Emergence of a giant fly triggers phoretic dispersal in the neotropical pseudoscorpion, *Semeiochernes armiger* (Balzan) (Pseudoscorpionida: Chernetidae)

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Summary

Field observations of the behaviours leading to phoretic dispersal in the neotropical pseudoscorpion *Semeiochernes armiger* (Balzan) were recorded from Panama. The pseudoscorpions formed high-density clusters around the larval and pupal holes (bores) excavated by the larvae of the giant wood-boring fly *Pantophthalmus tabaninus* Thunberg in a decayed *Ficus* trunk. Female *S. armiger* exhibited a strong preference to aggregate around pupal rather than larval bores. By contrast, an average of approximately one male occurred at each bore type, suggesting that males may compete for control of these sites. Within 48 h before emergence of the adult flies, pseudoscorpions became hyperactive. Pantophthalmid eclosion triggered group phoresy, with as many as 22 *S. armiger* attaching to a single fly. Whereas prolonged pseudoscorpion attachment was observed on several female flies, all phoretic individuals rapidly disembarked from an eclosing male. Phoretic specialisation on females appears to be adaptive since only female pantophthalmids visit trees suitable for colonisation by the pseudoscorpion. The findings of this study reveal that phoresy in *S. armiger* involves a complex suite of behaviours, closely attuned to the biology of the phoretic agent and functioning specifically for dispersal.

Introduction

Dispersal, potentially across relatively great distances, is essential for animals specialising on ephemeral, patchily-distributed habitats. In most of these species, habitat specificity necessitates sophisticated locomotor, sensory and physiological capacities for effectively locating appropriate new environments (Mitchell, 1970; Bartholomew & Lighton, 1986). However, many apterous arthropods have short-circuited these requirements by exploiting the greater dispersal capabilities of flying insects. Use of one animal by another for transport is known as phoresy (Wilson, 1980), and is common among mites (Lindquist, 1975), entomophagous insects (Clausen, 1976) and pseudoscorpions (Beier, 1948; Muchmore, 1971; Legg, 1975; Zeh & Zeh, 1991, in press a,b,c).

Equally critical to transient resource utilisation is the ability of a species to respond to environmental cues in timing its exodus from depleted habitats. Recent experimental evidence on the desert pseudoscorpion, *Dinocheirus arizonensis* (Banks), suggests that phoresy is triggered by eclosion of the phoretic agent from its pupal case (Zeh & Zeh, in press c). In the laboratory, incidence of phoresy was greater on eclosing cactus flies (*Odontoloxozus longicornis* (Coquillett)) than on post-teneral adults.

Here, we report field observations of phoretic behaviour triggered by host eclosion in the neotropical pseudoscorpion, *Semeiochernes armiger* (Balzan). We describe the suite of behaviours which enable this chernetid to disperse by attachment to the giant wood-boring fly, *Pantophthalmus tabaninus* Thunberg. Although *S. militaris* Beier has been reported as phoretic on a large brachyceran fly captured in a mist net (Mahnert, 1987), this paper provides the first detailed account of phoretic behaviour in the genus.

S. armiger is a large, heavily-sclerotised member of the chernetid subfamily, Hesperochernetinae. The species is highly sexually-dimorphic, with males possessing greatly enlarged chelae and chelal peg-like processes, absent in females (Beier, 1933; see Plate 1). Currently, three species of *Semeiochernes* are described in the literature, based on chelal size and presence/absence of the lateral process: *armiger* from Peru and Panama; *extraordinarius* Beier from Venezuela, and *militaris* from Brazil and Costa Rica (Beier, 1933, 1954; Mahnert, 1987). In examining hundreds of specimens from Panama, we found the entire range of 'interspecific' male variability (from small chelae without lateral processes to greatly enlarged chelae with pronounced lateral processes) in single populations of *S. armiger*. Based on a comparison of our specimens with those of museum collections, W. B. Muchmore has suggested that "there is probably just one very variable species involved here" (pers. comm.). Virtually nothing is known of the natural history of *Semeiochernes*.

The timber fly, *P. tabaninus*, is one of the largest flies in the world, with individuals ranging in mass from 0.91 to 2.80 g (Bartholomew & Lighton, 1986). Females oviposit on the bark of both standing and fallen trees. Development of the unusual wood-boring larvae, which excavate extensive galleries within the trunk, may require more than one year (Thorpe, 1934).

Methods

The research was conducted between May 1988 and July 1989 in moist lowland tropical forest of the Parque Nacional Soberania, Panama. We carried out extensive searches of a 60 ha tract of forest (Zeh & Zeh, in press a)
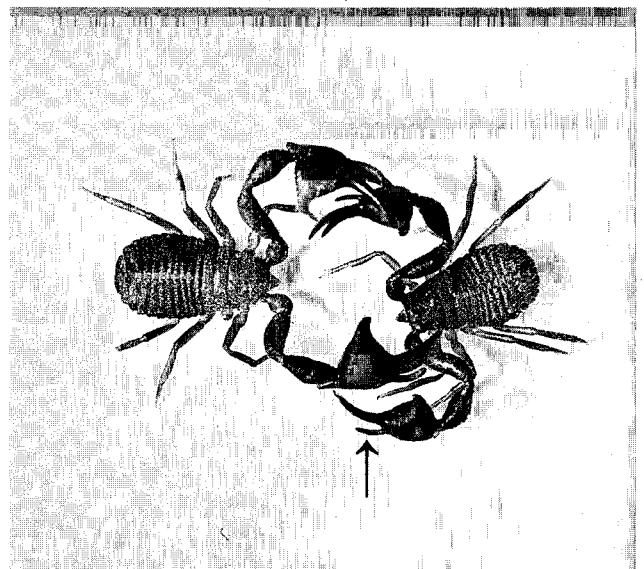

Plate 1: Two male *Semeiochernes armiger* (Balzan) engaged in combat. The chelal peg-like process is indicated by the arrow (lower right).

and located *S. armiger* populations in 14 naturally-occurring fallen or decaying trees. Observations of behaviour leading to phoresy were made in August 1988 when a large population was discovered in a dead, standing tree (FEF2) from which pantophthalmids were emerging.

P. tabaninus larvae excavate circular holes (bores) approximately 12 mm in diameter. Visual inspection enabled us to categorise the bores made in the FEF2 tree as either larval or pupal. Larvae are oriented head-first in the bores, with the posterior shield facing outwards (Thorpe, 1934). By contrast, pupae face outwards so that the sclerotised plate of the cephalic extremity is visible (Val, 1991). All active bores within a 0.55 m² area at the base of the tree were marked. The numbers of male and female *S. armiger* in and around each bore were counted at the beginning of the study. Since pseudoscorpions enter the approximately 10-cm deep bores, counting involved removing individuals by aspiration. Daily 2-hr observations, commencing 1 h before dusk, were carried out over a three-week period to monitor pseudoscorpion behaviour as pantophthalmids eclosed.

A two-way analysis of variance (ANOVA) was carried out to quantify the effect of pseudoscorpion sex and fly life-stage on number of individuals aggregating around pantophthalmid bores. Count data were $\sqrt{(Y)}+\sqrt{(Y+1)}$ transformed to normalise variance (Sokal & Rohlf, 1981). In addition, a chi-square was calculated to test for sex bias in pseudoscorpions phoretic on eclosed flies. Statistical analyses were carried out using SAS (SAS Institute, 1988).

Results

Tree populations of *S. armiger* were found only in decaying *Ficus* trees (*F. insipida* Willd. and other species, unidentified owing to absence of fruit and leaves). The fig trees were also inhabited by *Cordylochernes scorpioides* (Linn.), a chernetid pseudoscorpion which disperses under the elytra of the giant harlequin beetle, *Acrocinus longimanus* (Linn.) (Zeh & Zeh, 1991, in press a,b). *S. armiger* was most commonly located under loose sections of bark in the frass (sawdust) generated by pantophthalmid, harlequin beetle, and other dipteran and coleopteran larval activity. All *S. armiger* host trees exhibited evidence of pantophthalmid oviposition or larval boring. As with the pseudoscorpion, *P. tabaninus* was observed exclusively on *Ficus*.

Tree FEF2 was in an advanced stage of decay, with most of the *Cordylochernes* pseudoscorpions and all of the harlequin beetles having dispersed. Many of the vacated *Acrocinus* larval galleries were occupied by the large scorpion, *Opisthacanthus lepturus* (Beauvois). The giant amblypygid, *Paraphrynus laevifrons* (Pocock), was also abundant under remaining sections of loose bark. At dusk, the amblypygids moved out from under bark to occupy positions near pantophthalmid holes, and we observed one case of amblypygid predation on an eclosing *Pantophthalmus*.

Observation of *Semeiochernes* behaviour was greatly facilitated by the fact that large sections of bark had fallen away from the north face of FEF2 where pantophthalmid bores were concentrated. At first census, a total of 99

S. armiger were found in the 0.55 m² area, a density of 180/m². Overall, bore type was found to influence significantly the size of *S. armiger* aggregations, which were larger around pupal bores ($n=19$) than around larval bores ($n=11$) ($F_{1,56}=9.13$, $p=0.0038$). However, there was also a strong sex effect. Mean numbers ($\pm$SE) around pupae were 1.26 ± 0.36 males and 2.89 ± 0.36 females, compared with 0.91 ± 0.47 males and 0.91 ± 0.47 females around larvae. Response to bore type was highly significant in females ($p=0.0015$, Fisher's least significant difference statistic) but not in males ($p=0.553$).

As part of a study of dispersal-mediated sexual selection (manuscript in preparation), we photographed and marked the pseudoscorpions collected during this first census. Over the next 12 days, three further censuses were made before all newly-marked individuals were returned to the tree. At each census approximately 100 *Semeiochernes* were counted in the pantophthalmid emergence zone. Apparently, after each removal, the zone was re-colonised to saturation level by pseudoscorpions from a subcortical population of several hundred individuals.

The FEF2 tree was monitored for 15 days before fly emergence was observed. During this period, pantophthalmid bores were surrounded not only by *S. armiger* but also by thousands of an unidentified species of mite. Pseudoscorpions displayed a variety of behaviours while occupying the pantophthalmid emergence zone. The majority of females and a smaller fraction of males consistently remained inside or close to the bores. Other lone individuals, particularly males, moved freely within the zone without taking up residence at any particular bore. Individuals attempting to enter occupied bores were frequently repelled by both male and female residents (25 of 32 attempts). In several cases, mating was observed on the tree surface close to a bore entrance ($n=18$). Both males and females were occasionally seen to feed on the aggregating mites ($n=5$).

Several days before eclosion, fly pupae began engaging in repeated, piston-like, back-and-forth movements within their bores. When a pupa retracted into its hole, the pseudoscorpions and mites entered the bore and could be seen clustered on the wall and on the pupa's cephalic cap (Plate 2). On outward surges, the pupa moved forwards until its cephalic cap was flush with the bore opening, forcing the pseudoscorpions and mites out of the hole and on to the tree surface (Plate 3). In the 2–3 day period preceding fly eclosion, there was a sudden, dramatic shift in the behaviour of *S. armiger*. Activity in this usually slow-moving, cryptic species became frenetic, with individuals scrambling to occupy positions closest to the pupa. Activity among the mites also visibly intensified.

Two cases of fly emergence were observed on 24 August 1988 between 1820 and 1835. The first individual to eclose was a male which was photographed in the process of emergence (Plate 4) with at least 17 pseudoscorpions clinging to its legs, wings and body. Within 10 min, however, all the pseudoscorpions had disembarked while the fly was resting undisturbed on the trunk surface. At 1835, a female fly eclosed and was photographed shortly after emergence (Plate 5). In this case, 12 male and 10

female pseudoscorpions attached to the fly and remained phoretic until they were removed 2–3 h later in the laboratory.

Finally, two other instances of *S. armiger* phoresy on *P. tabaninus* were observed at other locations. In both cases, they involved post-teneral female flies seen after leaving their emergence trees. On 19 May 1988, two *S. armiger* females were observed to disembark from a fly ovipositing on a newly-fallen *Ficus insipida*. A second female fly, collected on 23 July 1989 by T. R. Dudley on Barro Colorado Island, was carrying 3 males and 7 females. Based on this study and the collection cited in Mahnert (1987), a total of 17 male and 26 female *Semeiochernes* have been found to be phoretic. Although the data suggest a female bias in incidence of phoresy, the trend is not statistically significant ($\chi^2 = 1.88, p > 0.05$)

Discussion

The findings of this study demonstrate that *S. armiger* engages in a complex set of behaviours which enable it to attach to pantophthalmid flies eclosing in old, depleted trees. Specialisation on newly-emerged flies is likely to result in a high probability of transport to fresh habitats. Our results are therefore consistent with the hypothesis that phoresy is a mechanism functioning specifically for dispersal (Beier, 1948; Weygoldt, 1969; Legg, 1975; Zeh & Zeh, in press c). As in other recent studies (Haack &

Wilkinson, 1987; Zeh & Zeh, 1991, in press a,b,c), the hypothesis that pseudoscorpion attachment to larger species is the accidental by-product of failed predation attempts (Vachon, 1940, 1954) was clearly not supported.

Moreover, our field observations indicate that phoresy in *S. armiger* is closely attuned to the biology of the dispersal agent. Of particular interest is our observation that pseudoscorpions disembarked rapidly after attaching to an eclosing male fly. Taken in conjunction with the fact that all cases of phoresy involved female pantophthalmids, this may suggest that *S. armiger* generally rejects males as dispersal agents. Evidence suggests that pseudoscorpion discrimination of host sex is adaptive. Mating in *P. tabaninus* has never been observed and apparently does not occur on oviposition trees (Val, 1991). Despite numerous observations of female pantophthalmids ovipositing on newly-fallen *Ficus*, we have never seen males in this habitat. Pseudoscorpions phoretic on male flies would therefore not be transported to appropriate new habitats.

A recent study of *C. scorpioides* investigated the morphological correlates of phoretic dispersal on harlequin beetles. Evidence indicated that males engaged in intense size-based competition to establish mobile mating territories on the abdomens of beetles, resulting in strong selection for large male size and fighting ability (Zeh & Zeh, in press a). In *S. armiger*, aggregation around pantophthalmid bores results in the high-density conditions which enable large males to monopolise females
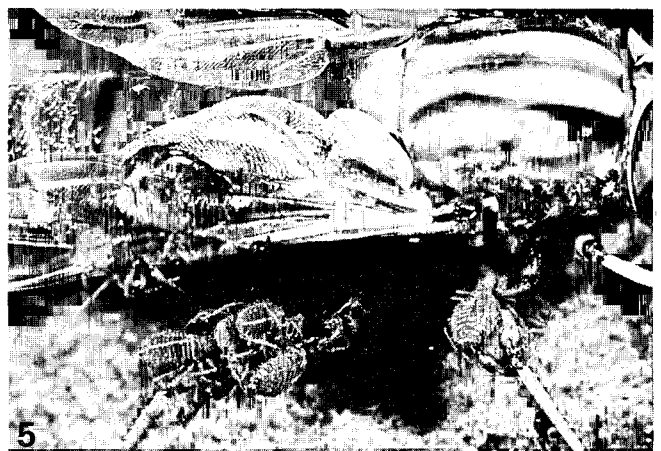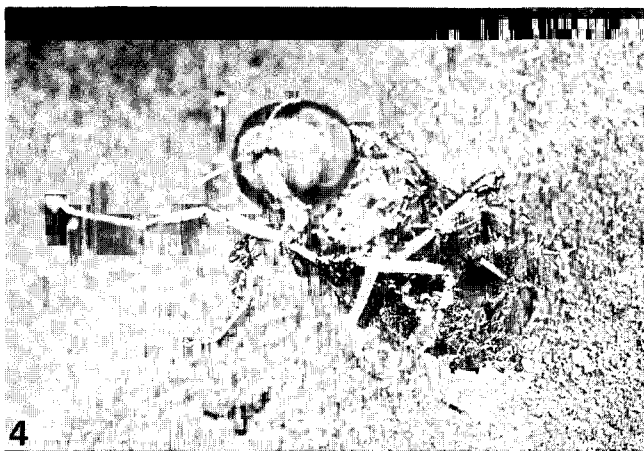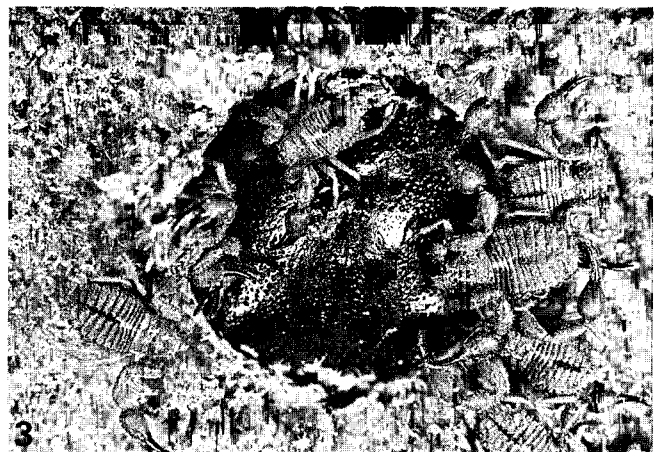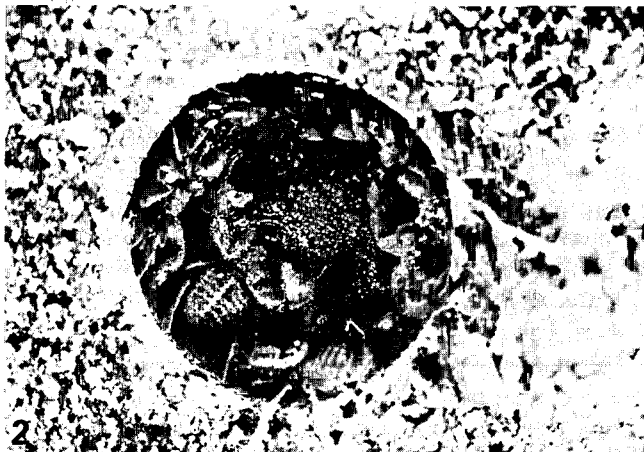
Plates 2–5: Phoretic behaviour in *Semeiochernes armiger*. 2 Pseudoscorpions cluster on the cephalic cap of a *Pantophthalmus tabaninus* pupa while it remains recessed within its bore; 3 Outward movement of the pupa forces pseudoscorpions out of the bore; 4 At least 17 *S. armiger* scramble on to a *P. tabaninus* male as it ecloses; 5 Several minutes after a *P. tabaninus* female ecloses, 22 *S. armiger* remain attached to the fly.

(Zeh, 1987; Zeh & Zeh, in press a). On the FEF2 tree, we observed numerous mating events in the zone of pantophthalmid emergence. We also noted a clear female bias in aggregations around pupal but not larval holes. The absence of a significant difference in numbers of males around larval versus pupal holes may indicate that males compete for control of these sites. These data suggest that the phenomenon of dispersal-generated sexual selection may also operate in *S. armiger*.

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