouch at the entrance. This silk pouch is camouflaged with bits of soil and debris. Of all the *Ephebopus* spp. studied, *E. rufescens* appears to have the most generalised retreat site placement and retreat architecture. The most recently de-

scribed *Ephebopus* species, *E. foliatus* (West *et al.*, in press) has not been observed in the field by us. Matjaz Kuntner (pers. comm., 2002) collected the male and female type specimens wandering on the trunks of small trees between 1–2 m off the ground in primary lowland tropical wet forest in the interior of Guyana. The retreats of *E. foliatus* have not been described, but Kuntner's collecting observations suggest an arboreal lifestyle. Collectively, the observations of *Ephebopus* ecology show a predominantly fossorial genus with individuals and life stages that will use above-ground sites. We are not aware of any other tarantula genus which exhibits this diversity of retreat architecture.

*Ephebopus* is a fossorial member of the otherwise arboreal tarantula subfamily Aviculariinae (West *et al.*, in press). The related genera *Avicularia*, *Tapinauchenius* and *Pachistopelma* are only known to build their retreats off the ground. We propose that the genus *Ephebopus* secondarily evolved the fossorial habit. We base this hypothesis on the observation that the burrows of *Ephebopus* in general, and *E. murinus* in particular, are unique in structure. *Ephebopus* is the only tarantula in the New World to construct a conspicuous flaring trumpet of silk at the burrow entrance. This is a feature seen in some Asian genera (e.g. *Haplopelma*, *Ornithoctonus*) which are unambiguously members of a different subfamily (Ornithoctoninae). Past studies of OHS have stressed the benefits of reduced intraspecific competition and risk of cannibalism/predation. For *Ephebopus* we propose a third possible mechanism: evolutionary history. *Ephebopus* may present us with the evolution of the fossorial habit from arboreal ancestors. This is the reverse direction from that proposed for the ancestral lineage of all spiders which is strictly fossorial.

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