ON THE FUNCTION OF HARLEQUIN BEETLE-RIDING IN THE PSEUDOSCORPION, *CORDYLOCHERNES SCORPIOIDES* (PSEUDOSCORPIONIDA: CHERNETIDAE)

David W. Zeh and **Jeanne A. Zeh**: Smithsonian Tropical Research Institute, Unit 0948, APO 34002-0948 USA, or, Apartado 2072, Balboa, República de Panama

ABSTRACT. The pseudoscorpion, *Cordylochernes scorpioides*, frequently occurs under the elytra of the giant harlequin beetle, *Acrocinus longimanus*. Here, we assess four hypotheses/scenarios which have been proposed to account for this phenomenon: (1) accidental boarding; (2) obligate symbiosis; (3) phagophily, and (4) phoretic dispersal. Field and laboratory observations of embarkation behavior clearly refute the accidental boarding hypothesis. Contrary to the obligate symbiosis scenario, pseudoscorpion offspring production does not occur on the beetle and the primary habitat of *C. scorpioides* is decaying trees. The phagophily hypothesis, i.e., that pseudoscorpions mount harlequins for the primary purpose of preying upon the beetles' phoretic mites, is also not supported. Pseudoscorpions collected from trees were found to be in better nutritional condition than beetle-riding individuals. Finally, evidence from a companion study supports the dispersal hypothesis, and also indicates that large male *C. scorpioides* defend beetles' abdomens as strategic sites for intercepting and inseminating dispersing females.

The reason why pseudoscorpions attach to other organisms (generally termed phoresy) is the subject of much debate and little data (see Muchmore 1971). In this paper, we evaluate several competing hypotheses put forward to explain the significance of the association between the chernetid pseudoscorpion, *Cordylochernes scorpioides* (L.), and the giant harlequin beetle, *Acrocinus longimanus* (L.) (Cerambycidae). *Cordylochernes scorpioides* is distributed throughout the tropical forests of Central and South America (Beier 1948) where it is frequently found under the elytra of harlequin beetles (Beier 1948; Beck 1968; Muchmore 1971; Zeh & Zeh 1991, 1992). This cerambycid also carries mites, occasionally in large numbers, both in small pits on the outer surface of its fore-elytra, and on its thorax, wings and abdomen (Fig. 1). It has been hypothesized that *C. scorpioides* climbs onto beetles: (1) accidentally; (2) for dispersal to new habitats, or (3) for "phagophily", i.e., to feed on the mites (for review see Muchmore 1971). The harlequin beetle/pseudoscorpion relationship has even been presented as obligate symbiosis in which the pseudoscorpions live exclusively on the beetles (Ricklefs 1979).

Our three-year study of *C. scorpioides* (Zeh & Zeh 1991, 1992) and *A. longimanus* (Zeh et al. 1992) has demonstrated that the primary habitat of this pseudoscorpion is decaying trees in the families Moraceae and Apocynaceae (e.g., *Ficus* spp. L. and *Parahancornia fasciculata* (Poiret)). Larval development of *A. longimanus* also occurs in these habitats (Duffy 1960; G. Tavakilian, pers. comm.; pers. obser.). While all pseudoscorpion life stages were collected from trees, no nymphs and only one newly-gravid female (N = 134 females) were taken from beetles, indicating that pseudoscorpion presence on beetles is strictly an adult phenomenon.

Field and laboratory observations in Panama and French Guiana were not consistent with the "accident" hypothesis. Pseudoscorpion embarkation involves a sequence of deliberate, stereotypical behaviors (Beck 1968) which appears to be triggered by olfactory cues and beetle stridulation (pers. obser.). Both in the field and when placed in laboratory containers with harlequin beetles, pseudoscorpions engaged in the characteristic lifting of pedipalps (so-called "beckoning" movements, see Weygoldt 1969) before moving rapidly to the posterior end of the beetle. There, pseudoscorpions gained access to the "subelytral space" by repeatedly pinching the beetle's abdomen, causing abdominal flexure and partial opening of the elytra (Fig. 2). In addition, in decaying *Ficus* trees, *C. scorpioides* occurs with several other pseudoscorpion species, e.g., *Lustrochernes* sp. Beier, *Parachernes plumosus* (With) and *Semeiochernes armiger* (Balzan). We have

Figure 1.—Harlequin beetle with elytra opened to display female *Cordylochernes scorpioides* and unusually heavy infestation of mites.

never found individuals of these species under the elytra of harlequin beetles ($N = 149$ beetles).

By contrast, results of our research clearly supported the dispersal hypothesis, demonstrating a pattern in which large numbers of adult pseudoscorpions boarded beetles on old, depleted trees and disembarked on newly-fallen trees. The study also revealed a novel aspect of the beetle/pseudoscorpion relationship. Large male *C. scorpioides* monopolize beetle abdomens as strategic sites for intercepting and inseminating dispersing females (Zeh & Zeh 1992).

METHODS

We tested the phagophily hypothesis by comparing pseudoscorpions taken from beetles with individuals collected from within decaying trees, using abdomen length as a measure of recent food consumption. In pseudoscorpions, no further molting occurs after the adult stage is reached so that the fully-sclerotized pedipalps and cephalothorax are fixed in size (Weygoldt 1969; Zeh 1987). However, the abdomen is only partially sclerotized and enlarges with food intake.

Measurement of the abdomen length of beetle-riding pseudoscorpions was restricted to individuals taken from beetles on newly-fallen, undecayed trees. We excluded pseudoscorpions from beetles collected on older, dead trees with evidence of beetle emergence. This was necessary to ensure that pseudoscorpion abdomen length reliably reflected the nutritional consequences of beetle-riding. Pseudoscorpions climb onto harlequins soon after the beetles eclose from pupal chambers within old trees (Zeh & Zeh 1992). The post-teneral beetles then rapidly fly off in search of newly-dead trees to mate and oviposit (Zeh et al. 1992). Pseudoscorpions collected from emerging beetles on old trees have therefore only just embarked and are in a nutritional state which largely reflects feeding within the tree and not on the beetle. By contrast, pseudoscorpions taken from a beetle captured on a new tree are likely to have spent a significant period on the beetle's abdomen during its search for a freshly-dead or dying tree.

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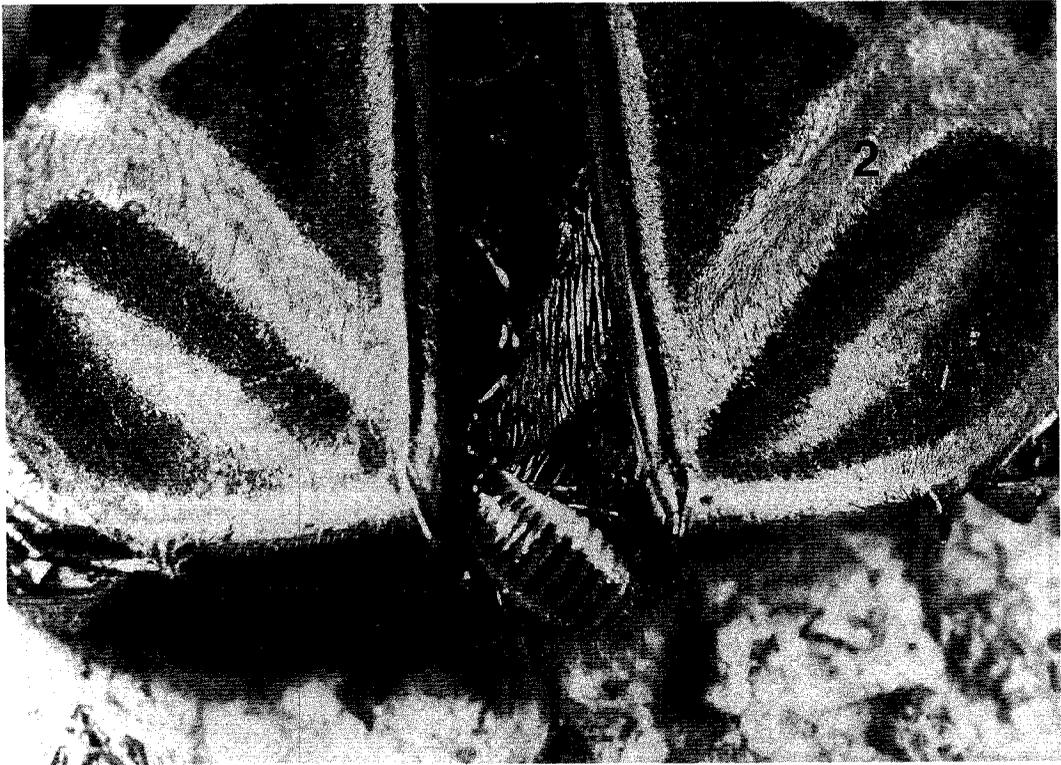
Figure 2.—Beetle-boarding behavior of *C. scorpioides* (see text).

Soberania. Eight female and 61 male pseudoscorpions were removed from 58 harlequin beetles taken from 7 newly-fallen, undecayed trees. Sixty-nine female and 100 male *C. scorpioides* were also collected from 16 tree populations in the area. In French Guiana, 30 females and 54 males were removed from 34 beetles collected from 3 newly-fallen trees along the Piste du Kaw, 50 km southeast of Cayenne. An equivalent number of males and females was collected from 12 sympatric tree populations.
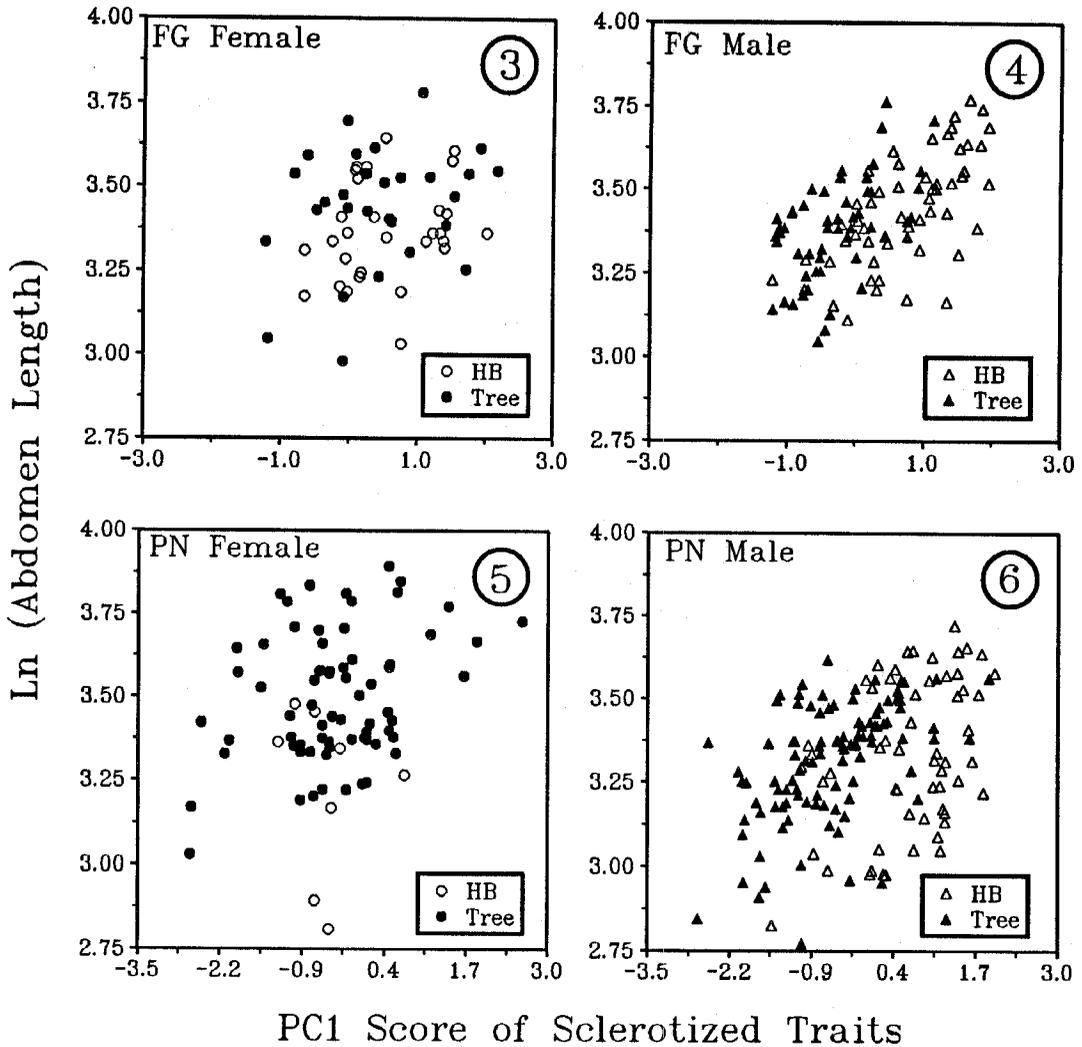
Two interrelated factors confound a direct comparison of the mean abdomen length of beetle-riding versus within-tree pseudoscorpions. First, although abdomen length varies with nutrition, there are also significant positive correlations between abdomen length and sizes of pedipalpal and cephalothorax traits. Second, for our analysis, it was particularly critical to take account of these correlations. Male pseudoscorpions compete to establish mating territories on the abdomens of beetles and, as a consequence, beetle-riding males are significantly larger overall than males randomly-sampled from trees (Zeh & Zeh 1992). Therefore, even in the absence of

nutritional differences, mean abdomen length is expected to be larger in beetle-riding pseudoscorpions.

Direct comparison of mean abdomen lengths

Table 1.—Results of principal components (PC) analysis of nine traits of the pedipalps and cephalothorax in *C. scorpioides*. PC analyses were carried out separately by gender and geographic location. Prop. = Proportion of total morphological variation explained by PC1.

Trait	Trait loading on PC1			
	FG female	FG male	PN female	PN male
MFL	0.140	0.080	0.135	0.080
HL	0.139	0.121	0.092	0.114
HD	0.131	0.230	0.147	0.204
TL	0.077	0.104	0.134	0.106
TD	0.180	0.160	0.179	0.197
FL	0.182	0.098	0.137	0.103
FD	0.094	0.104	0.203	0.129
CL	0.121	0.064	0.089	0.054
CW	0.186	0.093	0.156	0.072
Prop.	0.637	0.897	0.611	0.886

Figures 3–6.—Comparison of relative abdomen length in *C. scorpioides* from trees versus individuals from harlequin beetles (HB) (see text for explanation). Analysis carried out separately by gender and geographic location (FG = French Guiana; PN = Panama).

in the two environments was carried out, using an analysis of covariance (ANCOVA) which factored out the correlation between sclerotized trait size and length of the abdomen. The ANCOVA analysis is most clearly interpreted by first deriving a single, composite measure of size for the nine sclerotized traits we measured. This was obtained by performing principal components analysis (PCA) in which the first principal component (PC1) provides the single best measure of overall size (see Bookstein et al. 1985).

Sclerotized traits included in the analysis were: chelal movable finger length (MFL); chelal hand length (HL) and depth (HD); tibia length (TL) and depth (TD); femur length (FL) and depth (FD), and cephalothorax length (CL) and posterior width (CW) (see Chamberlin 1931). Measurements were taken from photographs of live individuals restrained with pedipalps fully extended under a glass slide (Kodak Technical Pan film, Nikon FE2 camera, 55 mm Micro-Nikkor lens with 55 mm extension). The negative image of each specimen was then projected onto a computer-linked digitizing tablet (Summagraphics MM 1201) and the coordinates of 38 anatomical landmarks on the dorsal outline of the body and

right pedipalp (plus two scale bar points) were recorded. The 9 traits were then computed from the coordinates. Principal component (PC) scores were calculated from the covariance matrix of ln-transformed measurements. All traits loaded positively on PC1 (Table 1) which therefore represents a composite measure of overall size (see Bookstein et al. 1985). To avoid negative values, the traits (measured in mm) were first multiplied by 10 before natural logarithmic transformation. Statistical analyses were performed using SAS© (SAS Institute, 1988).

RESULTS AND DISCUSSION

In the analysis of covariance, abdomen length represented the dependent variable, PC1 score of the sclerotized traits the covariate, and "environment", i.e., beetle versus tree, the independent categorical variable. Results demonstrated that, in both the Panamanian (PN) and French Guianan (FG) populations, adjusted mean abdomen length (least squares mean or LSM) of pseudoscorpions on trees (LSM_{Tree}) exceeded that of beetle-riding individuals (LSM_{HB}) in both females (FG: $LSM_{Tree} = 3.45$, $LSM_{HB} = 3.36$, $F_{1,57} = 4.60$, $P = 0.036$; PN: $LSM_{Tree} = 3.50$, $LSM_{HB} = 3.23$, $F_{1,74} = 13.88$, $P < 0.001$) and males (FG: $LSM_{Tree} = 3.44$, $LSM_{HB} = 3.36$, $F_{1,105} = 4.94$, $P = 0.028$; PN: $LSM_{Tree} = 3.36$, $LSM_{HB} = 3.26$, $F_{1,156} = 8.26$, $P = 0.005$) (see Figs. 3–6). This suggests that individuals within trees are better nourished than their counterparts on beetles. While our observations confirmed that beetle-riding pseudoscorpions do prey on the harlequin's mites, the results presented here were not consistent with Vachon's (1940) hypothesis that phagophily is the primary motivation for the association.

Finally, we suggest that, based on purely physiological considerations, the phagophily hypothesis seems flawed. Like other arachnids, pseudoscorpions feed by injecting digestive enzymes into their prey and then sucking out the dissolving tissue (Weygoldt 1969). External digestion enables *C. scorpioides* to exploit relatively large prey such as the dipteran and coleopteran larvae available in decaying trees. By contrast, such a feeding technique seems particularly ill-suited for specialization on the small mites resident on harlequin beetles.

LITERATURE CITED

Beck, L. 1968. Aus den Regenwäldern am Amazonas I. Natur und Mus., 98:24–32.

Beier, M. 1948. Phoresie und Phagophilie bei Pseudoscorpionen. Österreich. Zool. Z., 1:441–497.

Bookstein, F. L., B. Chernoff, R. L. Elder, J. M. Humphries, G. R. Smith & R. E. Strauss. 1985. Morphometrics in Evolutionary Biology: The Geometry of Size and Shape Change with Examples from Fishes. Acad. Nat. Sci. Philadelphia Spec. Publ. 15.

Chamberlin, J. C. 1931. The arachnid order Chelonethida. Stanford Univ. Publ. Biol. Sci., 7:1–284.

Duffy, E. A. J. 1960. A Monograph of the Immature Stages of Neotropical Timber Beetles. British Mus. Nat. Hist., London, U.K.

Muchmore, W. B. 1971. Phoresy by North and Central American pseudoscorpions. Proc. Rochester Acad. Sci., 12:79–97.

Ricklefs, R. E. 1979. Ecology, 2nd ed. Chiron Press, New York.

SAS Institute Inc. 1988. SAS/STAT User's Guide, Release 6.03 Edition. Cary, North Carolina.

Vachon, M. 1940. Remarques sur la phorésie des Pseudoscorpions. Ann. Soc. Ent. France, 109:1–18.

Weygoldt, P. 1969. The biology of pseudoscorpions. Harvard Univ. Press, Cambridge, Massachusetts.

Zeh, D. W. 1987. Life history consequences of sexual dimorphism in a chernetid pseudoscorpion. Ecology, 68:1495–1501.

Zeh, D. W. & J. A. Zeh. 1991. Novel use of silk by the harlequin beetle-riding pseudoscorpion, *Cordylochernes scorpioides* (Pseudoscorpionida, Chernetidae). J. Arachnol., 19:153–154.

Zeh, D. W. & J. A. Zeh. 1992. Dispersal-generated sexual selection in a beetle-riding pseudoscorpion. Behav. Ecol. Sociobiol., 30:135–142.

Zeh, D. W., J. A. Zeh & G. Tavakilian. 1992. Sexual selection and sexual dimorphism in the harlequin beetle *Acrocinus longimanus*. Biotropica, 24:86–96.

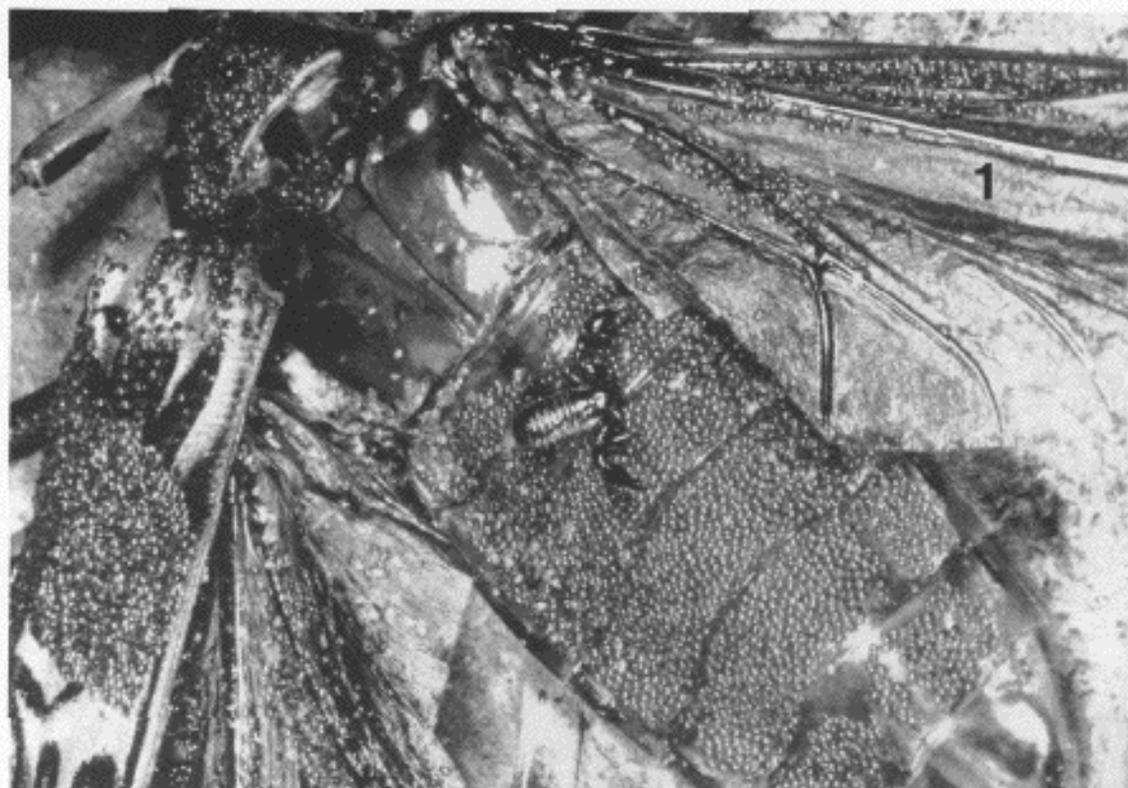*Manuscript received February 1991, revised April 1991.*

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