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Zeh, David Wayne

ECOLOGICAL FACTORS, PLEIOTROPY, AND THE EVOLUTION OF SEXUAL DIMORPHISM IN CHERNETID PSEUDOSCORPIONS

The University of Arizona PH.D. 1986

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ECOLOGICAL FACTORS, PLEIOTROPY, AND THE EVOLUTION OF SEXUAL DIMORPHISM IN CHERNETID PSEUDOSCORPIONS

by

David Wayne Zeh

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read the dissertation prepared by David Wayne Zeh

entitled Ecological Factors, Pleiotropy, and the Evolution of Sexual Dimorphism in Chernetid Pseudoscorpions

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

	11 Sept. 1986 Date
	9-11-86 Date
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Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

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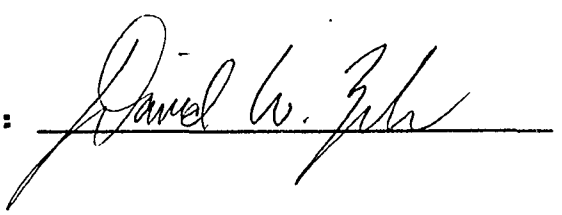
SIGNED: 

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ABSTRACT

The determinants of sexual dimorphism in a family of false scorpions (Pseudoscorpionida, Chernetidae) were investigated experimentally and with a literature analysis of comparative morphometric and habitat data. Species vary in the extent to which males and females differ in size of the conspicuous, prehensile pedipalps. Patterns within the Chernetidae suggest that dimorphism is a highly variable condition, relatively unconstrained by phylogenetic influences. The evolution of species with enlarged male pedipalps appears to be associated with a change from nonpairing to pairing sperm transfer behavior, and aggressive mate acquisition by males. Experiments with Dinocheirus arizonensis demonstrate a high correlation between male combat ability and chela size. Comparison of male and female life histories show prolonged development in males, and morphological comparisons implicate pedipalp dimorphism as a causative factor in this developmental rate difference. Prolonged development may be particularly costly to males, given the pattern of female sexual receptivity in this species. Females were found to become unreceptive soon after mating

and remain so throughout a protracted period of brood development. Experimental manipulations suggest that the male developmental rate cost is only outweighed under high density conditions when superior combat ability results in increased mating success. Repeated measures experiments failed to show any correlation between male pedipalp size and number of spermatophores accepted by a female. Parent-offspring regressions suggest the existence of additive genetic variance for male chela size and indicate a strong genetic correlation between this trait and cephalothorax length. Full-sib phenotypic correlations suggest that in D. arizonensis sexual divergence through sexual selection may be constrained by a high genetic correlation between males and females. Finally, the role of phoresy in the colonization of ephemeral, patchy habitats is investigated. Results support the hypothesis that attachment of pseudoscorpions to larger, more mobile arthropods represents a behavior functioning specifically for dispersal.

CHAPTER 1

SEXUAL SELECTION: AN OVERVIEW

Male animals produce small, motile sperm. Females produce large, nonmotile eggs. Because of this disparity, the sexes tend to differ in anatomical characteristics involved in copulation, gamete production and provisioning of offspring. In many species, however, males and females also differ in structures only secondarily associated with reproduction (Darwin 1871). For example, sexually dimorphic coloration is prevalent among birds (Selander 1972; Baker and Parker 1979), while in mammals (Ralls 1977; Alexander et al. 1979) and arthropods (Richards 1927; Ridley 1983) the sexes often differ in size. Members of one sex may even possess structures lacking in the other, e.g., antlers of deer stags (Clutton-Brock et al. 1982), bizarre eye stalks of male platystomatid flies (McAlpine 1979), or resonating air sacs of grouse cocks (Wiley 1974). These and other sexually dimorphic traits are thought to have evolved as a consequence of the economics of gamete production (see Parker 1984). Female reproductive success is usually limited by the resources available for egg production, whereas male reproductive

success is determined largely by the number of successful matings achieved (Bateman 1948; Trivers 1972). The mating tactics adopted by the sexes differ accordingly (Alexander and Borgia 1979; Parker 1983). The high cost of egg production predisposes females to safeguard their investment and discriminate between potential mates (Williams 1966). By contrast, the low cost of sperm production generally favors frequent, nonselective matings by males (for exceptions see Dewsbury 1982; Warner and Harlan 1982; Heiber and Cohen 1983; Gwynne 1984). Anisogamy tends to generate a bias in the operational sex ratio (ratio of receptive males to receptive females; Emlen and Oring 1977), with receptive females constituting the scarce resource for which males must compete.

Competing individuals are likely to vary in traits affecting their potential to achieve fertilizations. Through intrasexual competition and/or mate choice, (i.e., sexual selection, Darwin 1871), this existing variation in traits becomes realized as variation in male fertilization success (see Arnold 1983). If trait variation has a heritable basis (Falconer 1981), sexual selection may lead to the evolution of radical differences between the sexes (Lande 1980). Male-male competition as the force behind the evolution of enlarged male size and other traits related to combat ability has been well

established (Ghiselin 1974; Halliday 1983; Howard and Kluge 1985). However, the general significance of mate choice has been and continues to be the subject of much debate (e.g. Wallace 1889; Huxley 1938; Bateson 1983). Although sexual selection is frequently presented as the result of either choice or direct competition, in practice these processes are rarely mutually exclusive. Indeed, many dimorphic traits may well result from the complementary actions of male-male competition and female choice (Cox and Le Boeuf 1977; Borgia 1981). For this reason, the importance of female choice in sexual selection has proven difficult to assess (but see Downhower et al. 1983; Thornhill 1983; Kodric-Brown 1985).

Whatever the modus operandi, it is variation in reproductive success among individuals of one sex (usually males) that provides the raw material upon which sexual selection acts. The extent to which specialized adaptations for mate acquisition evolve in males (i.e., the degree of sexual dimorphism) should be determined in part by the extent to which males and females diverge in variance of reproductive success (Wade 1979; Wade and Arnold 1980; Arnold and Wade 1984). Genetic differences and environmental factors such as nutrition do inevitably generate a certain level of variation in both males and females (Kodric-Brown and Brown 1984). However, in males

this basic variability is augmented by variation in the number of successful matings achieved.

CHAPTER 2

AGGRESSION, DENSITY AND SEXUAL DIMORPHISM IN CHERNETID PSEUDOSCORPIONS

One approach to understanding the evolution of sexual dimorphism through sexual selection lies in an investigation of the factors influencing variation in male mating success (Orians 1969). In general, males endeavor to maximize number of matings by competing for females or for monopolization of the resources critical to female reproduction (see Williams 1975). Theory in behavioral ecology suggests that ecological constraints influence the extent to which males are successful in achieving these ends (Verner and Willson 1966; Orians 1969; Trivers 1972; Bradbury and Vehrencamp 1977; Emlen and Oring 1977; Borgia 1979; Wittenberger 1979; Thornhill and Alcock 1983). It is argued that spatial distribution of mates and/or resources and temporal patterns of female receptivity are of primary importance. Low density, uniform habitats and synchronous, short duration of female receptivity are predicted to be associated with sexually monomorphic species, since they render control by males either impossible or unprofitable. High density, patchy

habitats and asynchronous female receptivity, on the contrary, make monopolization by males possible, and should be associated with sexually dimorphic species.

In order to test the hypothesis that ecological factors constrain the extent to which sexual selection can operate, this paper documents patterns of sexual pedipalpal dimorphism in one family of pseudoscorpions, the Chernetidae. A conspicuous feature of all pseudoscorpions is their large, chelate pedipalps which serve as organs of prey capture (Chamberlin 1931). In the family Chernetidae, males invariably also use their pedipalpal chelae to forcefully grasp and maneuver females during spermatophore transfer (Weygoldt 1966a,b, 1969, 1970; Thomas and Zeh 1984; see Chapter 3). Various aspects of their biology make chernetids particularly suitable organisms for the study of sexual dimorphism. 1) They occupy a diversity of habitats, ranging from forest litter to clumps of rotting desert vegetation. 2) They occur at a wide range of population densities. 3) They exhibit varying degrees of sexual dimorphism in their pedipalpal chelae (see Chamberlin 1931; Muchmore 1974a; Fig. 1). 4) Sexual differences in chela size and morphology, if present, are primarily restricted to the adult stage (Weygoldt 1969; Chapter 5). Once adult, the individual undergoes no further molting.

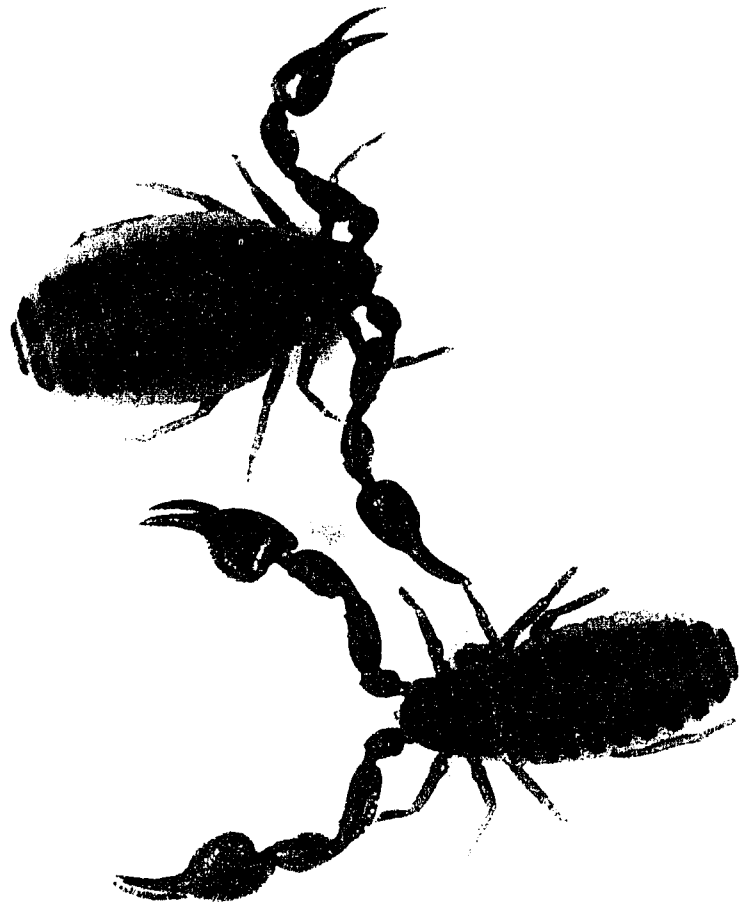


Fig. 1. Comparative Photographs of Male and Female Dinocheirus arizonensis.

Consequently, adult chela size (as measured for purposes of this paper, see Materials and Methods) is fixed and independent of age. 5) Postzygotic maternal investment is high (Chamberlin 1931; Weygoldt 1969; Zeh and Smith 1985), and females remain unreceptive throughout the development of their embryonic young (Chapter 3) which are nourished in a brood sac connected to the genital aperture. Since paternal care is absent, this female investment pattern tends to result in a highly biased ratio of receptive males to receptive females (operational sex ratio, Emlen and Oring 1977; reviewed by Sutherland 1985). In conjunction with patchy habitat utilization, this biased operational sex ratio is predicted to generate intense competition among males.

A literature analysis of the distribution of dimorphism among North American chernetid genera is presented, and the relationship between sexual dimorphism, body size and density is examined. Experimental manipulations are then used to evaluate the functional significance of dimorphic pedipalps in Dinocheirus arizonensis (Banks). This highly dimorphic chernetid species (Figs. 2 and 3) utilizes the ephemeral and spatially discontinuous habitat provided by rotting saguaro cacti (Carnegiea gigantea [Engelm]) in the Sonoran Desert. This research integrates experimental work

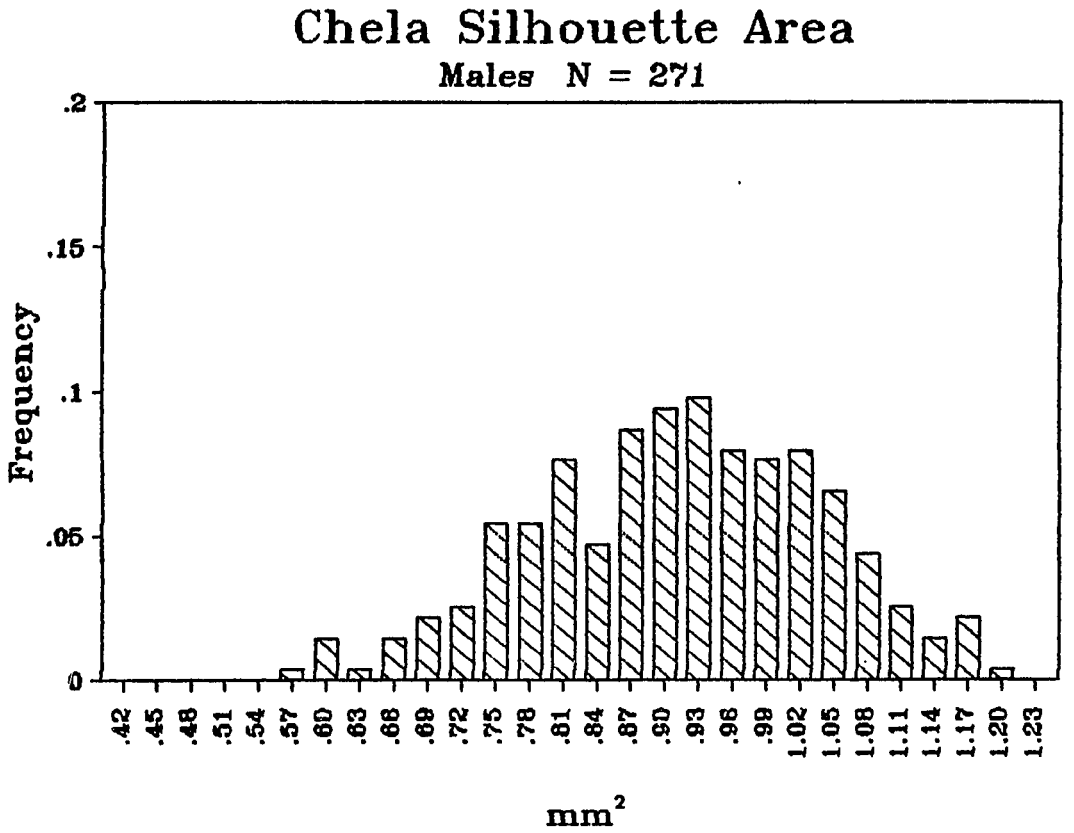


Fig. 2. Histogram of Male Chela Silhouette Area. Mean ± SE = 0.911 ± .008 mm².

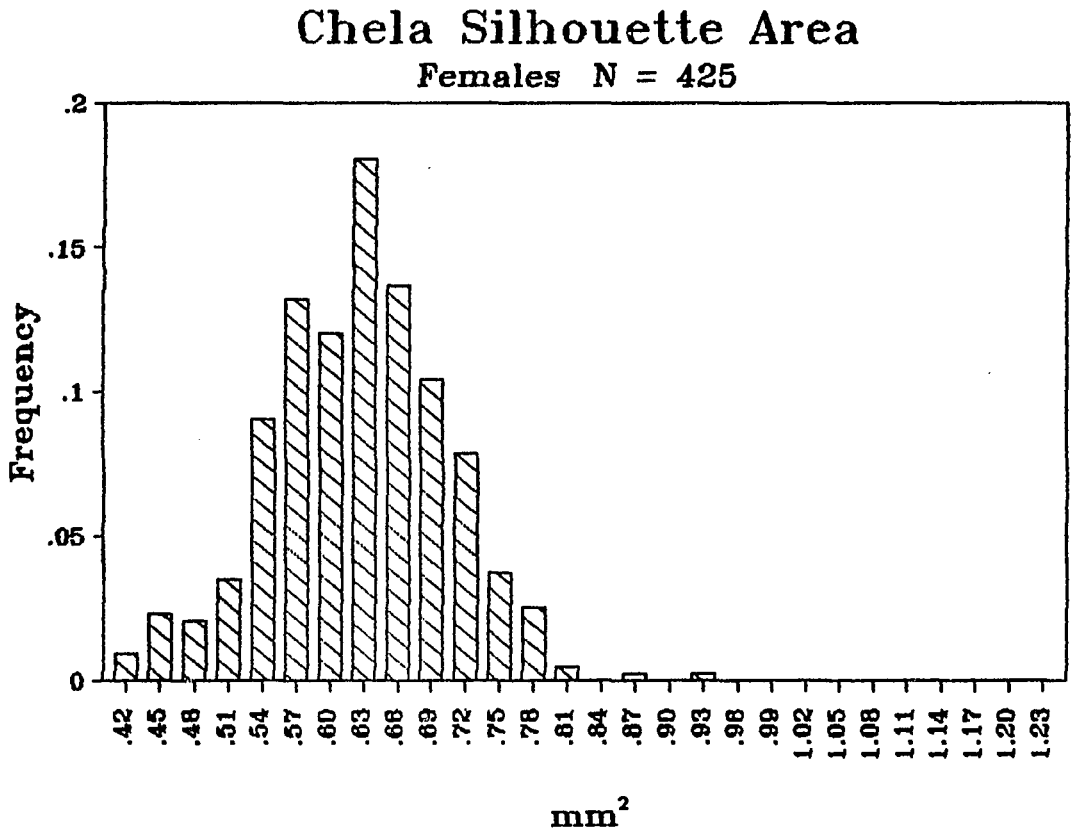


Fig. 3. Histogram of Female Chela Silhouette Area. Mean ± SE = .625 ± .004 mm².

on the behavior of a single species with comparative data on patterns of sexual dimorphism in the family as a whole. By combining analyses at two levels, the study attempts to assess the significance of behavior and ecology in the distribution of a sexually dimorphic trait among a clade of pseudoscorpion species.

Materials and Methods

In both the literature analysis and the experimental study, degree of sexual dimorphism was assessed in terms of difference between male and female chela (pincer) silhouette area (see below). The biological grounds for focusing on this trait rather than on some measure of body size such as cephalothorax length are as follows: first, the chelae function directly in male aggression (Thomas and Zeh 1984) and mate capture (Weygoldt 1969; Chapter 3), and are composed primarily of muscle tissue (Chamberlin 1931); second, across species, enlarged male chelae are not simply the allometric correlate of enlarged male body size (see Table 1); third, detailed morphological study of D. arizonensis has demonstrated that this trait provides a highly accurate measure of the proportions of nymphal soma allocated to body and pedipalps in the adult pseudoscorpion (Chapter 5); finally, in D. arizonensis sexual differences in total

Table 1. Comparison between Males and Females for Carapace Length and Chela Silhouette Area among North American Species of Chernetidae.

Character Measured	Number of species in which: Male Larger	Female Larger	Ties
A) Carapace Length	8	30	7
B) Chela Silhouette area	28	24	0

weight result entirely from the greater mass of the male pedipalp, and sexual chela differences account for 80% of this sexual disparity in pedipalp weight (Chapter 5).

Literature Analysis of North American Chernetidae

Generic Status, Scaling and Sexual Dimorphism. A list of all species inhabiting continental North America north of Mexico was compiled with the aid of Hoff (1958) and W.B. Muchmore (personal communication). The original data set consisted of 23 genera and 74 species. Only genera with two or more species, for which data included male and female morphometrics, were treated in the statistical analyses: a total of 10 genera and 51 species (Appendix 1). For each species and sex, chela silhouette area was estimated as the product of mean length and depth of the chelal hand (see Chamberlin 1931 for methods). Although detailed hand measurements are included in published species descriptions, frequently only the ranges for each sex and not the means are given. In these cases, the mean was interpolated as the midpoint of the range. The sexual difference in chela silhouette area (log [male chela silhouette area minus female chela silhouette area]) was then used as the measure of chelal dimorphism. When morphometric data for both males and females were available from multiple references, measurements were

weighted by sample size to determine average values for species. A one-way analysis of covariance (ANOCOVA) was used to partition variation in sexual dimorphism with genera as factor levels and log [female chela silhouette area] as a covariate (BMDP-83 P1V, Dixon 1983). A constant (1) was added prior to log-transformation of variables to eliminate undefined values.

Population Density and Sexual Dimorphism. Hoff's studies on the pseudoscorpions of Illinois, New Mexico and Colorado (1949, 1956, 1959, 1963) provided data on density for approximately 50% of the species used in this analysis. Other important sources included Benedict and Malcolm (1982), Nelson (1975), Hoff and Clawson (1952), and Chamberlin (1952). Unfortunately, sampling methods vary between species and among investigators. It was assumed that inconsistent sampling between species was random with respect to the true relationship between sexual dimorphism and density. This inconsistency probably contributed to error variance, thereby reducing the power of the test. Because of probable lower error variance associated with sampling from discrete habitats, data analysis was also conducted on a subset consisting of nest-inhabiting species. Density was calculated by dividing total individuals collected (adults and nymphs) by number of collections (see Appendix 1) and was

determined for 42 of the 51 species. Ambiguous data (e.g., "great numbers" in one of six collections of Acuminochernes crassopalpus, Hoff 1949) were excluded from the analysis. A stepwise linear regression (BMDP-83, P2R) was performed with log [density] and log [female chela silhouette area] as independent variables, and chelal dimorphism (log [male chela silhouette area minus female chela silhouette area]) as the dependent variable.

Experiments with Dinocheirus arizonensis

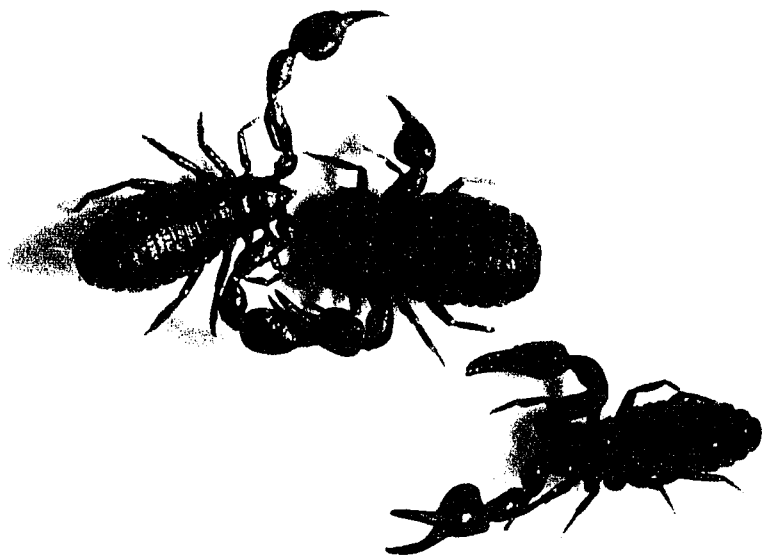
All experiments were carried out with pseudoscorpions collected from natural populations in the vicinity of Tucson, Arizona. Experiments were conducted in the laboratory because of the difficulties associated with observing behavior in the field. Since males and females readily mate in encounter arenas, and females produce offspring which develop to maturity under laboratory conditions, it was assumed that these results reasonably depict processes occurring in the field. Only individuals in apparent vigorous physical condition were utilized in the experiments. Those incapable of rapidly righting themselves when overturned were excluded. Healthy individuals were kept in isolation with ample food (Drosophila melanogaster) and moisture for an adjustment period of at least 24 hr.

Male Aggression and Relative Chela Size.

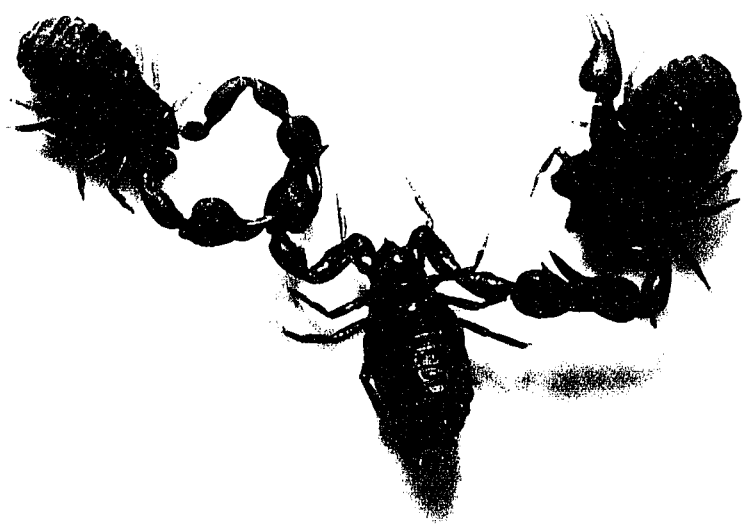
Collections were made between March 1980 and February 1981. Twenty-three pairs of males (46 different individuals) were chosen randomly and possible territorial influences on behavior were avoided by simultaneously introducing two individuals into a 50 mm diameter petri dish. When three aggressive encounters between the males had been observed, the identities of the aggressor and the subordinate were recorded. During the last 19 of these trials, combat duration was also recorded. On completion of the experiments, chela size was measured. Males were anesthetized with CO_2, and camera lucida outlines were made of a lateral view of the right chelal hand with the aid of a Wild M5D stereomicroscope. The silhouette area of the chelal hand was calculated by planimetry of the outline.

Effects of Relative Chela Size and Density on Mating Success. Individuals were collected as tritonymphs (the third and final nymphal stage) between September and November 1983, and underwent their terminal molt in isolation to ensure virginity. Anesthetized individuals were marked on the cephalothorax or abdominal tergites with nontoxic paint (see Fig. 4 in Thomas and Zeh 1984). Chela size was determined by the camera lucida/planimetry method, and 40 males were ranked from smallest to largest

on the basis of chela size. Males were then divided into two groups: ranks 1 to 20 = "small;" ranks 21 to 40 = "large." To maintain an approximately constant difference between the chela sizes of large and small males in each replication, small individuals with ranks 1 through 4 were matched with large individuals with ranks 21 through 24, and so on. Within each replication, density treatments were randomly assigned to experimental units. No systematic color coding scheme was used to differentiate between large and small males to avoid possible observer bias. Two large and two small males were added to an observation chamber containing two females, and interactions were observed for a period of one hour. For each male the following data were recorded: 1) attack behaviors (against males, females, and/or mating pairs); 2) successful displacements of males engaged in mating (= "takeovers", see Fig. 4), and 3) number of spermatophores transferred (see Chapter 3 for detailed discussion of sperm transfer behavior). In these observations, number of spermatophores deposited was equated with number of spermatophores actually transferred to the female. Male positioning of the female over the spermatophore after deposition makes direct observation of transfer difficult (personal observation). However, the assumption was partially tested by isolating post-experimental females in



A



B

Fig. 4. Mating Competition in D. arizonensis. A) Lone male at lower right approaches mating pair. B) Lone male (at upper left) grasps chela of paired male (at lower center) in an attempted mating takeover. The paired male maintains his grasp on the chela of the female (at upper right).

environments conducive to brood sac development. Nineteen of 20 mated females produced broods, indicating that insemination had occurred in nearly every case. The effect of density on these variables was examined by varying the size of the observation chamber. The low density treatment utilized an arena of 60 cm^2, while the high density treatment took place in an area of 30 cm^2. Five replications at each density were carried out. A two-way ANOVA (BMDP-83, P2V, Dixon 1983) on summed output of each size class was used to assess the effects of relative chela size and density. In order to stabilize variance, data on spermatophores transferred and takeovers were $\sqrt{[Y + 0.5]}$ transformed for statistical analysis (where Y = value of dependent variable; see Sokal and Rohlf 1981).

Results

Literature Analysis of North American Chernetidae

Generic Status, Scaling and Sexual Dimorphism. A graph of the distribution of chelal dimorphism among chernetids illustrates wide variation in levels of dimorphism within genera (Fig. 5). In Fig. 5, a ratio measure of sexual dimorphism is used only to facilitate visual comparison. Although mean levels of dimorphism

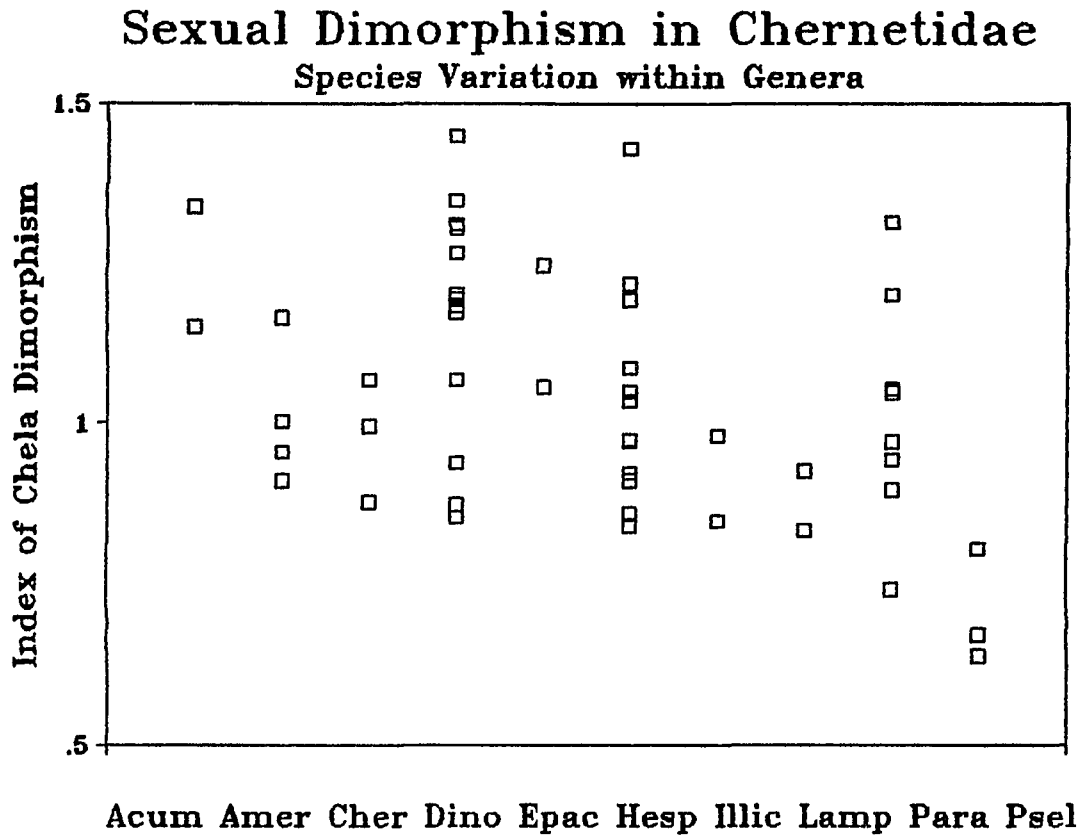


Fig. 5. Patterns of Sexual Dimorphism in Chernetidae: Species Variation within Genera. Abbreviations for genera as follows: Acum = Acuminochernes; Amer = Americhernes; Cher = Chernes; Dino = Dinocheirus; Epac = Epactiochernes; Hesp = Hesperochernes; Illic = Illichernes; Lamp = Lamprochernes; Para = Parachernes and Psel = Pselaphochernes.

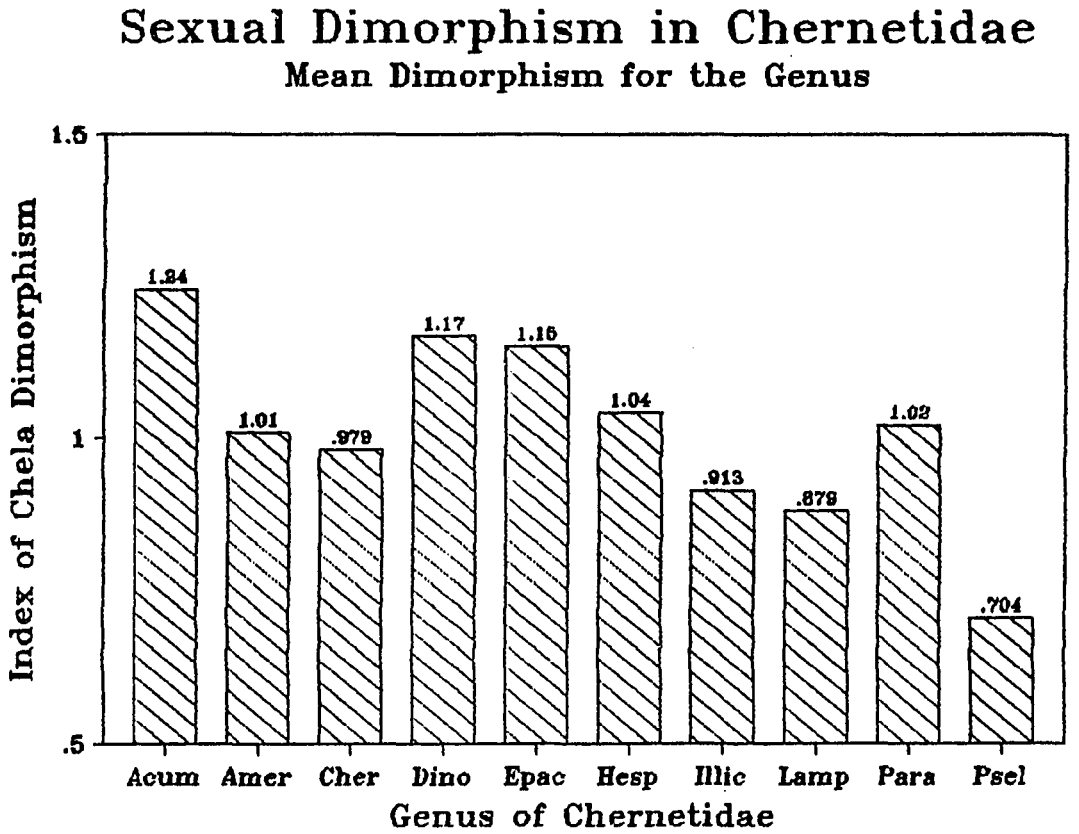


Fig. 6. Patterns of Sexual Dimorphism in Chernetidae: Mean Dimorphism for the Genus. Abbreviations as in Fig. 5.

differ somewhat between genera (Fig. 6), these differences are not significant, especially when the relationship between dimorphism and female chela silhouette area is taken into account (Table 2, ANOCOVA: $F_{9,40} = .9408$, $P = .502$). Sexual differences in chela silhouette area increase with female chela size (regression coefficient = .279, $F_{1,40} = 10.53$, $P = .0024$), indicating that larger species tend to be more dimorphic (Fig. 7). Female chela size is highly correlated with cephalothorax length, i.e., with overall body size ($r = .921$, $P << .001$). The slopes of dimorphism versus female chela size do not differ between genera ($F_{9,31} = .5651$, $P = .815$). Finally, differences between generic means for sexual dimorphism are only marginally significant if female chela size is not included as a covariate in the analysis (ANOVA: $F_{9,41} = 1.8253$, $P = .0927$).

Population Density and Sexual Dimorphism. A weak but significant correlation exists between dimorphism and density ($r = .305$, $P = .047$). Taken together in a stepwise linear regression, female chela size and density account for 36% of the total variation in sexual dimorphism (see Table 3, $F_{2,39} = 10.89$, $P = .0002$). If the regression analysis is restricted to species collected from nests, the partial correlation of density with dimorphism increases from .266 to .384 (Table 3), and female chela

Table 2. Comparison of Generic Means for Sexual Dimorphism.

A) Analysis of Covariance with female chela silhouette area as the covariate. B) Analysis of variance on same data without including the covariate.

Source	SS	df	MS	F	P
A) ANOCOVA					
Between Genera	.0025	9	.0003	.9408	.5015
Covariate (Slope)	.0031	1	.0031	10.5262	.0024
Error (Among Species)	.0118	40	.0003		
Equality of Slopes	.0017	9	.0002	.5651	.8147
Error	.0101	31	.0003		
B) ANOVA					
Between Genera	.0060	9	.0007	1.8253	.0927
Error (Among Species)	.0149	41	.0004		

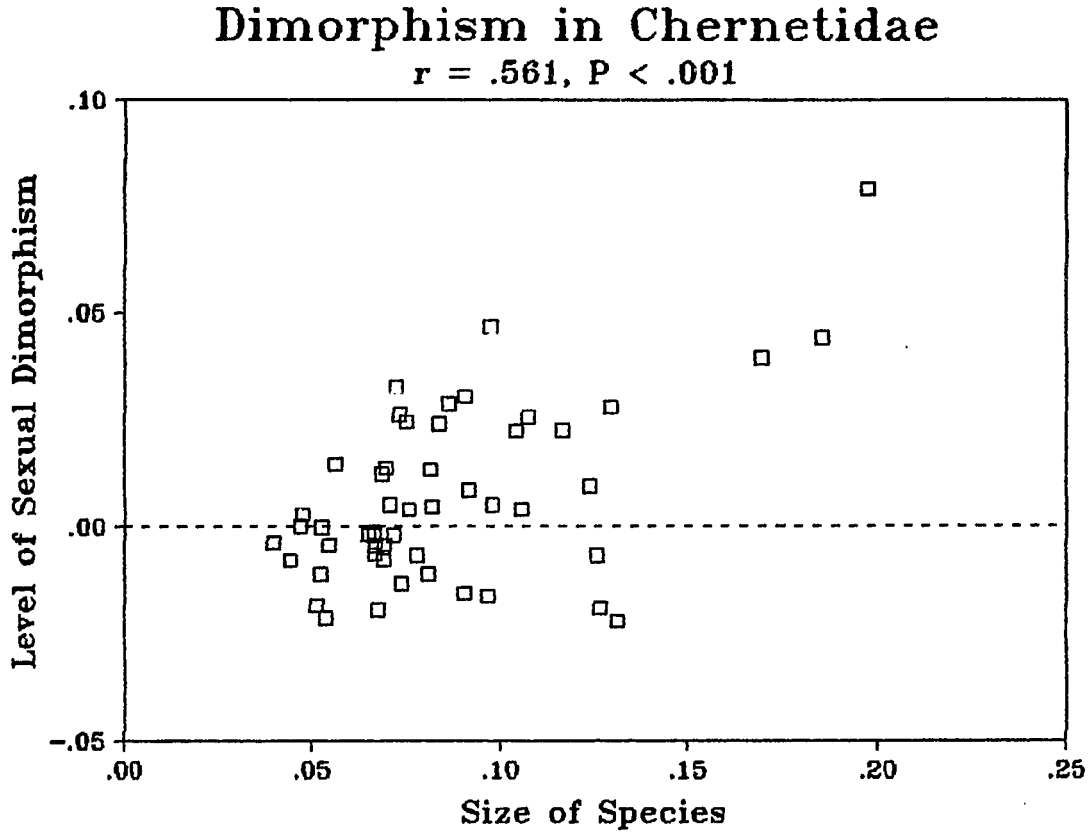


Fig. 7. Level of Sexual Dimorphism versus Size of a Species in Chernetidae. Size = log (female chela silhouette area + 1) and level of sexual dimorphism = log [(male minus female chela silhouette area) + 1].

size and density account for a greater proportion of total variance in dimorphism (R^2 = .543, $F_{2,8}$ = 4.76, $P < .05$, see Appendix 1 for raw data).

Experiments with Dinocheirus arizonensis

Male Aggression and Relative Chela Size.

Encounters between males invariably result in aggression, consisting of a two-step sequence (for photographs, see Thomas and Zeh 1984:Fig. 4). Upon approach, males halt and engage briefly (< 5 seconds) in an apparent appraisal of one another, involving slow, jerking movements of their raised chelae. Then, sudden, forceful grasping of each other's chelae is followed by a chela-pulling struggle, as each male attempts to gain a solid hold (this sudden grasping behavior will subsequently be referred to as "attack"; similar forms of male aggressive behavior have been observed in other chernetids, e.g., Weygoldt 1966a,b 1969). One individual is eventually overpowered, and either flees by pulling away or submits by remaining motionless. The quantitative results demonstrate a strong association between chela size and fighting ability: males with larger chelae were dominant in 18 of the 23 encounters (X^2 = 7.35, $P < .01$, Table 4). This relationship becomes more apparent when outcomes are categorized by difference in chela silhouette area of the two combatants

Table 3. Summary of Stepwise Linear Regression Indicating Correlations between Sexual Dimorphism and Density or Size of a Species.

A) Analysis based on entire data set. B) Analysis restricted to species collected from nests.

Source	SS	df	MS	F	P
A) DATA FROM ALL COLLECTIONS					
Regression	.0066	2	.0033	10.89	.0002
Residual	.0118	39	.0003		
Multiple R = .5986					
Multiple R^2 = .3583					
Partial Correlations with Sexual Dimorphism					
Variable:	Density		Female Chela Silhouette Area		
Regression Step					
0	.3055		.5563		
1	.2660		.5563		
2	.2660		.5406		
B) COLLECTIONS FROM NESTS					
Regression	.0016	2	.0008	4.76	<.05
Residual	.0013	8	.00017		
Multiple R = .7370					
Multiple R^2 = .5432					
Partial Correlations with Sexual Dimorphism					
Variable:	Density		Female Chela Silhouette Area		
Regression Step					
0	.6665		.6812		
1	.3843		.6812		
2	.3843		.4220		

Table 4. Morphological Traits as Predictors of Male Aggressive Ability in *D. arizonensis*.

Trait	Number of Encounters in Which Trait of Dominant Male Was		X^2(1 df)
	Larger	Smaller	
Chela Silhouette Area	18	5	7.35 (P < .01)
Cephalothorax Length	15	8	2.13 (P > .10)
Total Body Length	13	10	.393 (P >.50)

(Fig. 8). Dominance by males with smaller chelae occurred only when chela differences were slight. Furthermore, the duration of the struggle between males is inversely related to the difference in their chela size (Fig. 9). Total body length is a poor predictor of aggressive ability (X^2 = .391, n.s., Table 4) and is only weakly correlated with chela silhouette area (Chapter 5). Although cephalothorax length is significantly correlated with chela silhouette area (Chapter 5), it is a less reliable indicator of aggressive ability (X^2 = 2.13, $P > .10$).

Effect of Relative Chela Size and Density on Mating Success. Examination of main effects reveals that number of spermatophores transferred is significantly affected by relative chela size ($F_{1,16} = 17.23$, $P = .0008$) i.e., males with large chelae transfer more spermatophores (Tables 5 and 6). However, the significant interaction between density and relative chela size ($F_{1,16} = 12.58$, $P = .0027$) and the simple comparisons of the effects of relative chela size (low density: $F_{1,16} = .0915$, n.s.; high density: $F_{1,16} = 14.81$, $P < .01$) indicate that size advantages are manifested only at high density (see Table 6). The greater success in spermatophore transfer among large males apparently results from both their higher attack rates ($F_{1,16} = 3.05$, $P = .100$), and greater ability

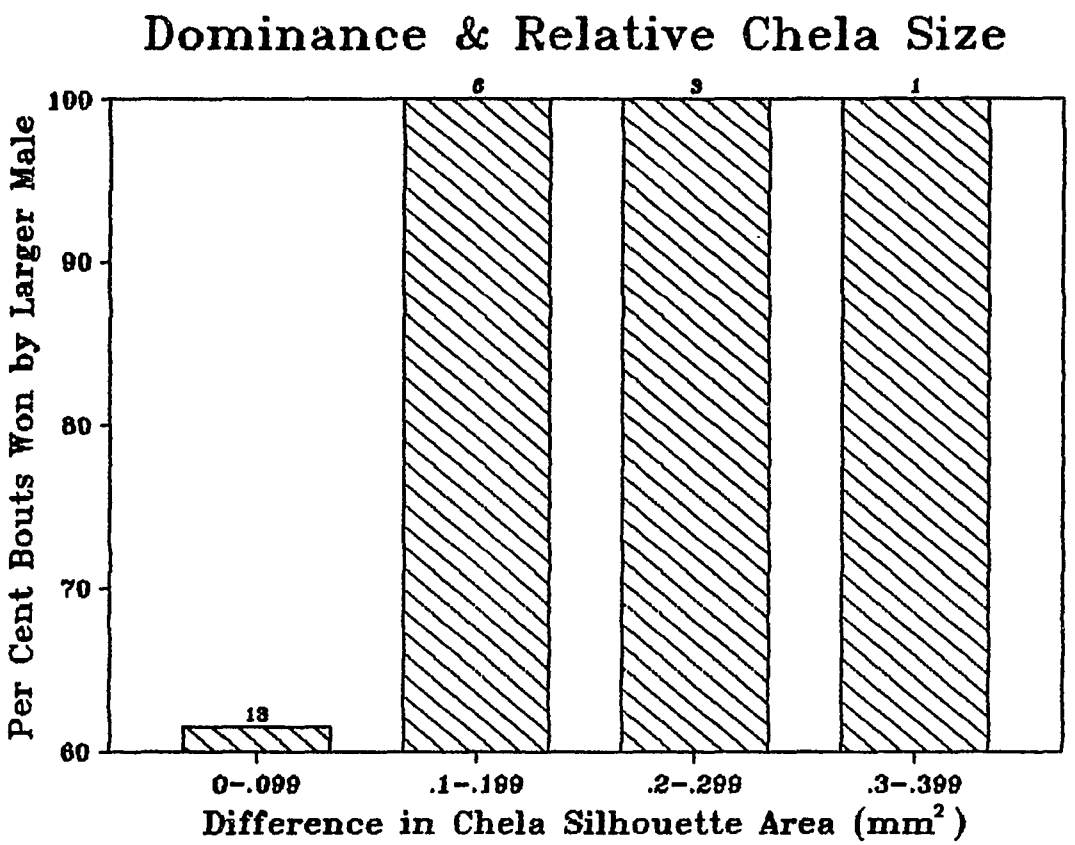


Fig. 8. Dominance and Relative Chela Size. Bar graph categorizing percent of encounters in which males with larger chelae were dominant by difference in chela sihouette area of two combatants. Numbers above bars indicate sample size.

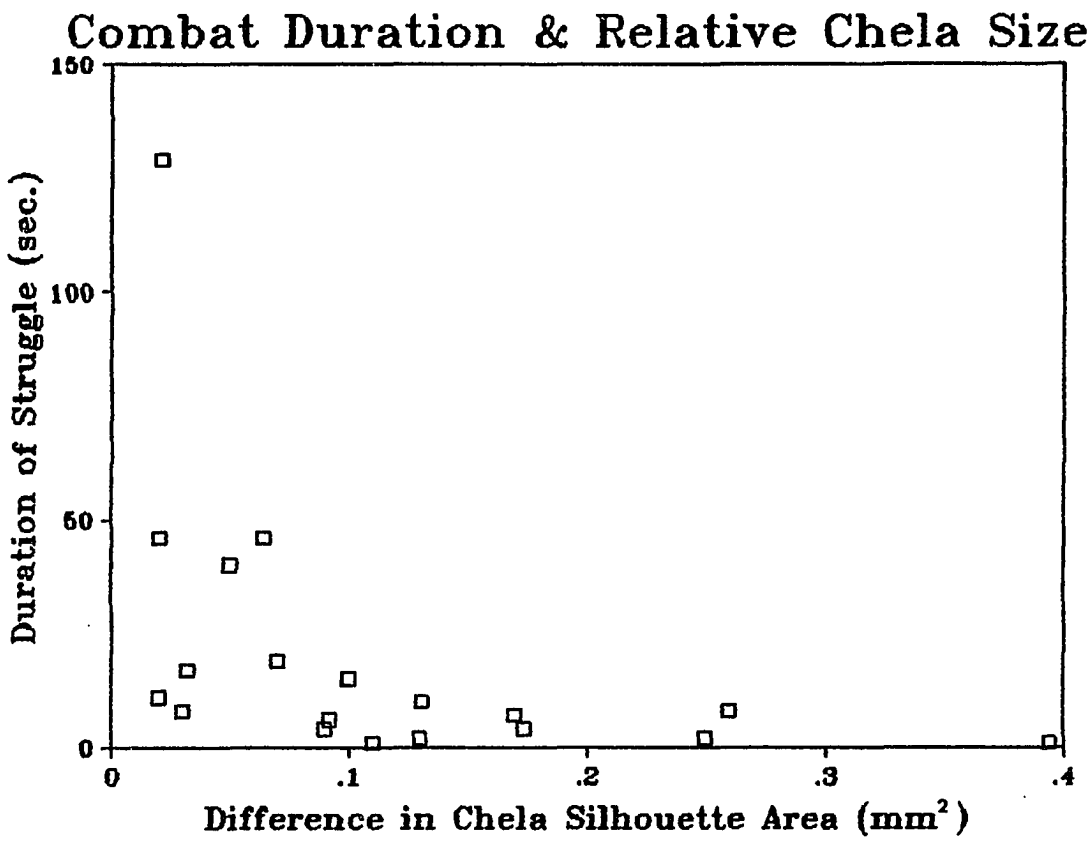


Fig. 9. Combat Duration and Relative Chela Size. Duration of struggle between males as a function of difference in their chela silhouette areas. For log-transformed data, $R^2 = 0.442$, N = 19.

to displace other males through takeovers ($F_{1,14} = 9.23$, $P = .0064$).

Discussion

The literature analysis revealed that pedipalpal dimorphism in the family Chernetidae is a highly variable condition with male chela silhouette area ranging from 60% to 150% of that of the female. Partitioning of the variation into between- and within-genera components indicates that sexual dimorphism is not well defined along taxonomic lines. Since the distribution of this character is inconsistent with the phylogeny, it seems valid to conclude that historical origins are unlikely to have strongly influenced patterns of dimorphism in these species (see Dobson 1985). Moreover, the extreme variability in levels of dimorphism within genera (Fig. 5) suggests that this conclusion would be robust to modifications in the phylogeny of the group. Historical factors (i.e., descent from a common ancestor) could, of course, account for sexual dimorphism in those chernetids not included in this analysis, such as the monotypic genera. Cladistic investigation of the hierarchical relationships between all genera in the family would enable a more precise assessment of the role of historical factors in chernetid sexual dimorphism (see Eldredge and

Table 5. Two-way ANOVA Summary of the Main and Interactive Effects of Relative Chela size (Relchela) and Density.

A) number of spermatophores transferred (Nsperm); B) number of attack behaviors (Attacks) and C) number of successful takeovers (Takeovers)(see Methods for definitions).

Source	SS	df	MS	F	P
A) NSPERM					
Density	.1163	1	.1163	2.54	.1309
Relchela	.7904	1	.7904	17.23	.0008
D X R	.5768	1	.5768	12.58	.0027
Error	.7339	16	.0459		
B) ATTACKS					
Density	31.25	1	31.25	3.05	.1000
Relchela	31.25	1	31.25	3.05	.1000
D X R	1.25	1	1.25	.12	.7315
Error	164.00	16	10.25		
C) TAKEOVERS					
Density	.07036	1	.07036	.63	.4387
Relchela	1.09624	1	1.09624	9.23	.0064
D X R	.24676	1	.24676	2.21	.1563
Error	1.78445	16	.11153		

Table 4. Treatment Means ± SE for Two-way ANOVA Experiment on Behavioral Effects of Density and Relative Chela Size.

Abbreviations as defined in Table 3.

	LOW DENSITY			HIGH DENSITY		
RELCHELA	Nopers	Attacks	Takeovers	Nopers	Attacks	Takeovers
SMALL	1.8 ± .85	6.0 ± 1.4	.55 ± .39	.40 ± .85	9.0 ± 1.4	.55 ± .39
LARGE	8.0 ± .85	9.0 ± 1.4	.84 ± .39	8.60 ± .85	11.0 ± 1.4	1.34 ± .39

Cracraft 1980; Ridley 1983; Carothers 1984).

Across chernetid species, sexual dimorphism was found to vary positively with size (as measured by female chela silhouette area). This relationship is pervasive among animal taxa and has been attributed to both adaptive (Clutton-Brock 1985) and nonadaptive causes (Huxley 1932; Maynard Smith 1978). Recent quantitative genetic models suggest that genetic correlations between the sexes can greatly restrict the evolution of sexual dimorphism, especially when selection is weak and environmental fluctuations prevent attainment of genetic equilibrium (Lande 1980). In D. arizonensis preliminary quantitative genetic studies have provided evidence of such a genetic correlation for chela size between the sexes (Chapter 5). Most recently, Leutenegger and Cheverud (1982, 1985) have proposed the variance dimorphism hypothesis to explain the correlation between size and dimorphism within clades. According to this view, greater trait variance in one sex (males) would enable that sex to respond more strongly to directional selection. Paradoxically, even in the absence of sexual selection, natural selection for increased size in both sexes could transform an originally monomorphic species into a dimorphic one.

Although nonadaptive causes (genetic correlation between the sexes, see Chapter 5) may be implicated

in the size-dimorphism correlation within the Chernetidae, variance dimorphism does not appear to have played a significant role. Evidence bearing on this question comes from the relationship between size and dimorphism in the Cheiridioidea (Fig. 10), a group closely related to the Chernetidae (Weygoldt 1966b). Males in this taxon deposit structurally simple spermatophores on the substrate, and do not physically interact with the female during sperm transfer (Weygoldt 1966b, 1969, 1970; Thomas and Zeh 1984). Sexual dimorphism is common in these nonpairing species: males are <u>smaller</u> than females (Chamberlin 1931; see Fig. 10). Enlarged male size is virtually unknown in the Cheiridioidea and, moreover, there is a highly significant relationship between species' size and sexual dimorphism ($r = -.947$, $P < .001$; data in Appendix 2). The larger the species, the smaller is the male relative to the female. This relationship contradicts the prediction of the variance dimorphism hypothesis which assumes a greater variance in males (Cheverud et al. 1985). Natural selection for smaller size, acting on a subset of monomorphic species, should produce a lineage in which males smaller than females occur in smaller-sized species. Rather, the negative correlation in Cheiridioidea between species' size and size of male relative to female suggests that reduced male size is the result of sexual selection

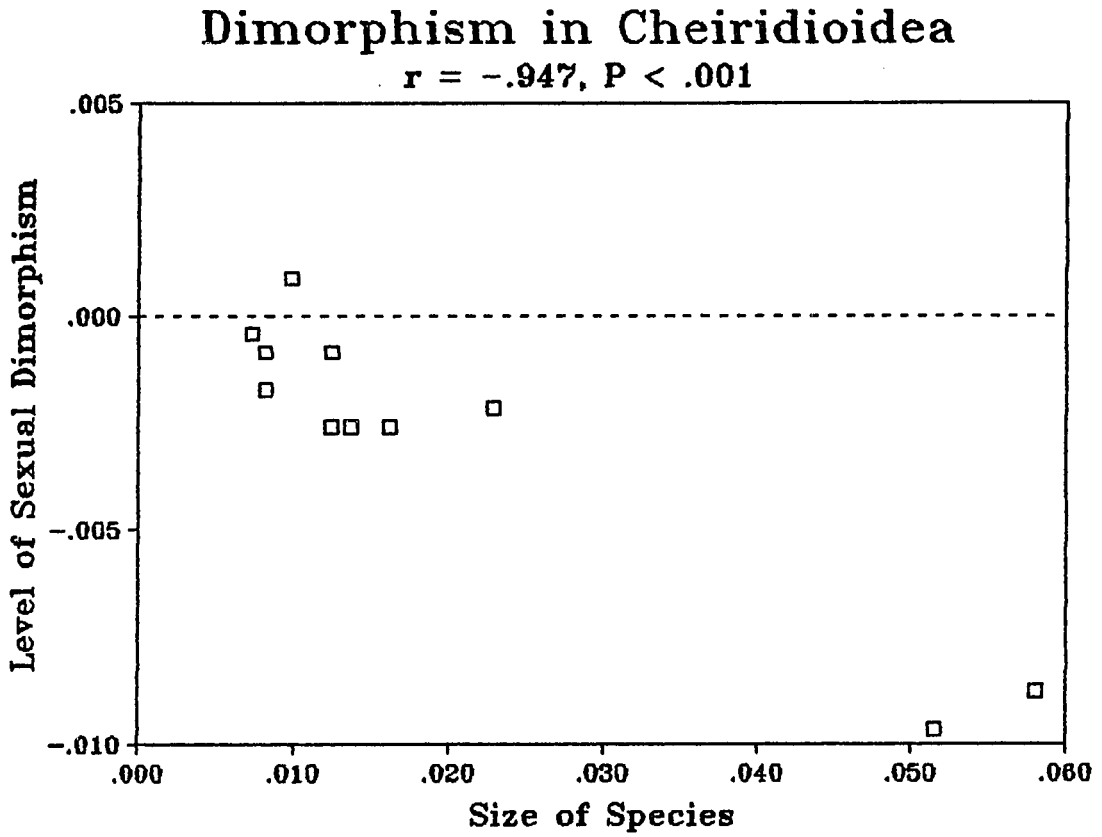


Fig. 10. Level of Sexual Dimorphism versus Size of Species in Cheiridioidea. Size = log (female chela silhouette area + 1) and level of sexual dimorphism = log [(male minus female chela silhouette area) + 1].

acting uniformly on cheiridioidean species. Consistent with this interpretation is the nonsignificant relationship between size and dimorphism in Cheiridioidea when a ratio measure of sexual dimorphism is used ($r = -.273$, $P = .377$). It is hypothesized that small male size is a consequence of sexual selection for more rapid development in males, thereby increasing the probability that spermatophores are encountered by receptive females (Thomas and Zeh 1984; Zeh and Smith 1985; also see Wiklund and Fagerstrom 1977). Nonpairing behavior is generally considered to represent an ancestral condition in pseudoscorpions (Chamberlin 1931; Beier 1932; Weygoldt 1966b; Schaller 1979). An outgroup comparison (see Maddison et al. 1984) with the Cheiridioidea suggests that sexual dimorphism in the form of smaller males is the primitive condition in Chernetidae. The evolution of species with enlarged male pedipalps following a change from nonpairing to pairing behavior strongly implicates sexual selection as a cause of chernetid dimorphism.

Results of the experiments reported here on Dinocheirus arizonensis provide evidence that sexual selection in the form of male combat has been a significant force in the evolution of sexual dimorphism, and that male aggressive ability is reliably predicted by relative chela size. Processes other than sexual selection

could explain such sexual divergence in morphology (see Price 1984). For example, direct ecological forces could lead to sexual divergence, if dimorphism resulted in reduced competition and increased foraging efficiency in members of a breeding pair (Temeles 1985). This mechanism can be eliminated as a cause of chernetid dimorphism since in pseudoscorpions social bonds approaching this complexity are known only in the family Atemnidae (Brach 1978). A recent genetic model by Slatkin (1984) suggested that ecological forces (e.g., competition for food), acting directly on each sex, could not only maintain but actually provide the initial impetus for sexual differences in a quantitative character. It seems unlikely, however, that enlarged male chelae in chernetids have evolved to reduce competition between males and females. Dimorphism is primarily restricted to the adult stage (Chamberlin 1952; Weygoldt 1969; Chapter 5) whereas feeding by males is most intense during nymphal stages when the sexes are morphologically similar. Experimental work on D. arizonensis also indicated that the mating advantage conferred by large chelae depends strongly on density. This relationship is explicable in terms of 1) aggressive mate acquisition behavior of males and 2) methods of sperm transfer and characteristics of mating behavior (see Thomas and Zeh

1984; Chapter 3). In the absence of competition, mating events, involving the transfer of multiple spermatophores, may last as long as two hours (Chapter 3). Males generally seem unable to distinguish sex without contact, and use their pedipalpal chelae to forcefully grasp the chelae of any individual encountered (see Fig. 4). In probabilisitic terms, the potential for takeovers of mating pairs by large males must increase with density. Similar effects of density on mating success have been reported for dung flies (Borgia 1980) and wood frogs (Howard and Kluge 1985). Ghiselin (1974) has argued that throughout the animal kingdom density increases the importance of male combat, and consequently acts as a primary determinant of male reproductive tactics. If this density effect has been a significant factor in the evolution of sexual dimorphism in Chernetidae, then dimorphic species should occur at higher local population densities than monomorphic species, especially during breeding periods. A positive correlation between density and dimorphism was, in fact, detected in the comparative analysis of chernetid species.

In the Chernetidae pairing behavior involving aggressive capture of mates (Weygoldt 1966a,b, 1969; Chapter 3) provides the potential for male combat to become a significant selective force for increased chela size. The fact that in many chernetid species males are

smaller than females indicates that pairing is not the sole factor determining levels of dimorphism. Studies of the life history consequences of dimorphism suggest that another decisive factor may be the cost of enlarged male chela size in terms of prolonged development (Chapter 5). This developmental rate cost seems particularly acute, given the pattern of female sexual receptivity in D. arizonensis. Females become unreceptive soon after mating and remain so throughout an extensive period of brood sac development (Chapter 3). The findings reported here suggest that it is only at high density that this cost of sexual dimorphism is outweighed by the benefit of increased male mating success.

CHAPTER 3

AN EXPERIMENTAL STUDY OF FEMALE SEXUAL RECEPTIVITY

Male competition as the force behind the evolution of enlarged male size and other traits related to combat ability has been well established (Ghiselin 1974; Halliday 1983; Howard and Kluge 1985). However, the general significance of mate choice has been and continues to be the subject of much debate (e.g., Wallace 1889; Huxley 1938; Bateson 1983). Although sexual selection is frequently presented as the result of either choice or direct competition, in practice these processes are rarely mutually exclusive. Indeed, many dimorphic traits may well result from the complementary actions of male competition and female choice (Cox and Le Boeuf 1977; Borgia 1981). For this reason, the importance of female choice in sexual selection has proved difficult to assess (but see Thornhill 1983; Kodric-Brown 1985). This paper examines the potential influence of female choice on a sexually dimorphic trait which is known to function in male combat (Chapter 2) in the pseudoscorpion, D. arizonensis (Banks).

Among pseudoscorpions, great diversity exists in mating behavior and methods of sperm transfer. At one extreme, males deposit spermatophores in the absence of females, e.g., Tridenchthoniidae, Chthoniidae, Neobisiidae, Garypidae, Pseudogarypidae, Cheiridiidae and some Olpiidae (Weygoldt 1966b 1969 1970; Schaller 1979; Thomas and Zeh 1984). At the other extreme, male and female cheliferids engage in complex pairing behavior following elaborate courtship by the male (Weygoldt 1969). Courtship involves display of the ram's horn organs, a pair of erectile tubes originating from the genital atrium. After depositing a spermatophore on the substrate, the male grasps the female, and uses modified foretarsi to assist in sperm uptake (see Kew 1912; Vachon 1949; Weygoldt 1969). Mating behavior has been most extensively studied in the family Chernetidae (Weygoldt 1970), which includes the species examined here. In all 10 chernetid genera investigated, pairing occurs with little or no courtship (Kew 1912; Levi 1953; Weygoldt 1970). Males generally seem unable to distinguish sex without contact, and use their pedipalpal chelae to forcefully grasp the chelae of any conspecific encountered (Figs. 11 and 12). Contact between males generally results in combat (Weygoldt 1966a; Chapter 2), and unreceptive females also respond aggressively. Males maintain their hold on

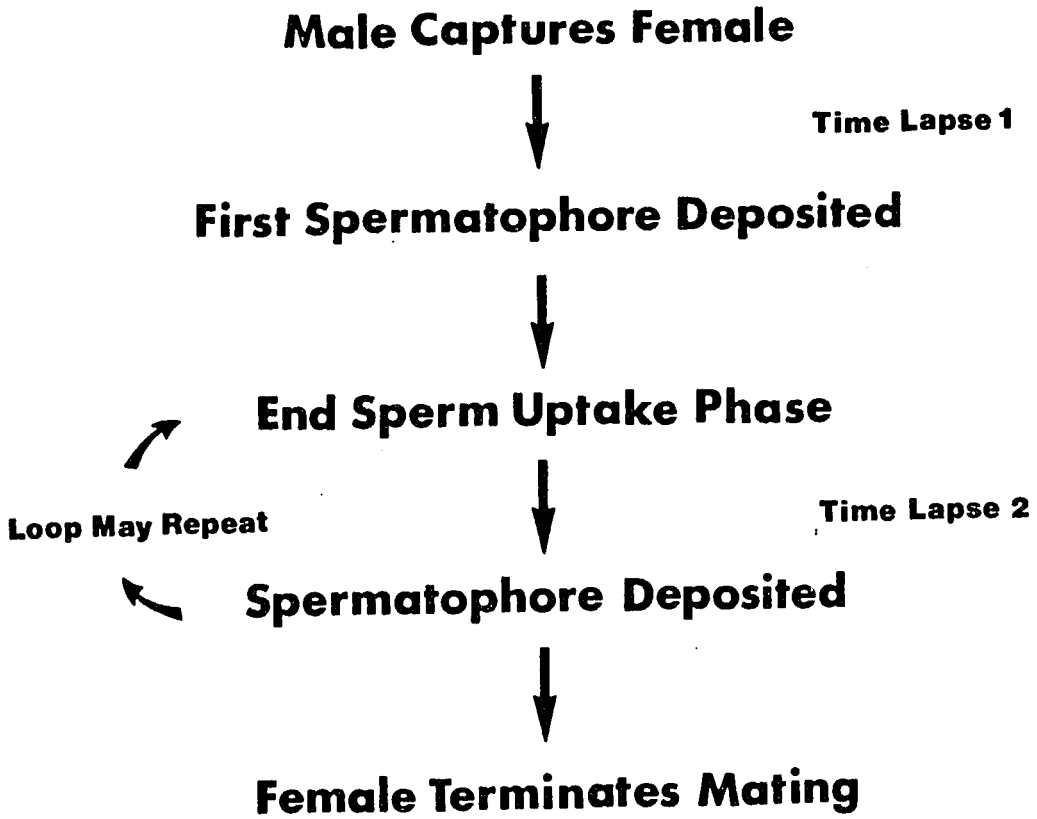


Fig. 11. Summary of the Major Stages in the Pairing Behavior of D. arizonensis.

receptive females throughout a protracted "mating dance" which may involve the deposition and uptake of several spermatophores. Although males position the female over the spermatophore, they do not otherwise assist in sperm uptake.

Marked sexual dimorphism is apparent in D. arizonensis and many other chernetid species: males possess heavier pedipalps with the greatest difference apparent in the large, prehensile chelae (Muchmore 1974; Chapter 5). By contrast, in terms of overall body size (cephalothorax length), in most species females are larger than males: enlarged male pedipalps are not simply the result of allometry (Chapter 2). Recent experiments with D. arizonensis show a strong association between relative male chela size and combat success (Chapter 2). In addition, males with larger chelae have greater mating success under conditions of high density. Thus, pedipalpal dimorphism is functionally significant in the context of sexual interference between males (Chapter 2). Potentially, enlarged male pedipalps could also function directly in mating, either by enabling males to prolong their grasp on females, or by influencing female choice. In these organisms, it is important to distinguish the components of female choice. In the classic sense (Darwin 1871), females may choose among males prior to forming

pairs. In D. arizonensis, this component of choice is highly constrained by the mate acquisition behavior of males and by male-male interference (Thomas and Zeh 1984). However, female choice may also involve decisions such as the duration of the mating event (Sakaluk 1984) or, in matings with multiple spermatophore transfer, the number of sperm packets accepted. This latter component of choice may be significant in chernetid pseudoscorpions. The purpose of this study was twofold: 1) to evaluate the relationship between male chela size and number of spermatophores transferred in the absence of male-male interactions, and 2) to quantitatively examine changes in female receptivity through time and as a result of previous mating experience. The results are then considered in the general context of pseudoscorpion reproductive biology. Several additional questions regarding female receptivity emerge from these experiments and avenues for future research are suggested.

Materials and Methods

Mating Experience and Female Receptivity

For these experiments individuals were taken from the F_1 generation of a breeding program conducted to estimate heritability of chela and body size (Chapter 5).

Between April and June 1985 tritonymphs were obtained from rotting saguaro cacti (Carnegiea gigantea [Engelm]) in the vicinity of Tucson, Arizona. Sibling offspring from matings between these field-collected pseudoscorpions provided the individuals used in this investigation. Ten broods were selected randomly from 36 broods reared. From each of the 10 broods, two females were chosen at random and separated into two treatment categories. In all cases, individuals had eclosed no more than two weeks prior to selection. The same randomization procedure was used to select males. In both treatment categories each female was mated a total of three times and on each occasion was paired with a virgin male: 20 females and 60 males were used in the experiment. The treatments differed in time interval between successive matings: 24 hr versus 48 hr; for the interim period females were returned to individual rot-provisioned gallon jars. The design was thus a single factor experiment with repeated measures on the same individuals (Winer 1971). Pedipalpal dimorphism was quantified on the basis of silhouette area of the chelal hand. The chela constitutes the largest component of the pedipalp: 61.4% and 52.8% of total pedipalp weight in males and females, respectively (Chapter 5). Its weight is highly correlated with that of the total pedipalp ($r = .994$, see Chapter 5). In fact, 80% of the sexual

difference in pedipalp weight is accounted for by differences in chela weight (Chapter 5). Chelae consist primarily of muscle tissue (Chamberlin 1931), and function directly in male aggression and mate capture (Fig. 12, see Chapter 2). Potential differences among males, other than those of cephalothorax length and chela size, were minimized by pairing each female with sibling males. The effect of male chela size was evaluated by including male minus female chela silhouette area as a covariate in the analysis (BMDP-83, Program 2V, see Dixon 1983). The influence of male body size was also evaluated: sexual difference in cephalothorax length was included as a covariate in a separate analysis. Individuals were placed in 50 mm diameter petri dishes and the total number of spermatophores transferred during mating was recorded. Each observation was continued until mating was aggressively terminated by the female (Fig. 12). Morphometrics were obtained from CO_2-anesthetized individuals upon completion of the experiments. A Wild M5D stereomicroscope equipped with an ocular micrometer was used to measure cephalothorax length. Each camera lucida outline of a lateral view of the chelal hand was measured with a LI-3100 area meter (LI-COR, INC.) to determine chelal hand silhouette area.

A B

C D

Fig. 12. Photographic Sequence of Mating in D. arizonensis. A) Male initiates mating by grasping both chelae of the female. B) Male leads female to mating site. C) Male holds female over spermatophore during sperm uptake phase. D) Female rejects male.

Spermatophore Deposition Rate and Female Receptivity

Data on the duration of mating stages were recorded i.e., time elapsed between successive spermatophore depositions (see Fig. 11). Because of the low number of spermatophores transferred in second and third matings, only first matings were considered in this analysis. Data on first matings were extracted and pooled with 24 observations on virgin female matings made in 1984. These pooled data were used to examine correlations between time to spermatophore deposition and female receptivity (BMDP-83, Program 6D).

Results

Mating Experience and Female Receptivity

The raw data and ANOVA summary are presented in Tables 7 and 8 respectively. Female receptivity was quantified as the number of spermatophores transferred during a mating event. The effect of mating experience was highly significant: female receptivity decreased linearly with number of previous matings (main effect: $F_{2,35} = 41.94$, $P < .0001$, see Fig. 13). Linearity was confirmed by partitioning the mating experience sum of squares into linear and quadratic contrasts ($F_1 = 87.98$, $P < .0001$, see Table 9a). The main effect of time interval between

Table 7. Results of Repeated Measures Experiment on Female Receptivity.

Data in each cell represent the total of 10 replications. The data were √[Y + .5] transformed for statistical analysis, where Y = number of spermatophores accepted by a female.

	Factor B: Mating Experience			
Factor A: Interval	First	Second	Third	Row Total
24 hour				
Raw Data	31.0000	20.0000	7.0000	58.0000
√ Transformed	18.7479	15.1829	9.9829	43.9137
48 hour				
Raw Data	35.0000	18.0000	0.0000	53.0000
√ Transformed	19.7624	14.2697	7.0711	40.7560
	Column Totals			Grand Total
Raw Data	66.0000	38.0000	7.0000	111.0000
√ Transformed	38.5104	29.4526	17.0540	84.6697

matings was not significant ($F_{1,17}$ = .83, P = .376). This main effect, which measures interval influence on receptivity averaged over the three levels of mating experience, was subdivided into its component simple effects (interval influence at a single level of mating experience). Interval had no significant effect at the first and second matings (P > .50), but approached significance at the third ($F_{1,35}$ = 2.845, P = .100, Table 9B). Male chela size had no consistent effect on number of spermatophores transferred when included as a covariate in the analysis (pooled regression coefficient = -.25812, n.s.). Enlarged male chelae thus conferred no advantage at any level of female mating experience (Figs. 14 - 16). The same conclusions held for cephalothorax length (pooled regression coefficient = .89961, n.s.).

Spermatophore Deposition Rate and Female Receptivity

Prior to pooling, the 1984 observations again showed no relationship between number of spermatophores accepted and male chela size (r = -.0077, P = .971). In the pooled observations on 44 virgin female matings, the number of spermatophores transferred ranged from one to seven. There was a significant negative correlation between time taken by males to deposit the initial spermatophore and number of spermatophores ultimately

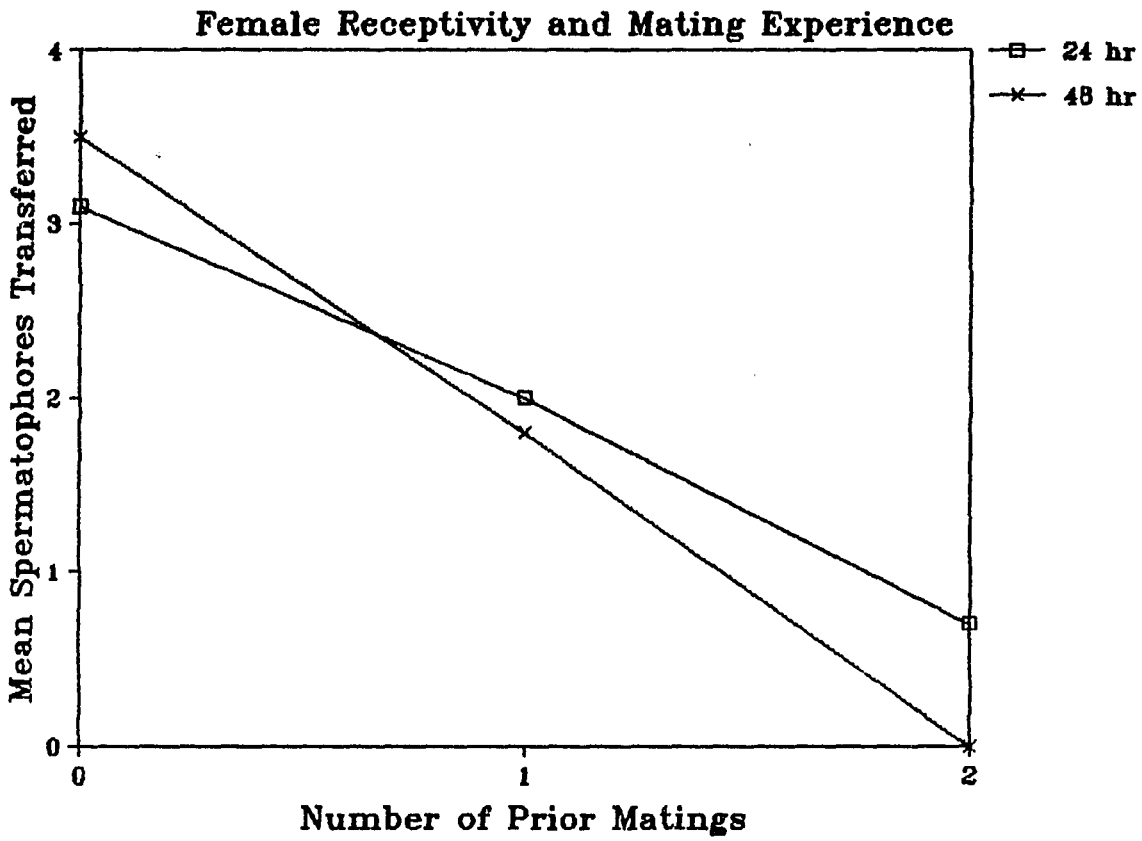


Fig. 13. Female Receptivity versus Mating Experience.

Table 8. ANOCOVA Summary of the Effects of (1) Time Interval between Matings and (2) Mating Experience on Female Receptivity.

The covariate included here is sexual difference in chela surface area. Analysis is unchanged by including sexual difference cephalothorax length as a covariate (see text).

Source	SS	df	MS	F	P
Between individuals					
Time interval between matings	.15435	1	.15435	.83	.3756
Covariate (reg. coeff. = .99498)	.28677	1	.28677	1.54	.2317
Error 1 (indiv. within groups)	3.16900	17	.18461		
Within individuals					
Mating experience	10.97312	2	5.48656	41.94	<.0001
Interaction (interval x experience)	.55188	2	.27594	2.11	.136*
Covariate (reg. coeff. = -1.16755)	.38183	1	.38183	2.92	.0964
Error 2 (experience x indiv. within groups)	4.57868	35*	.13082		

Pooled Regression Coefficient for Covariate = -.25812

* Incorporates Huynh-Feldt epsilon factor degrees of freedom adjustment (see Huynh and Feldt 1976; Frane 1980).

accepted ($r = -.536$, $P < .0001$, Fig. 17). This correlation suggests that deposition rate may be a criterion by which females determine duration of mating events. The link between deposition rate and receptivity is further suggested by examining data grouped according to the number of spermatophores transferred (Figs. 18 and 19, see Table 10 for ANOVA summary). In all groups, a significant increase was apparent in time lapse between the penultimate and final spermatophore accepted by the female (see contrasts in Table 11).

Discussion

These experiments failed to show any effect of either male cephalothorax length or sexually dimorphic pedipalps on female acceptance of spermatophores. Results did indicate, however, that mating experience, spermatophore deposition rate, and interval between matings all influence female receptivity to some degree. Two aspects of the reproductive biology of pseudoscorpions may explain these findings. First, morphological studies have shown that in pairing pseudoscorpions females possess well developed spermathecae (see Legg 1974; Muchmore 1975). Pseudoscorpion sperm are encased in proteinaceous cysts, which, in addition to protecting sperm during the interval between spermatophore deposition and sperm uptake

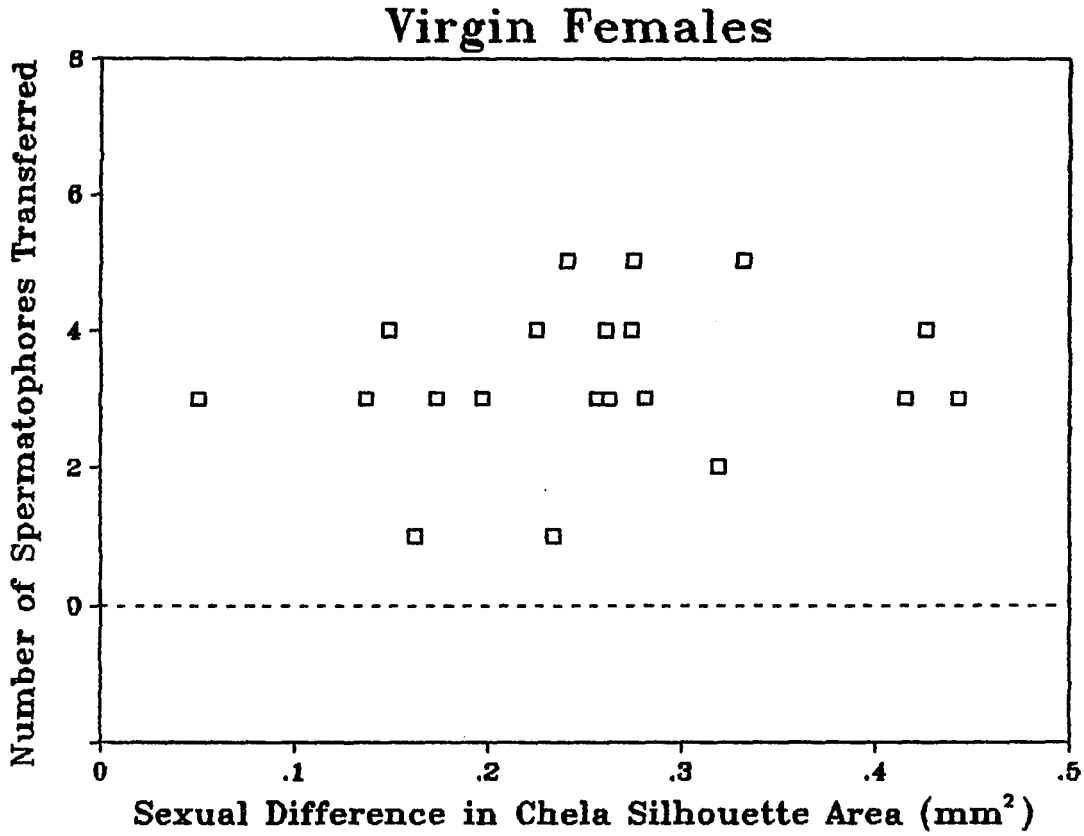


Fig. 14. Female Receptivity versus Sexual Difference in Chela Size: Virgin Females.

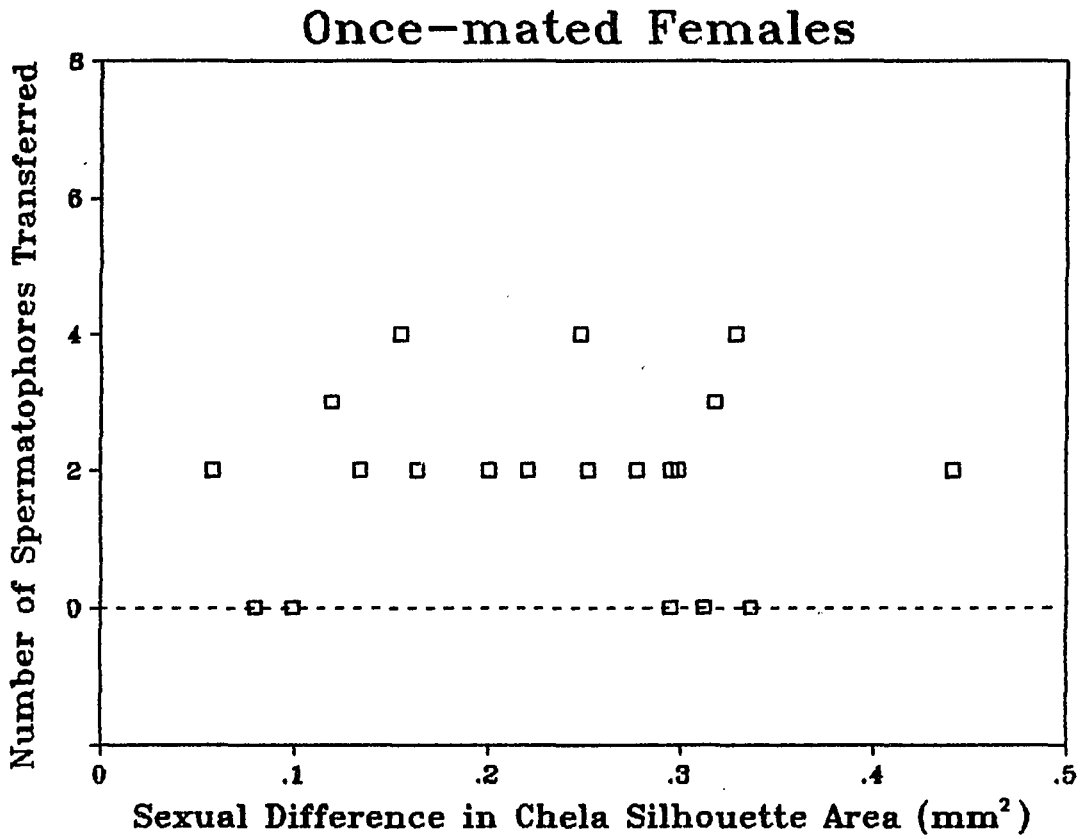


Fig. 15. Female Receptivity versus Sexual Difference in Chela Size: Once-mated Females.

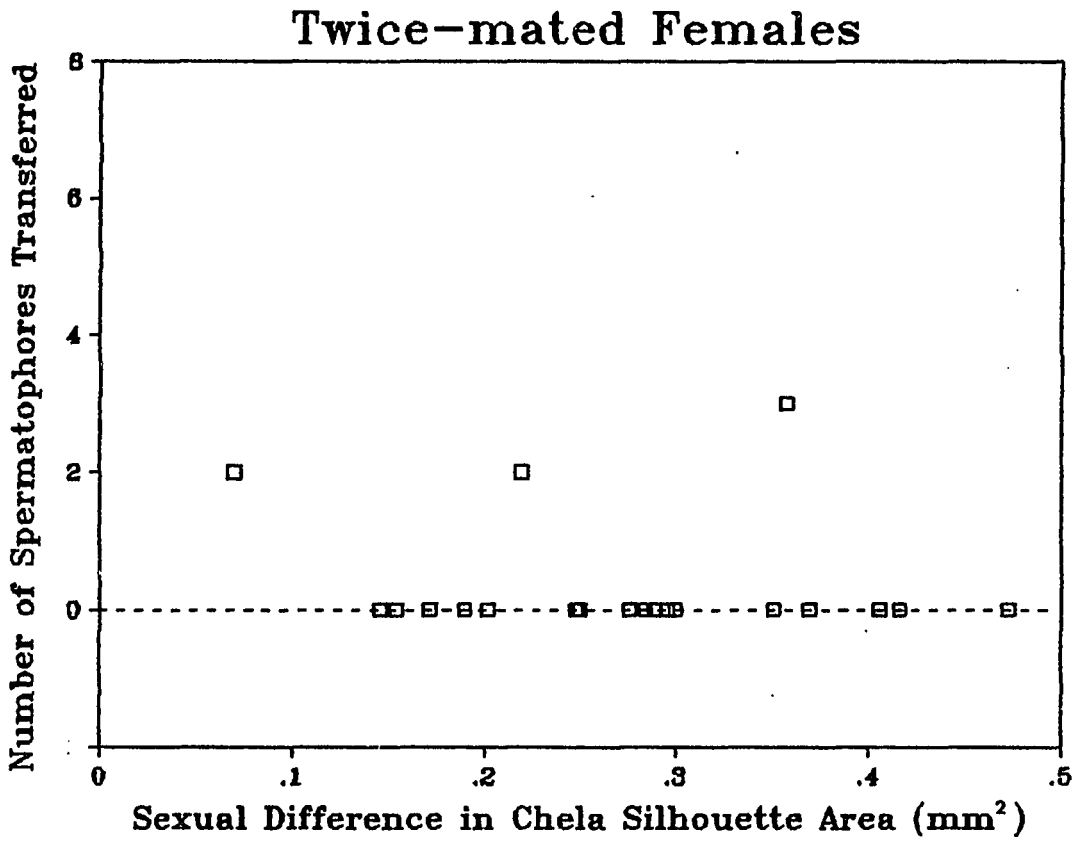


Fig. 16. Female Receptivity versus Sexual Difference in Chela Size: Twice-mated Females.

(Legg 1973), may allow sperm to remain viable for extended periods in the female reproductive tract. Observations made during heritability experiments (Chapter 5) demonstrated that sperm storage in D. arizonensis enables females to produce at least three broods from a single mating (personal observation). Second, all pseudoscorpions nourish embryos within a brood sac which covers the genital aperture (Vachon 1938; Zeh and Smith 1985). Gravid females are completely unreceptive (based on 20 observations, unpublished data) and could only take up spermatophores by brood sac abortion. The first brood sac becomes visible five days after virgin mating, irrespective of the number of subsequent matings. While females in the 24 hr treatment showed limited receptivity two days after first mating, the 48 hr treatment demonstrated that females had become completely unreceptive by the fourth day (see Fig. 13). Embryonic development within the brood sac requires approximately three weeks (27 °C), after which protonymphs emerge and cluster on the mother's body for an additional two days before dispersing (personal observation). Second and third brood sacs were formed within two days of protonymph dispersal. These observations suggest that: 1) one or two matings may provide adequate sperm for the reproductive life of the female, and 2) a critical point is reached

Table 9. Main Effect of Mating Experience Partitioned into Linear and Quadratic Contrasts.

B) Tests of the simple effects of interval between matings.

A) Mating Experience (Factor B with q Levels)

Contrast	First	Second	Third	SS_c	F	P
C_1	1	0	−1	11.509	87.98	<.0001
C_q	1	−2	1	.093	.71	>.5000

$$F_{1,35} = \frac{MS_c}{MS_{error2}}$$

MS_c = contrast mean square

MS_{error2} = Mean square of error 2 (Table 8)

B) Time Interval (Factor A with p Levels)

Level of Factor B	$T_{24,q}$	$T_{48,q}$	F	P
First mating	18.7479	19.7624	.345	>.500
Second mating	15.1829	14.2697	.279	>.500
Third mating	9.9829	7.0711	2.845	.100

where $T_{p,q}$ = Total for cell at level p of Factor A and level q of Factor B (from Table 7).

$$F_{1,35} = \frac{(T_{p,q} - T_{p',q})^2}{2nMS_{wcell}}$$

MS_{wcell} = weighted average of two error mean squares from Table 8 (see Winer 1971:529-532)

Table 10. Repeated Measures ANOVA on Time Lapse between Successive Spermatophore Depositions during Single Mating Events.

Results are based on virgin female matings observed in 1984 and 1985. Data are grouped according to the number of spermatophores transferred (=Nsperm) and only groups with >2 observations were analyzed.

Nsperm	Source	SS	df	MS	F	P
3	Between	265.65	12	22.14		
	Depositions	101.55	2	50.77	3.91	.0661*
	Error	311.63	24	12.98		
4	Between	519.30	13	39.95		
	Depositions	903.30	3	301.10	15.16	.0007*
	Error	774.36	39	19.86		
5	Between	103.54	6	17.26		
	Depositions	254.11	4	63.53	21.21	.0016*
	Error	71.89	21	2.99		
7	Between	54.11	3	18.04		
	Depositions	427.86	6	71.31	22.08	.0012
	Error	58.14	18	3.23		

* Incorporates Huynh-Feldt epsilon factor degrees of freedom adjustment (see Huynh and Feldt 1976; Frane 1980).

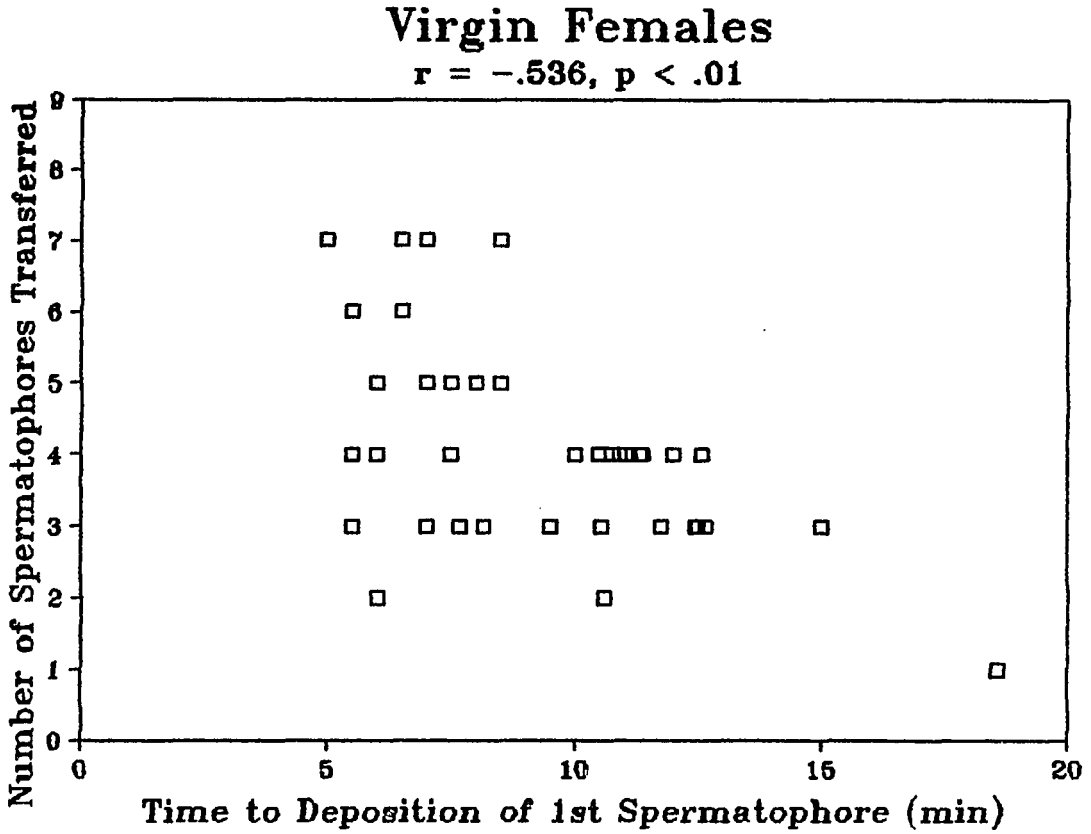


Fig. 17. Female Receptivity versus Spermatophore Deposition Rate.

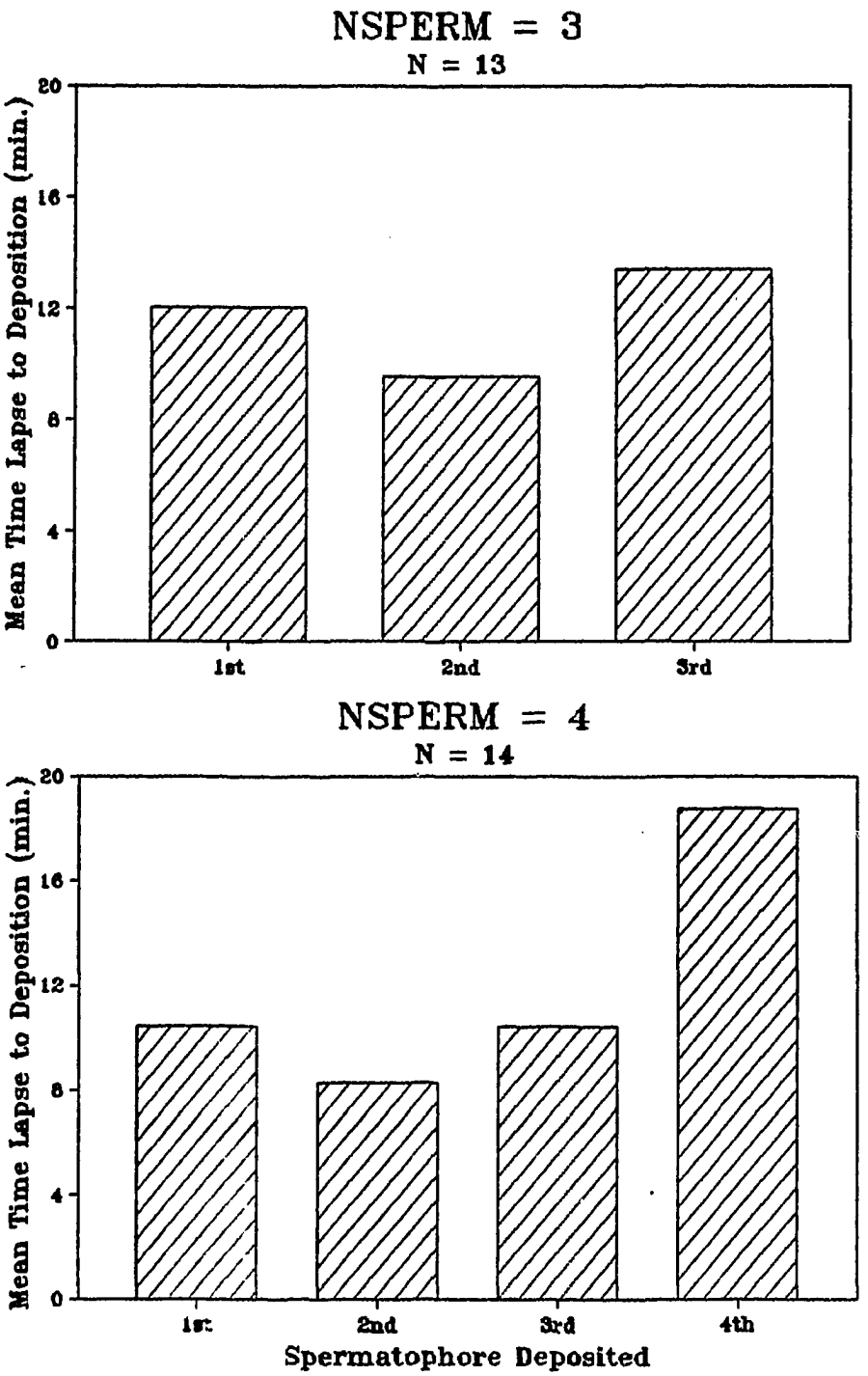


Fig. 18. Time Elapsed between Successive Spermatophore Depositions versus Spermatophore Deposited: 1. NSPERM = total number of spermatophores accepted.

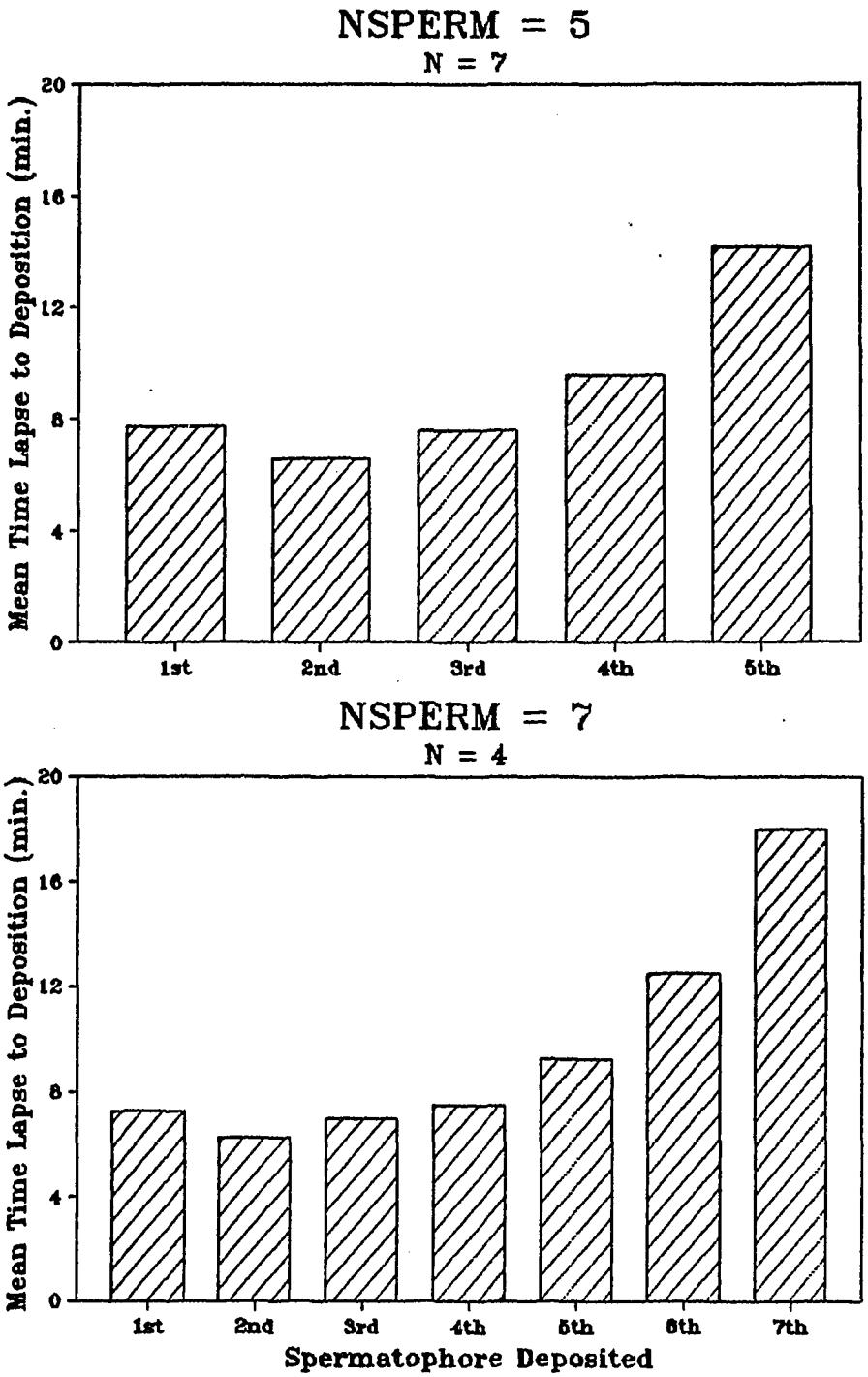


Fig. 19. Time Elapsed between Successive Spermatophore Depositions versus Spermatophore Deposited: 2.

between the second and fourth day after initial mating, beyond which further mating is detrimental to brood development. This would explain why the effect of interval was restricted to third matings: these occurred before the critical point in the 24 hr treatment and after in the 48 hr treatment.

Physiological constraints therefore appear to result in a "receptivity window." This study suggests that it is within this window that spermatophore deposition rate and mating experience exert their influence on female receptivity. Deposition rate was related to receptivity in two ways. I) There was a negative correlation between time to first deposition and total spermatophores transferred (Fig. 17), and II) females invariably terminated mating following a significant increase in time taken to deposit a spermatophore (Figs. 18 and 19, Table 11). Several hypotheses can be evaluated based on their ability to explain relationships I and II above. According to the simplest hypothesis, females allocate a fixed length of time to mating. This hypothesis is consistent with relationship I but not II, i.e., it does not predict rejection by the female following a significant increase in the time elapsed between spermatophore depositions, irrespective of the absolute number of spermatophores

Table 11. Orthogonal Contrasts for Each ANOVA Presented in Table 10.

For each Nsperm category, the most significant increase in time elapsed between successive depositions occurs with the final spermatophore deposited.

	Spermatophore Deposited 1ST 2ND 3RD 4TH 5TH 6TH 7TH									
Nsperm	Contrast Coefficient							SS_c	F	P*
3	-1	-1	2					60.25	4.64	.050
	-1	1	0					41.30	3.18	.100
4	-1	-1	-1	3				860.52	43.34	<.001
	-1	-1	2	0				10.21	0.51	>.500
	-1	1	0	0				32.57	1.64	>.100
5	-1	-1	-1	-1	4			221.26	73.87	<.001
	-1	-1	-1	3	0			27.43	9.16	<.050
	-1	-1	2	0	0			0.86	0.29	>.500
	-1	1	0	0	0			4.57	1.53	>.250
7	-1	-1	-1	-1	-1	-1	6	323.15	100.04	<.001
	-1	-1	-1	-1	-1	5	0	85.01	26.32	<.010
	-1	-1	-1	-1	4	0	0	16.20	5.02	<.100
	-1	-1	-1	3	0	0	0	1.33	0.41	>.500
	-1	-1	2	0	0	0	0	0.17	0.05	>.900
	-1	1	0	0	0	0	0	2.00	0.62	>.500

deposited. In addition, duration of mating event and success in sperm transfer are not independent, as would be predicted ($r = .658$, $P < .001$, Fig. 20). A second hypothesis proposes that deposition rate signals overall male quality since ability to rapidly produce and deposit spermatophores may, for example, reliably reflect success in resource acquisition. This hypothesis cannot stand as a complete explanation since, again, it predicts I but not II. A possible causal link between male nutrition and spermatophore deposition rate could be investigated through experimental manipulation of diet. Finally, according to a third hypothesis, deposition rate signals spermatophore quality, e.g., sperm concentration within the packet. Relationships I and II follow from this hypothesis which would also give an explanation for female acceptance of spermatophores from second males encountered. Further testing of this hypothesis requires dissection of spermatophores to determine sperm content.

Overall, this study found no functional significance to pedipalpal dimorphism in the context of female choice. Rather, results suggest that rapid reproduction provides the main impetus for female mating decisions in D. arizonensis. Such female behavior is compatible with the exigencies of reproduction in the ephemeral and unpredictable environment of the cactus

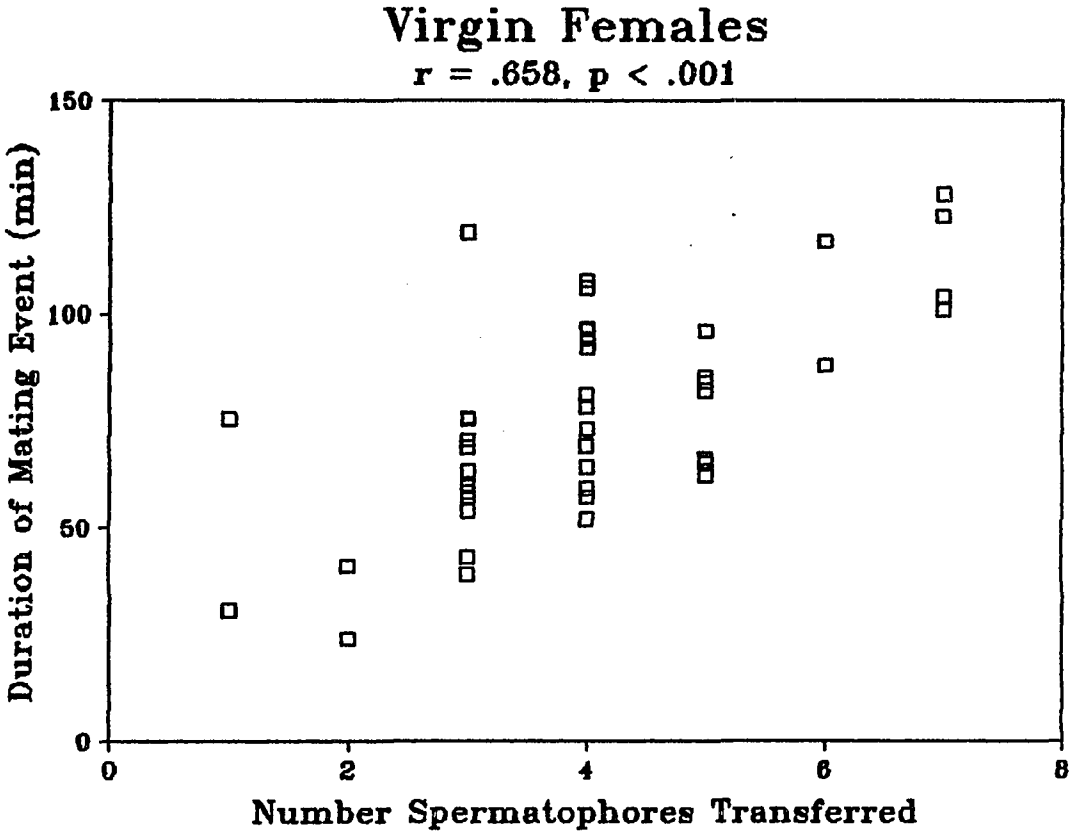


Fig. 20. Duration of Entire Mating Event versus Number of Spermatophores Accepted by Virgin Females.

rot (Chapter 4). The moist, arthropod-rich habitat of a rotting saguaro cactus deteriorates to dried-out ribs and integument within one to several months (Steenbergh and Lowe 1977). Rapid reproduction is especially crucial in D. arizonensis because dispersal, as in many monosphyronid pseudoscorpions (see Beier 1948, Muchmore 1971, Legg 1975), occurs through phoresy, i.e., by attachment to larger, more mobile species, usually flying insects. The phoretic agent in this case is the cactus fly, Odontoloxozus longicornis Hennig (Neriidae) which undergoes larval development and pupation in saguaro rots (see Ryckman and Olsen 1963; Mangin 1979 1984 for data on O. longicornis). Adult pseudoscorpions grasp a hind leg of the neriid fly soon after it ecloses and in this way are transported to a fresh rot (Chapter 4). Hence, offspring failing to mature and disperse before desiccation of the rot will not successfully reproduce. These findings underscore the need to take account of the environmental and life history constraints acting on organisms when considering the nature and importance of female choice in sexual selection (see Parker 1983).

CHAPTER 4

THE PSEUDOSCORPION, THE SAGUARO AND THE FLY: PHORETIC DISPERSAL IN A DESERT ARACHNID

The structuring of the physical environment into discrete, habitat "patches" may have profound evolutionary consequences for life history patterns, reproductive tactics and species interactions (Levins 1968; Parker and Stuart 1976; Wilson 1983). Of obvious importance to organisms dependent on ephemeral, discontinuously distributed habitats is the capacity for effective dispersal. Recent game theory models suggest that dispersal from even stable habitat patches can result in increased fitness (Hamilton and May 1977). Development of specialized mechanisms for dispersal may, however, be costly. This is particularly evident in terrestrial arthropod species exploiting patchy microhabitats which deteriorate through time. Traits necessary for dispersal may seriously hamper efficient foraging in confined microhabitats. Terrestrial arthropods have evolved various adaptations in response to these conflicting requirements. For example, the holometabolous mode of development allows larval insects to burrow into solids, such as soil, and plant and animal tissues, unencumbered by external

wing pads (Hinton 1977). Allocation of resources to dispersal mechanisms may also compromise reproductive output. The pervasive phenomenon of environmentally-cued wing polymorphism among insects appears to represent a tactic for minimizing such trade-offs (see reviews in Hamilton 1978; Matsuda 1979).

Apterous arthropods inhabiting discontinuous terrestrial habitats face an even greater challenge. Despite inherently limited dispersal capabilities, many wingless species have overcome obstacles to patchy habitat utilization by exploiting the greater mobility of other species. Known as phoresy, this use of one animal by another for transport (Wilson 1980) is well documented among mites (Lindquist 1975) and entomophagous insects (Clausen 1976). The importance of phoresy in mite dispersal has been clearly established. Some pyemotids are known to produce environmentally induced dispersal phenotypes ("phoretomorphs," see Moser and Cross 1975; Smiley and Moser 1976), and genetically based polymorphism for carrier preference has been demonstrated in Peochilochirus necrophori which is phoretic on several species of burying beetles (Wilson 1982). By contrast, although phoretic pseudoscorpions were observed as long ago as the eighteenth century (Poda 1761 cited in Beier 1948), the significance of phoresy in this arachnid order

remains controversial (see review in Muchmore 1971, Lloyd and Muchmore 1975). Many authors regard pseudoscorpion phoresy as a behavior functioning specifically for dispersal ("The Dispersal Hypothesis," Beier 1948; Weygoldt 1969; Legg 1975). However, since pseudoscorpions typically attach to arthropods almost small enough to be preyed upon, other authors view such phoresy as the accidental byproduct of an unsuccessful predation attempt ("The Predation Hypothesis," Vachon 1940,1954; Muchmore 1971). Less commonly, pseudoscorpions are found attached to larger animals, e.g., cerambicid beetles (Beck 1968), mice (Muchmore and Hentschel 1982) and rats (Muchmore 1972). These relatively long term associations are less controversial and are known to involve a predator/prey relationship: the pseudoscorpion consumes ectoparasites of the host (Beier's (1948) phagophilie).

Although taxonomically widespread among pseudoscorpions, phoresy appears to be most common in the family Chernetidae (see Beier 1948; Muchmore 1971,1982). Chernetids represent 21% of all pseudoscorpion species (Chamberlin and Malcolm 1960), but account for approximately 55% of those which are known to engage in phoresy (Legg 1975). Species in this family occupy a diversity of habitats, ranging from persistent accumulations of forest litter to transient clumps of

decaying vegetation (Hoff 1959; Legg 1975). This paper examines the role of phoresy in Dinocheirus arizonensis (Banks), a chernetid pseudoscorpion utilizing the ephemeral and spatially discontinuous habitat provided by rotting saguaro cacti (Carnegiea gigantea [Engelm]) in the Sonoran Desert. These cactus rots are also utilized by the neriid fly, Odontoloxozus longicornis Hennig, which mates and oviposits on the rot surfaces (Mangin 1979; 1984). Larval and pupal stages develop within the rots, and D. arizonensis has been found phoretic on adult flies in the field (N = 7; personal observation and R.L. Smith and M. McGee personal communication). Under laboratory conditions, the pseudoscorpions may also prey on adult neriid flies (see Fig. 21). This system is therefore particularly well suited for comparing predictions of the predation and the dispersal hypotheses. The determinants of phoretic and predatory behavior were assessed experimentally. Two experiments were conducted. One compared the incidence of phoresy on post-teneral adult versus eclosing flies. The second incorporated a repeated measures approach to examine the effects of gender and social context on the rate of attachment, and changes in phoretic behavior through time. The results are compared to patterns of colonization by D. arizonensis of artificially induced rots monitored in the field. Finally,

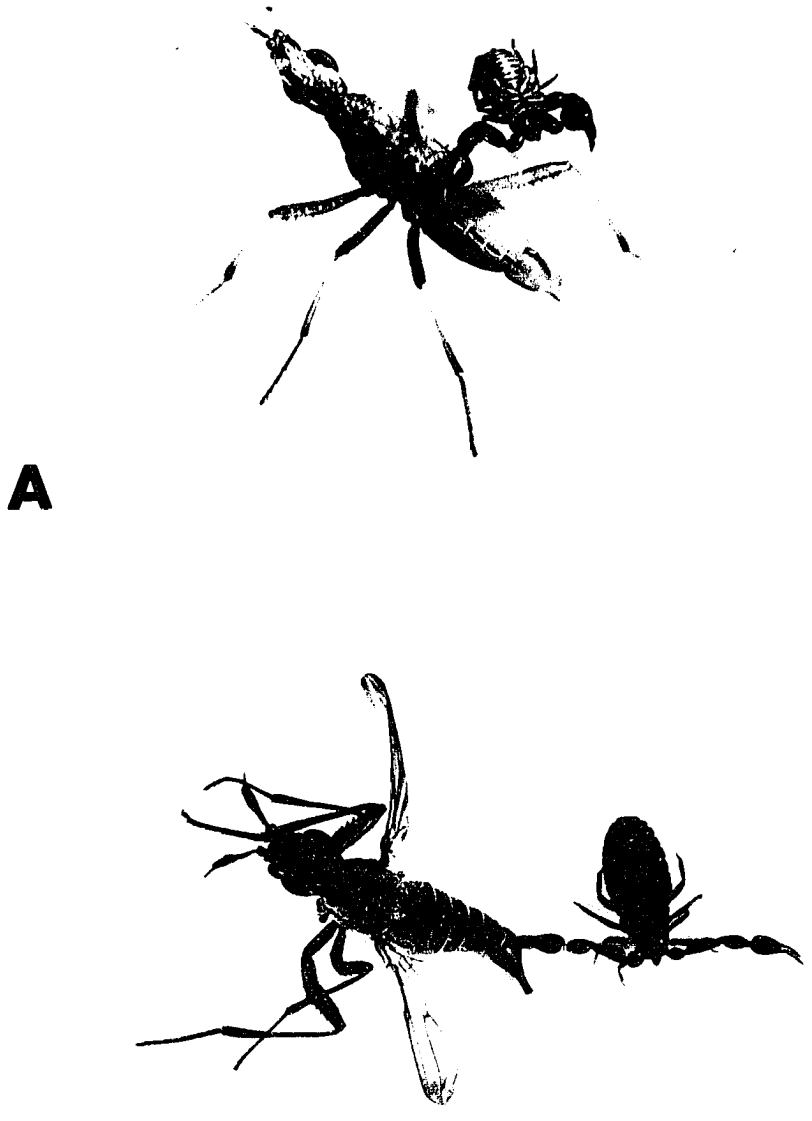


Fig. 21. Phoresy versus Predation. A) Male D. arizonensis phoretic on female neriid fly, O. longicornis. B) Female pseudoscorpion preying upon neriid fly.

the predation/dispersal debate over pseudoscorpion phoresy is reconsidered in the light of these experimental findings.

Materials and Methods

Pseudoscorpions and neriids used in the phoresy experiments (Experiments 1 and 2) were derived from natural populations inhabiting rotting saguaro cacti in the vicinity of Tucson, Arizona. Experiment 1 was conducted in November/December 1985, using pseudoscorpions which were laboratory-bred F1 offspring of field-collected individuals. Experiment 2 was carried out between February and August 1985. Pseudoscorpions were collected as deutonymphs (second nymphal stage) and molted to maturity in the laboratory. All replications of the phoresy experiments were established in 5 cm (single-individual treatments) or 10 cm (paired-individual treatments) diameter petri dishes (observation arenas). Neriid pupae were obtained by rearing field-collected larvae on a mixture of standard Drosophila medium and liquid extract of rotting saguaro. Replications were monitored three times per day from initiation of each experiment to its termination 48 hr after eclosion or addition of a fly. Behaviors were scored as no response, phoresy, or predation. In predation, the pseudoscorpion uses its

pedipalpal chelae to grasp and its chelicerae to puncture and consume the body (usually the abdomen) of the fly. This behavior is clearly distinct from phoresy in which the pseudoscorpion uses a chela to maintain a grasp on the trochanter of a fly's hind leg (see Fig. 21). For hypothesis testing, it was assumed that phoresy and predation were independent to the extent that predation events did not bias incidence of phoresy among treatment categories. This assumption was supported by the results of Experiment 2: predation occurred randomly with respect to all treatment categories (see Results). The study of colonization patterns was conducted between March 1983 and June 1984 in the Tucson Mountain Unit of Saguaro National Monument. D. arizonensis remains reproductively and probably phoretically active throughout the year. Phoretic individuals have been observed in the field in February, March, May and September.

Experiment 1: Do Pseudoscorpions Preferentially Prey on or Attach to Newly Eclosed Neriids?

This experiment compared the proportion of individuals engaging in phoresy and predation in two treatment groups, one exposed to eclosing flies, the other to post-teneral adults. Each replication involved placing a male and a female D. arizonensis in an observation

arena. In the treatment group to be exposed to newly eclosed flies, one neriid pupa was added to each petri dish. Time to eclosion could not be precisely controlled; therefore, duration of male/female interaction preceding exposure to a neriid was standardized between treatment groups by pairing replications. Twenty-four hours following eclosion in a first treatment replication an adult fly was added to its second treatment counterpart. (This procedure controlled for potential diel patterns of attachment). Twenty replications were established for each treatment group and maintained at 27 ± 1°C on a 12 hr light:12 hr dark photoperiod. One-tailed Fisher's exact tests were used to compare the incidence of phoresy and predation in the two groups.

Experiment 2: Do Gender and Social Context Influence the Incidence of Phoresy and Predation?

Observation arenas were set up as follows for each of 23 replications: male alone; female alone; male pair; female pair; and male/female pair (i.e., 182 experimental units at the outset due to the mortality in one female pair replication before completion of the first trial). All pseudoscorpions had undergone their final molt within two weeks of the first trial of the experiment. One neriid pupa was added to the single-individual treatments and two

pupae to two-individual treatments. To examine changes through time, the experimental procedure was repeated approximately six weeks after termination of the first trial. The same pseudoscorpions were used and were not fed between trials. Because of instances of mortality among the pseudoscorpions, there were 19 or 20 replications for the second trial. The experiment was originally conceived as a two-way ANOVA repeated measures design with gender and social context as factors, and rate of phoresy or predation (cases of phoresy or predation per individual) as the response variable. However, this design generated discrete values of the dependent variables. First and second trial results were therefore summed (cases of phoresy per individual in two trials) to provide a closer approximation to a continuous distribution. Finally, significant results were checked using nonparametric measures of association (Fisher's exact test). ANOVAs were performed on square root transformed data and the analyses were carried out with BMDP 1983, programs 2V and 4F (Dixon 1983).

Colonization Study: Do Colonization and Dispersal Patterns Reflect Gender Differences in Phoretic Behavior?

Determining the precise age of natural rots is difficult; therefore the decomposition process was

artificially induced by injecting rot extract (presumably containing the bacterium Erwinia carnegieana, see Steenbergh and Lowe 1977) into damaged regions of freshly fallen cactus. Quantitative pseudoscorpion samples were obtained by sieving and sorting sawn-off .235 m^2 sections of rot (based on formula for the lateral surface area of a cylinder, $2\pi rh$). This destructive technique limited the number of samples per rot to three: 1. one month after rot initiation; 2. during prime decomposition state and peak arthropod abundance, three to seven weeks after the first sampling, and 3. in final stages of rot desiccation, three to seven weeks after the second sampling. A total of nine rots, from 4 m to 10 m in composite length, were sampled in this manner. Intervals between samplings differed as a result of seasonal variation in the rate of saguaro rot progression. However, for each rot the time lapse between successive samplings was held constant. A repeated measures ANOVA design was used to examine changes in density and sex ratio through sampling periods (BMDP 1983, Program 2V). Ratios were arcsin transformed for statistical analyses.

Table 12. Comparison of the Incidence of Phoresy and Predation on Eclosing versus Post-teneral Flies.

Fly Category	Category of Pseudoscorpion Response		
	No Phoresy	Phoresy	Total
A) INCIDENCE OF PHORESY			
Eclosing	32	8	40
Adult	38	2	40
	70	10	80

	Category of Pseudoscorpion Response		
	No Predation	Predation	Total
B) INCIDENCE OF PREDATION			
Eclosing	36	4	40
Adult	37	3	40
	73	7	80

Results

Experiment 1: Do Pseudoscorpions Preferentially Prey on or Attach to Newly Eclosed Neriids?

Eclosing and teneral flies are more vulnerable to capture and injury than are post-teneral adults. Thus, with emerging flies, the predation hypothesis predicts a higher incidence of mortality, while the dispersal hypothesis predicts a higher incidence of phoresy. The rate of predation did not differ between the two treatments (P = .500, Table 12), but phoresy occurred significantly more often in the group exposed to eclosing flies (P = .0436, Table 12).

Experiment 2: Do Gender and Social Context Influence the Incidence of Phoresy and Predation?

The ANOVA on data pooled from both trials (Table 13) indicates that gender exerted a significant main effect on rate of phoresy ($F_{1,112}$ = 4.63, P = .0336) but that social context did not ($F_{2,112}$ = .06; P = .940). In all social contexts there were more cases of phoresy by females than by males (see Fig. 22). Neither gender ($F_{1,112}$ = .0035, P = .953) nor social context ($F_{2,112}$ = 2.07, P = .1309) significantly influenced rate of predation (Table 14; Fig. 23). The repeated measures ANOVA (Table 15) showed a marginally significant increase in

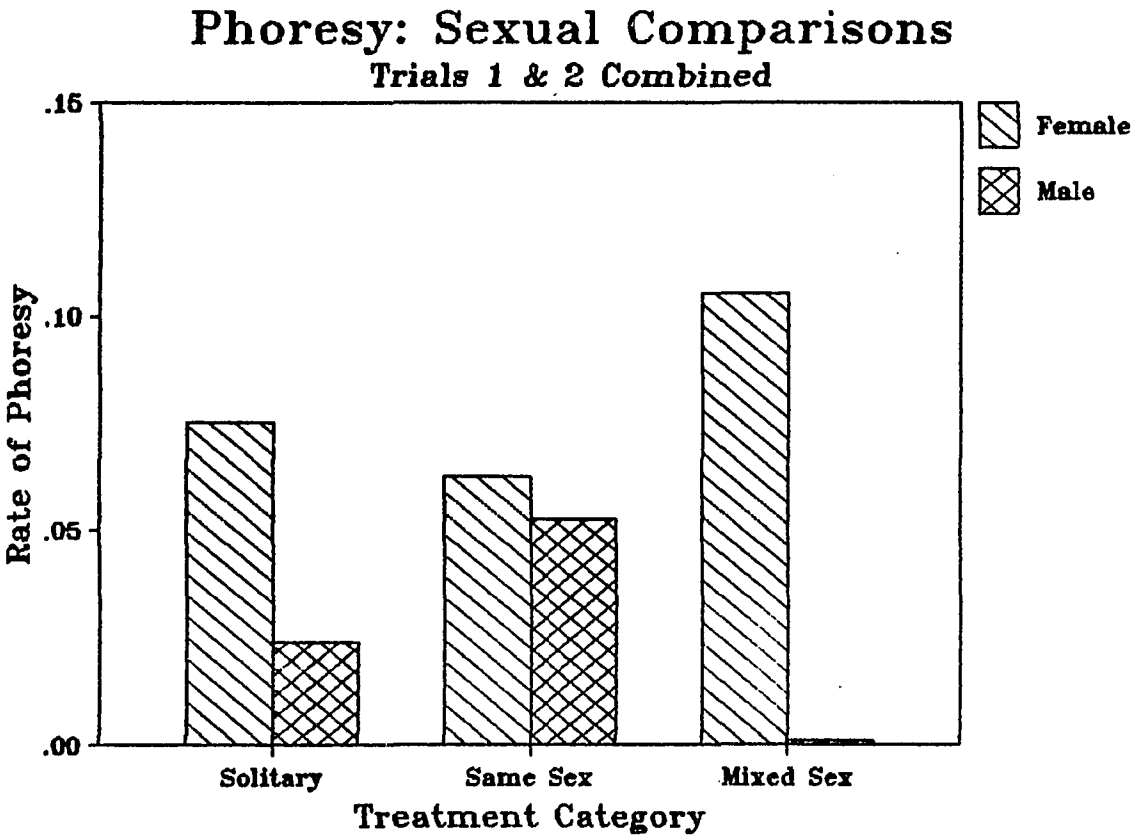


Fig. 22. Comparison of Male versus Female Phoresy Rates.

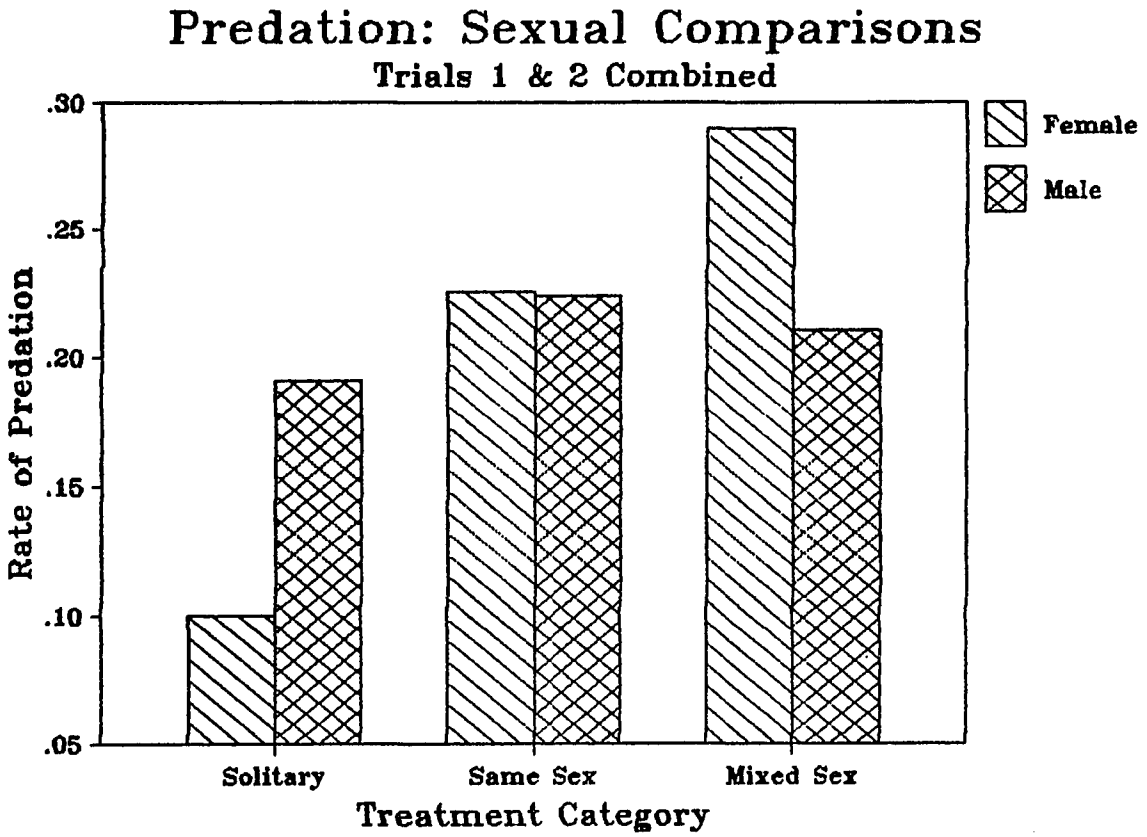


Fig. 23. Comparison of Male versus Female Predation Rates.

overall (male and female) phoresy rate for the second trials ($F_{1,112} = 3.05$, $P = .0837$). However, this overall effect masked a significant difference between the sexes in the effect of trial. A 2-tailed Fisher's exact test (data provided in Table 13) showed a highly significant increase in phoresy among females during the second trials ($P = .0137$) whereas male incidence of phoresy remained unchanged ($P = 1.00$). Predation rates did not vary significantly between trials for either sex (Table 15). In all cases the nonparametric tests corroborated the results indicated by the ANOVAs. Since social context consistently had no effect on rate of phoresy or predation, data were lumped for these tests (Table 13).

Colonization Study: Do Colonization and Dispersal Patterns Reflect Gender Differences in Phoretic Behavior?

Density of adult D. arizonensis varied significantly between sampling periods (Table 16), with greatest abundance occurring in second samples (Fig. 24). Comparison of linear and quadratic contrasts (see Rosenthal and Rosnow 1985) confirmed the humped shape of the relationship ($F_1 = .319$, $P > .5$; $F_q = 12.12$, $P < .005$). By contrast, the proportion of females in the population declined linearly with sample period (Table 16; Fig. 25; $F_1 = 21.41$, $P < .001$; $F_q = 2.60$, $P > .10$). In

Table 13. Summary of Results of Experiment 2 Showing Incidence of Phoresy and Predation among Males and Females in the Two Trials.

For simplicity, categorization by social context is omitted, since this treatment had no effect on the response variables (see Table 14 and text).

Trial		Category of Pseudoscorpion Response		
		No Phoresy	Phoresy	Total
A) PHORESY				
Trial 1	Female	88	2	90
	Male	89	3	92
Trial 2	Female	70	10	80
	Male	76	2	78
		Category of Pseudoscorpion Response		
		No Predation	Predation	Total
B) PREDATION				
Trial 1	Female	72	18	90
	Male	76	16	92
Trial 2	Female	61	19	80
	Male	61	17	78

Table 14. ANOVA Summary Table Showing the Main and Interactive Effects of Social Context and Gender on Rate of Phoresy and Predation.

The sum of each individual's response in trials 1 and 2 was used as the dependent variable and only complete cases were included.

SOURCE	SS	df	MS	F	P
A) RATE OF PHORESY					
Context	.00292	2	.00146	.06	.9400
Gender	.10909	1	.10909	4.63	.0336
C X G	.03842	2	.01921	.82	.4452
Error	2.63947	112	.02357		
B) RATE OF PREDATION					
Context	.27006	2	.13503	2.07	.1309
Gender	.00023	1	.00023	.00	.9526
C X G	.13105	2	.06553	1.00	.3694
Error	7.30362	112	.06521		

Table 15. Repeated Measures ANOVA Summary Table for Experiment 2.

In addition to evaluating the effects of social context and gender, this analysis examines change in individual's response from trial 1 to trial 2.

SOURCE	SS	df	MS	F	P
A) RATE OF PHORESY					
Context	.00478	2	.00239	.19	.8268
Gender	.04515	1	.04515	3.60	.0605
C X G	.02716	2	.01358	1.08	.3425
Error	1.41868	113	.01255		
Trial	.03371	1	.03371	3.05	.0837
T X C	.02999	2	.01499	1.35	.2622
T X G	.07608	1	.07608	6.87	.0100
T X C X G	.01025	2	.00512	.46	.6306
Error	1.25084	113	.01107		
B) RATE OF PREDATION					
Context	.16880	2	.08440	2.14	.1230
Gender	.00002	1	.00002	.00	.9835
C X G	.07688	2	.03844	.97	.3813
Error	4.42643	112	.03952		
Trial	.01220	1	.01220	.42	.5186
T X C	.00320	2	.00160	.05	.9466
T X G	.00710	1	.00710	.24	.6222
T X C X G	.20748	2	.10374	3.57	.0315
Error	3.25711	112	.02908		

addition, female density was significantly greater than male density for the initial samples (paired t test, t = 2.98, P = .0175, 2-tailed), but this relationship reversed for the second sampling period (t = -2.53, P = .0353). Nymphs were only observed in second and third samplings.

Discussion

Experimental results and those of the colonization study indicate that phoretic behavior may explain colonization patterns in D. arizonensis. Of the two sexes, females were more likely to engage in phoresy and were more influenced by time and food deprivation. As rots progressed, the ratio of females to males declined in a linear fashion. Taken together, these findings suggest a dispersal system in which there is a tendency for phoretic females to be the first to colonize and the first to abandon the transient habitat of a cactus rot. Comparative observations show that phoresy among pseudoscorpions is most common in inseminated and gravid females (Beier 1948). The experiments conducted here were not specifically designed to isolate differences in the phoretic behavior of virgin versus mated females. Nevertheless, mated females (in male/female pairs) did exhibit a slightly higher rate of phoresy than unmated females (female alone; female pair; see Fig. 22). The

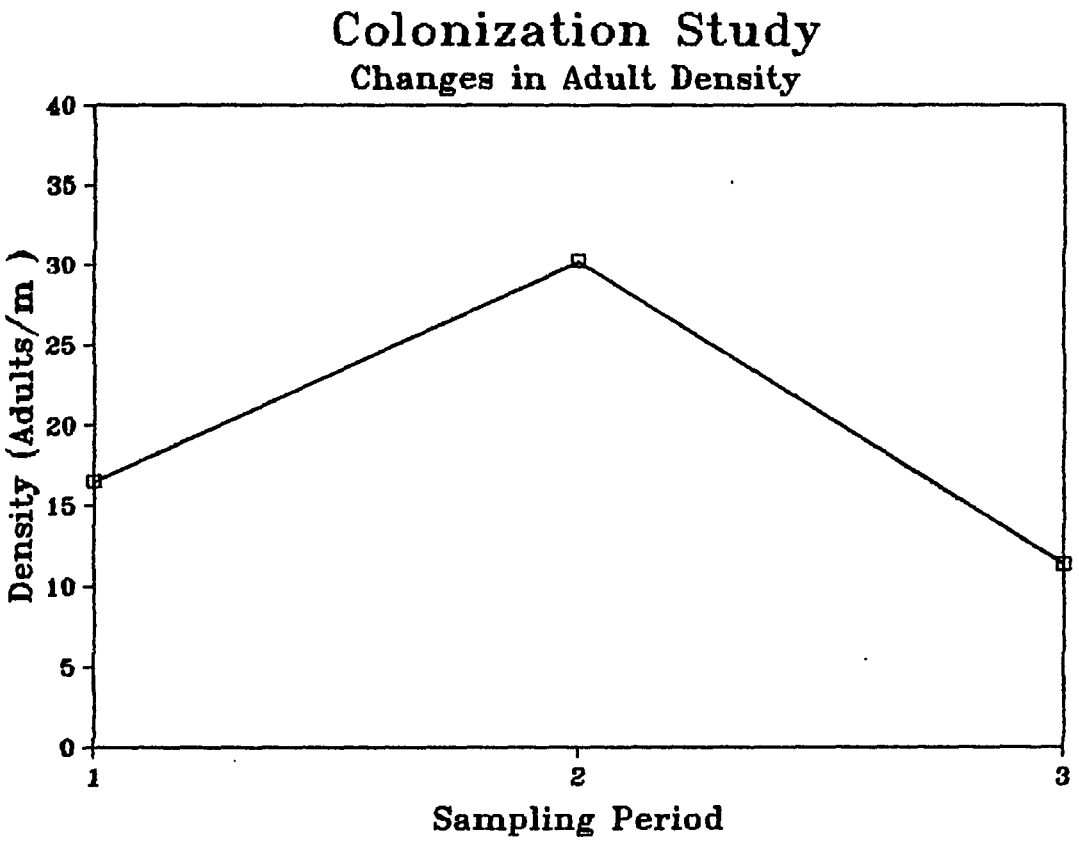


Fig. 24. Changes in Adult Density through Three Successive Sampling Periods.

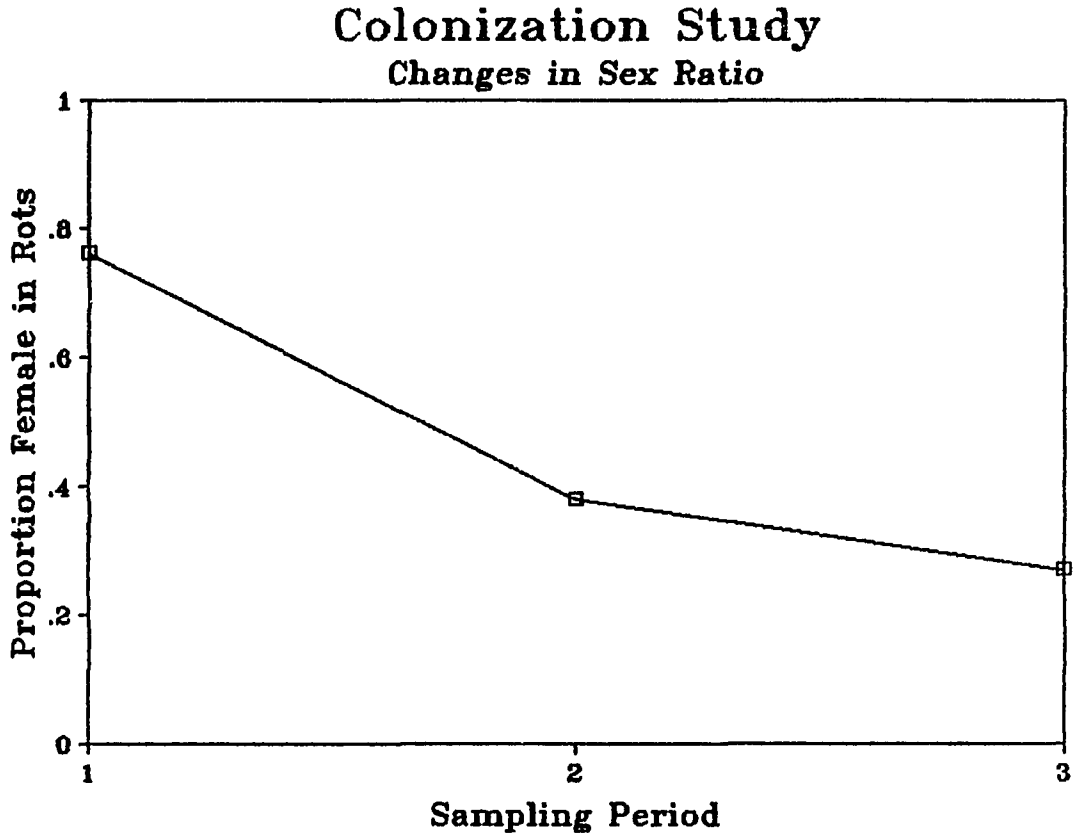


Fig. 25. Changes in the Proportion of Females in Rot Populations through Sampling Periods.

female bias in dispersal patterns may perhaps be best understood in the context of pseudoscorpion reproductive biology. Females store sperm for prolonged periods and can produce several broods from a single mating. Maternal investment is high: embryos are nourished for two to three weeks within a brood sac carried on the underside of the female's abdomen (Weygoldt 1969). Initiation of a brood sac late in the progression of a rot may result in offspring that fail to mature and disperse. The higher propensity for phoresy among females would seem to be evolutionarily stable (sensu Maynard Smith 1982): females must disperse to ensure the successful development of their offspring. Given this behavior and the very limited period of sexual receptivity in females (Chapter 3), male reproductive success may be best achieved by deferring phoresy in order to mate with females about to disperse. Finally, the absence of nymphs from the first set of samples supports the assertion that phoresy in pseudoscorpions is limited to adults (Beier 1948; Weygoldt 1969).

The results presented here show that D. arizonensis is most commonly phoretic on eclosing neriid flies, upon which it can and does also prey. This apparent preference could simply stem from eclosing flies' susceptibility to attachment. Alternatively, the higher incidence of phoresy

Table 16. Repeated Measures ANOVA Summary of the Colonization Data.

Changes in adult density and proportion of females in rots through sampling periods are evaluated. Through time, adult density follows a quadratic curve while proportion of females decreases linearly.

SOURCE	SS	df	MS	F	P
A) ADULT DENSITY					
Between Rot Error	3489.40741	8	436.17593		
Sampling Period	1406.19907	2	703.09954	6.22	.0100
Linear	36.12517	1	36.12517	.32	NS
Quad.	1370.07380	1	1370.07380	12.12	<.005
Within Rot Error	1808.92593	16	113.05787		
B) PROPORTION OF FEMALES IN ROTS					
Between Rot Error	.28443	8	.03555		
Sampling Period	1.26050	2	.63025	12.01	.0007
Linear	1.12383	1	1.12383	21.41	<.001
Quad.	.13666	1	.13666	2.60	>.100
Within Rot Error	.83978	16	.05249		

on eclosing flies may represent an active preference which increases the efficiency of phoresy as a dispersal mechanism. Because rots decay through time, eclosing flies are more likely to disperse to new rots than would a randomly selected member of the adult neriid population. These findings do not support the suggestion that transport of pseudoscorpions by other arthropods is accidental, motivated by hunger, and occurs simply because pseudoscorpions are incapable of consuming their hosts (Vachon 1940; Muchmore 1971). Were this the case, predation should have been highest on vulnerable eclosing flies, and phoresy most common on active post-teneral adults. The predation hypothesis would also presumably predict an increase in rate of predation on eclosing flies with time and food deprivation. In fact, the predation rate remained unchanged while female phoresy rate increased. By contrast, this experimental study supports the conclusion reached by Beier (1948), Weygoldt (1969), and Legg (1975) that the attachment of pseudoscorpions to the appendages of flies and other arthropods represents a behavior functioning specifically for dispersal. The dual predatory/phoretic nature of the relationship between D. arizonensis and O. longicornis may also explain in part the long-standing predation/dispersal controversy in the literature. Isolated observations of either phoresy or

predation could lead to opposing interpretations based on accurate but incomplete evidence.

Still to be determined is the nature of the cues which induce phoretic behavior in pseudoscorpions. Initial observations suggest that olfactory stimuli released by eclosing and teneral flies might play an important role. Preliminary experiments were therefore conducted in which neriid pupae were crushed and the resultant slurry applied to adult flies. No significant increase in rate of phoresy occurred when pseudoscorpions were exposed to these as opposed to untreated flies. The greater rate of attachment to eclosing flies observed in Experiment 1 may indicate that pseudoscorpions use behavioral as well as olfactory cues when engaging in phoresy. Olfaction clearly affects detachment of the pseudoscorpion from the fly (personal observation). Phoretic female pseudoscorpions, which were transferred from petri dishes to gallon jars containing dried-out saguaro tissue, remained attached for up to 17 days. In each case (N = 5) when liquid rot extract was added to the dried out tissue, the pseudoscorpion "disembarked" within 10 minutes.

Despite the disagreement over current function generated by the predation/dispersal controversy, it is generally accepted that pseudoscorpion phoresy had its evolutionary origin in predatory behavior (Beier 1948;

Weygoldt 1969). Assuming this hypothesis to be correct, small size, prehensile chelae and predacious habit constitute exaptations (sensu Gould and Vrba 1982) for pseudoscorpion dispersal. Vrba (1983) argues that exaptations may often have major consequences for macroevolutionary patterns such as magnitude of speciation in a lineage. Patterns in pseudoscorpion diversification appear to be consistent with this view (Legg 1975). The Pseudoscorpionida, with its 2000+ species (Muchmore 1982) is considerably more diverse than its sister taxon (Weygoldt and Paulus 1979), the Solpugida (900+ species, Muma 1982). Solpugids differ from pseudoscorpions in lacking prehensile chelae, an important exaptation for phoretic dispersal. Single comparisons are, of course, of limited utility: pseudoscorpions and solpugids also differ in several traits unrelated to dispersal. Nevertheless, diversification can be strongly linked to effective dispersal mechanisms in several independent lineages of terrestrial arthropods. Evidence in support of this link is provided when a contrast approach (Felsenstein 1985) is used to compare species richness in sister taxa: 1. Insecta (800,000) vs. Entognatha (2540) (Hennig 1981); 2. Araneae (35,000) vs. Amblypygi (70) (Platnick and Gertsch 1976; Levi 1982), and 3. Acari (30,000) vs. Ricinulei (33) (Weygoldt and Paulus 1979; Johnston 1982; Levi 1982). In

each contrast the taxon possessing the greater number of species also possesses more highly specialized mechanisms for dispersal: flight in the insects; ballooning in the spiders, and phoresy in the mites. Phoresy provides species otherwise confined by their limited sensory and locomotor capacities with the ability to exploit transient and discontinuous habitats (Mitchell 1970). As a result of rare, long-distance dispersal events, phoretic inseminated females could also act as propagules in founding new populations, thereby facilitating speciation (J.H. Brown personal communication). Such a mechanism would explain the existence of species apparently endemic to small islets in the Florida Keys (e.g., Parachernes bisetus, see Muchmore and Alteri 1974). Thus, at the macroevolutionary level, phoresy may have been a significant factor in the diversification of the Pseudoscorpionida.

CHAPTER 5

LIFE HISTORY CONSEQUENCES OF SEXUAL DIMORPHISM IN A CHERNETID PSEUDOSCORPION

Response to natural selection may be severely restricted by trade-offs between fitness components (Williams 1966; Gadgil and Bossert 1970; Antonovics 1976; Charlesworth 1980; Rose 1982; Schaffer 1983). Lande (1982) has argued that genetic correlations among life history traits influence the direction and rate of character change under selection, and that these correlations ultimately stem from pleiotropic effects exerted by many loci. Strong genetic correlations between homologous traits in males and females may also restrain their evolutionary divergence through sexual selection (Lande 1980; Leutenegger and Cheverud 1982; Cheverud et al. 1985). Conversely, in nonequilibrium populations sexual dimorphism could evolve even in the absence of differential selection. Greater trait variance in one sex would enable it to respond more fully to directional selection acting equally on both sexes (Leutenegger and Cheverud 1985). Consequently, species' attributes may be as much the products of phylogenetic history and genetic constraints as they are adaptive responses to recent

environments (Gould and Lewontin 1979; Cheverud et al. 1985).

The general significance of these constraints in natural populations may be best determined by empirical research which combines the correlative methods of comparative studies (e.g., Baker and Parker 1979; Ridley 1983; Felsenstein 1985) with quantitative genetic analyses. Such research would involve formulation of hypotheses concerning the functional or ecological utility of characters based on nonrandom associations between traits and environments. Mating designs and artificial selection experiments (Falconer 1981) would then be conducted on a subset of the species to establish the extent of genetic variance and covariance underlying the traits in question (see Palmer and Dingle 1986). Unfortunately, however, little empirical work has been directed towards identifying taxa amenable to both levels of analysis. One family of arachnids, the chernetid pseudoscorpions, is particularly well suited for comparative ecological study and for quantitative genetic investigation. The Chernetidae comprises more than 390 species (Chamberlin and Malcolm 1960), 75 of which occur throughout North America over a wide range of habitats (W.B. Muchmore personal communication). The small size, high fecundity and relatively short life cycles of

these pseudoscorpions enable multi-generation selective breeding programs. Presented here are preliminary findings of research whose ultimate objective is to assess the importance of genetic versus ecological factors (sensu Emlen and Oring 1977) in the evolution of sexual dimorphism in Chernetidae. Two previous papers (Chapters 2 and 3) explored the functional significance of sexually dimorphic pedipalps (Fig. 26) in the chernetid Dinocheirus arizonensis, a species inhabiting rotting saguaro cacti in the Sonoran Desert. Enlarged male pedipalps enhance aggressive ability and increase mating success under conditions of high density (Chapter 2). Female reproductive behavior, including high levels of maternal investment and short duration of sexual receptivity, appears to indirectly influence sexual selection by intensifying male combat. However, experimental work failed to show any direct effect of enlarged pedipalps on female mating decisions (Chapter 3). All chernetid males use their chelae to initiate mating by forcefully grasping the female (Weygoldt 1966,1969,1970; Thomas and Zeh 1984; Chapters 2 and 3). Despite this shared mating behavior, pedipalpal dimorphism among chernetids is highly variable with male chela size ranging from 60% to 150% of that of the female (Chapter 2). Partitioning of the variation into between- and within-genera components suggests that

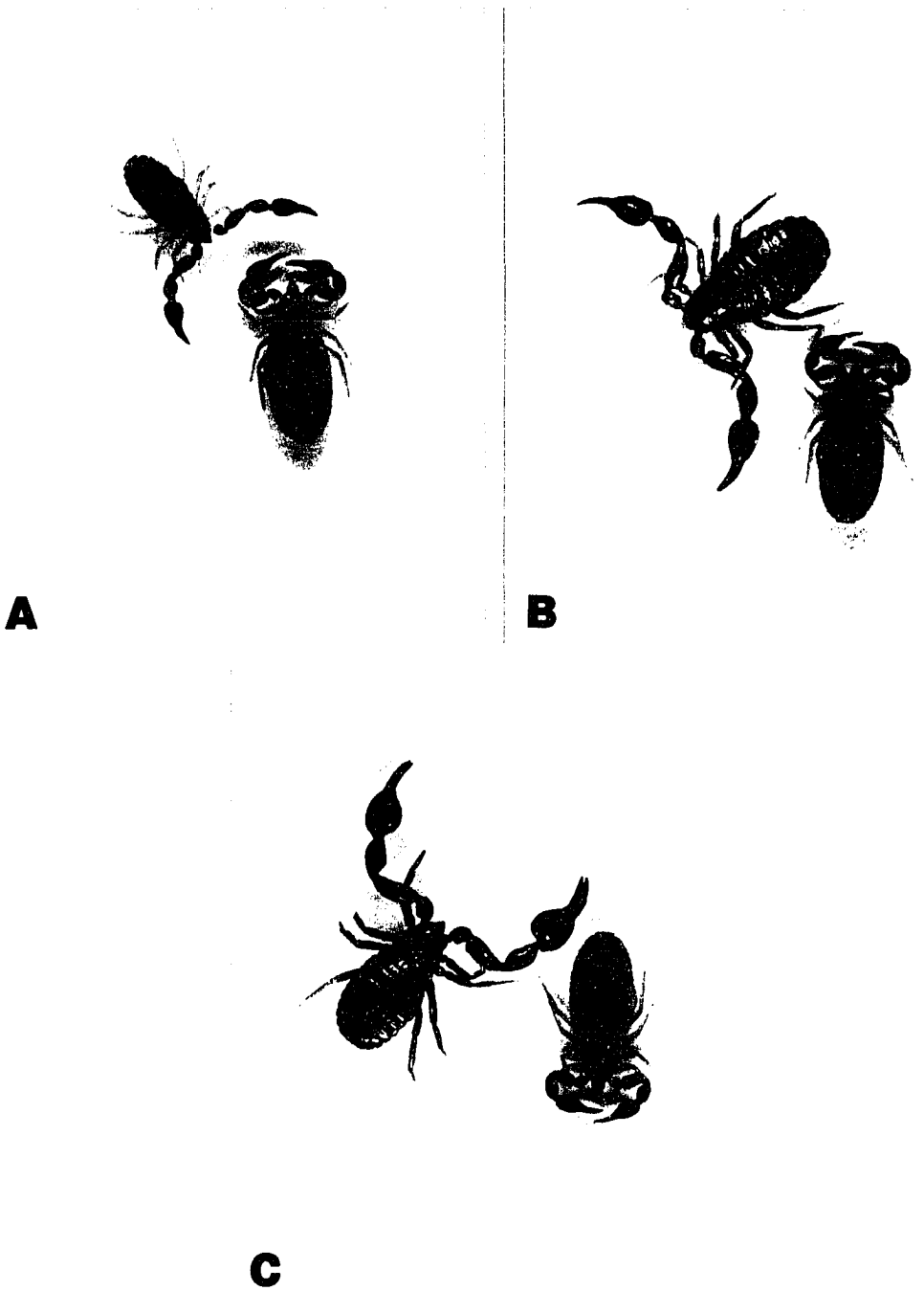


Fig. 26. Comparison between the Sexes for Pedipalp Morphology. A) young tritonymph; B) adult female, and C) adult male.

the distribution of sexual dimorphism in Chernetidae is not constrained by phylogeny (Chapter 2). This paper examines the life history consequences of sexually dimorphic pedipalps in Dinocheirus arizonensis. Two studies were conducted. One provided a detailed analysis of male versus female allocation of nymphal soma to various morphological characters of the adult stage (i.e., proportion of total mass committed to body, pedipalps and chelae). The second compared male and female adult morphologies, in addition to determining sexual differences in developmental periods (fertilization to adult). Parent-offspring regressions are used to provide initial estimates of heritability and other quantitative genetic parameters. Finally, the factors influencing sexual dimorphism in Chernetidae are considered in the light of these findings.

Materials and Methods

Experimental Populations

D. arizonensis nymphs were collected from natural populations inhabiting rotting saguaro cacti (Carnegiea gigantea [Engelm]) in the vicinity of Tucson, Arizona. Pseudoscorpions pass through three instars prior to the terminal adult molt: proto-, deuto- and tritonymph. For

the somatic allocation comparison, 42 tritonymphs matured in separate 5 dram vials at 23 ± 2°C. Each individual was provided with 2 to 3 cm^3 of larvae-rich medium taken from high density Drosophila melanogaster cultures. Sections of fibrous brown paper were crumpled to provide nesting substrate for nymphal molts. The parental generation of the developmental period/heritability study (84 individuals) was established from deutonymphs, using the same method.

Experimental Design

Somatic Allocation Comparison. At the onset of molting torpidity (see Weygoldt 1969), 24 males and 19 females were deprived of food. Within 24 hr of completion of the adult teneral period, individuals were killed with ethyl acetate, and immediately weighed on a Cahn 29 Automatic Electrobalance. Both pedipalps of each individual were severed at the proximal end of the coxo-trochanteral joint (see Chamberlin 1931) under a dissecting microscope and weighed. Chelae were then removed at the tibio-chelal joint and also weighed. Incisions were slightly biased to prevent leakage of body fluids from the segments to be measured. The following traits were assessed for each individual: total, body, pedipalp and chela weights; pedipalp mass and chela

mass as percents of total; chela mass as percent of pedipalp; adult and tritonymph chela silhouette areas (for methods see Chapter 2), and adult cephalothorax and total body lengths. Tritonymph chela silhouette area was measured from exuviae.

Developmental Period/Heritability Study. The parental generation consisted of forty-two individuals of each sex randomly paired in 5 cm diameter petri dishes. Thirty-six of the inseminated females subsequently produced 696 F_1 offspring which were reared to the deutonymphal stage as full sib families in gallon jars. D. arizonensis shows 90% to 100% survivorship when raised through one or two nymphal stages on Drosophila (personal observation). However, earlier attempts to rear individuals from fertilization to maturity on this single prey item resulted in high mortality and incomplete sclerotization in the tritonymph to adult molt (personal observation). For this reason each jar was provisioned (on two occasions) with 500 cm^3 of saguaro rot which had been mixed to ensure homogeneity and sorted to remove large insects and pseudoscorpion contaminants. Deutonymphs were transferred to individual vials to complete maturation and were maintained throughout development at 27 ± 1°C. The duration of development from fertilization to adulthood was determined to the nearest day for each individual.

Chela silhouette area and cephalothorax length of each adult were also measured, as described elsewhere (Chapter 2).

Statistical Analysis

Somatic Allocation Comparison. Comparisons between males and females were made for all 12 traits, using two-sample t-tests (BMDP Program 3D, Dixon 1983). Correlation matrices of the 12 traits were calculated separately for each sex. A repeated measures ANOVA was used to compare chela silhouette areas of males and females at the tritonymph and adult stages (BMDP 1983, Program 2V, Dixon 1983).

Developmental Period/Heritability Study. Developmental periods, chela silhouette areas and cephalothorax lengths of F_1 generation males and females were compared, using a two-way ANOVA (BMDP-83, Program 2V). For hypothesis testing, the interaction between sex and family (35 d.f.) was used as the error term since siblings were reared together during early development. Offspring-on-sire regressions weighted according to family size and intraclass correlation coefficients were used to estimate heritabilities of chela silhouette area and cephalothorax length (see Falconer 1963:203-205). Because of sexual differences in trait variance, regressions were

calculated separately for each sex with adjustment made for variance differences, as described by Falconer (1981:153-154) (analysis was carried out with BMDP 1983 Program 1R, using case weight option). The offspring-on-sire regression provides a "clean" estimate of heritability (Mitchell-Olds 1986) since it avoids potential covariance due to an environmental maternal effect. Heritabilities and their standard errors were obtained by doubling the regression coefficient and its standard error (Falconer 1981). The genetic correlation between cephalothorax length and chela silhouette area was computed, using arithmetic means of weighted cross-covariances in offspring and sires (Reeve 1955).

Results

Somatic Allocation Comparison

Overall, males weighed significantly more than females (t = 1.81, P = .0392; see Table 17), the difference being attributable to higher pedipalp mass (t = 6.11, P < .0001). Body mass (total mass minus pedipalp weight) did not vary significantly between the sexes (t = -.12, P = .4519). Although there was a positive correlation between body mass and cephalothorax length in both sexes (males: r = .657, females: r = .739), it was

Table 17. Comparison of Mean Values for Male versus Female Morphological Characters Based on Somatic Allocation Study.

Significance levels from one-tailed *t*-tests. Length in mm, mass in mg, surface area in mm^2.

Trait	Male	Female	*t*	P
Total mass (TM)	3.674	3.249	1.81	.0392
Pedipalp mass (PM)	1.384	.939	6.11	< .0001
Chela mass (CM)	.853	.496	7.75	< .0001
Proportion TM in palps (PM÷TM)	.381	.290	8.62	< .0001
Proportion PM in chelae (CM÷PM)	.614	.528	16.69	< .0001
Proportion TM in chelae (CM÷TM)	.234	.153	11.89	< .0001
Body mass (TM-PM)	2.289	2.311	- .12	.4519
Cephalothorax length (CL)	1.210	1.192	.62	.2711
Total body length (TBL)	3.163	3.309	-1.02	.1594
Chela silhouette area nymph (CSA_{ny})	.221	.179	4.88	< .0001
Chela silhouette area adult (CSA_{ad})	.744	.502	8.07	< .0001

pedipalp mass which showed the strongest correlation with cephalothorax length in males (r = .846). The greater somatic allocation to pedipalps of males relative to females (38% vs. 29% of total weight) was primarily associated with males' more massive chelae: sexual chela differences accounted for 80% of the difference in adult pedipalp weight. Variation in chela silhouette area between males and females at the tritonymph stage was significant, although small compared to adult differences. This ontogenetic divergence in chela size of the sexes is reflected in the highly significant interaction between gender and developmental stage ($F_{1,36}$ = 40.49, P < .0001, Table 19). Mass measures were generally highly inter-correlated (Table 18), with the strongest relationship existing between chela and pedipalp mass (male: r = .9941; female: r = .9902). Chela silhouette area and mass measurement were also highly correlated in both sexes (males: r = .9474; females: r = .9119). Body mass and pedipalp or chela mass were more weakly correlated in males (r = .6758, r = .6760, respectively) than in females (r = .8973, r = .8678, respectively).

Developmental Period/Heritability Study

Sexual comparisons for chela silhouette area and cephalothorax length in F_1 individuals (Figs. 2, 3 and 28)

Table 18. Phenotypic Correlations Matrices Computed Separately for A) Male and B) Female Traits Measured in the Somatic Allocation Study.

Trait	TM	PM	CM	PM+TM	CM+PM	CM+TM	TM-PM	CL	TBL	CSAny
A) CORRELATION MATRIX FOR MALES										
PM	.9354									
CM	.8334	.9940								
PM+TM	-.3984	.1628	.1400							
CM+PM	.4814	.5738	.4548	.1262						
CM+TM	-.2642	.2878	.2044	.9725	.3525					
TM-PM	.9697	.6758	.6759	-.6071	.2904	-.4824				
CL	.7702	.8448	.8387	.0413	.4830	.1458	.6548			
TBL	.5458	.3052	.3114	-.5026	.1723	-.4288	.5962	.0742		
CSAny	.3335	.4803	.4501	.2224	.0755	.2253	.2311	.5894	-.2425	
CSAad	.7859	.9436	.9474	.1701	.6471	.3134	.6344	.7395	.2976	.4181
B) CORRELATION MATRIX FOR FEMALES										
PM	.9451									
CM	.9805	.9901								
PM+TM	-.2314	.0892	.1833							
CM+PM	.1476	.2960	.4258	.2967						
CM+TM	-.1489	.1687	.2365	.9593	.5539					
TM-PM	.9923	.8974	.8679	-.3462	.1142	-.2650				
CL	.7512	.7312	.6875	-.2989	.0580	-.2212	.7384			
TBL	.5278	.4807	.4627	-.3930	.0646	-.3152	.5293	.0136		
CSAny	.5250	.5142	.4414	-.2273	-.2391	-.2440	.5151	.4754	.2843	
CSAad	.8449	.9800	.9119	-.1554	.3247	-.0201	.7978	.6107	.5490	.6524

Table 19. Repeated Measures Analysis of Variance Comparing Chela Silhouette Area of Males and Females at the Tritonymph and Adult Life History Stages.

SOURCE	SS	df	MS	F	P
Gender	.36121	1	.36121	50.95	<.0001
Error 1	.25522	36	.00709		
Life stage	3.31322	1	3.31322	761.86	<.0001
G x Ls	.17609	1	.17609	40.49	<.0001
Error 2	.15656	36	.00435		

matched those reported above: chelae were significantly larger in males ($F_{1,35}$ = 596.51, P < .0001; Table 20), while cephalothorax length did not vary between the sexes ($F_{1,35}$ = 1.35; P > .10; Table 20). The estimates obtained suggest low heritability for and high genetic correlation between chela silhouette area and cephalothorax length. The son-on-sire estimate showed chela size to be moderately heritable ($\underline{h}^2$ = .351, SE = .176; Fig. 29), although the daughter-on-sire regression produced a nonsignificant result ($\underline{h}^2$ = .074, SE = .148). A similar pattern was evident for cephalothorax length (son-on-sire: $\underline{h}^2$ = .235; SE = .168; daughter-on-sire: $\underline{h}^2$ = .090, SE = .132). The genetic correlations between chela silhouette area and cephalothorax length were positive and highly significant: son-on-sire: r_B = .874 ± .010; daughter-on-sire: r_B = .982 ± .035. Because of potential bias by both dominance and maternal environmental effects, estimates of genetic correlations based on full-sib phenotypic covariance were excluded from the analysis. At the phenotypic level, however, correlation between the sexes for chela silhouette area based on family means was highly significant (r = .481, P =.006). (The upper limit to the genetic correlation between the sexes for chela silhouette area is thus $2r_{FB}$ = .962).

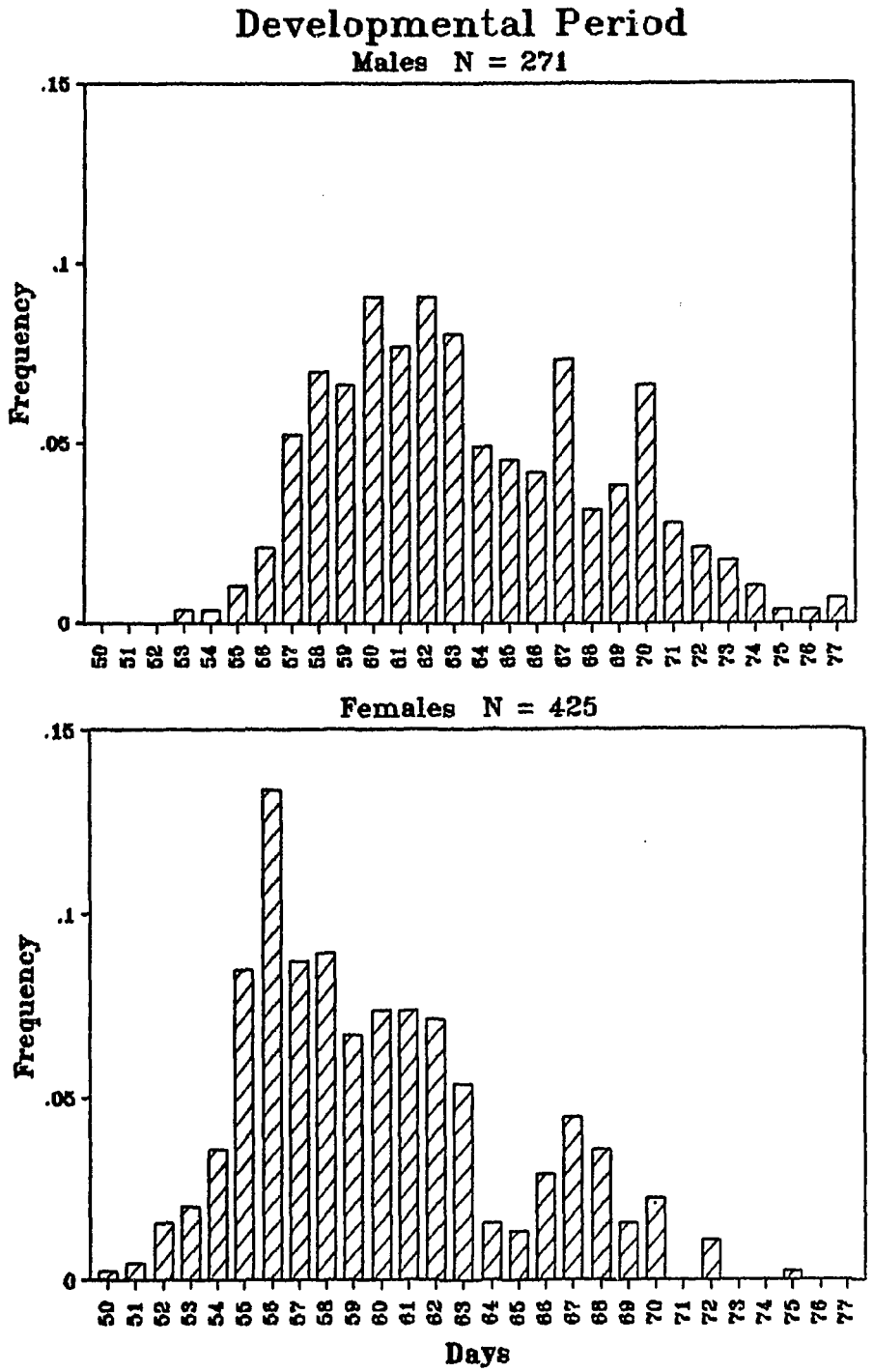


Fig. 27. Male versus Female Developmental Period.

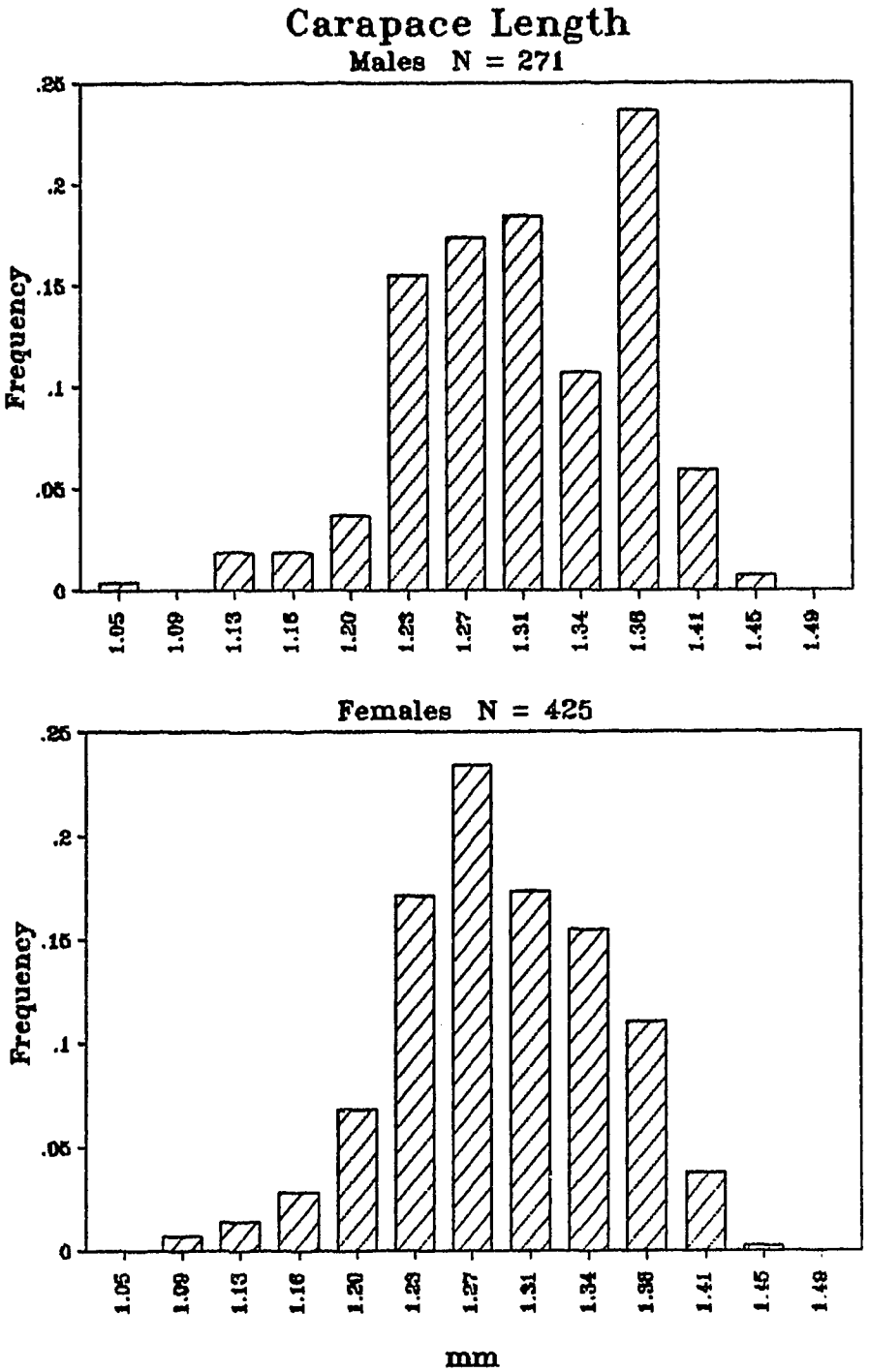


Fig. 28. Male versus Female Cephalothorax Length.

At 63.27 days, mean duration of male development was 3.20 days longer than that of the female ($F_{1,35}$ = 84.75, P < .0001; Fig. 27; Table 20). Using weighted family means, there was a marginally significant positive phenotypic correlation between developmental period and chela silhouette area in males (r = .269, P = .502). Within families, sexual dimorphism in developmental period was also positively correlated with sexual difference in chela silhouette area (r = .300, P = .038; Fig. 30).

Discussion

The morphological and life history findings reported here demonstrate that sexual dimorphism in D. arizonensis is essentially an adult phenomenon, not fully manifested until the final molt, and representing a costly investment for males. Enlarged male pedipalps enhance fighting ability and mating success (Chapter 2), but are apparently acquired at the cost of prolonged nymphal development during which males accumulate more food resources and allocate a greater proportion of these resources to adult pedipalps than do females.

It could be argued that sexual disparity in duration of development in D. arizonensis is not causally related to pedipalpal dimorphism but stems from other differences between males and females. Such a hypothesis is, however,

Table 20. Two-way Analysis of Variance Summary Table of Sexual Comparisons in the F_1 Generation of the Heritability Study.

SOURCE	SS	df	MS	F	P
A) DEVELOPMENTAL PERIOD					
Family	5196.99036	35	148.48544	12.29	<.0001
Gender	1321.93172	1	1321.93172	109.38	<.0001
F x G	423.01559	35	12.08616		
Error	9732.78057	624	15.59740		
B) CHELA SILHOUETTE AREA					
Family	1.41284	35	.04037	2.79	<.0100
Gender	8.61959	1	8.61959	596.51	<.0001
F x G	.50586	35	.01445		
Error	5.11380	624	.00820		
C) CEPHALOTHORAX LENGTH					
Family	.59891	35	.01711	3.89	<.0100
Gender	.00596	1	.00596	1.35	>.2500
F x G	.15415	35	.00440		
Error	2.18140	624	.00350		

inconsistent with: 1. the positive correlation between sexual difference in developmental period and sexual dimorphism in chela size, and 2. the absence of sexual differences in body mass after removal of the pedipalps. In fact, among arachnids it is generally the female rather than the male which is larger and matures more slowly (Thomas and Zeh 1984). This protandry (early emergence of males) is predicted to occur in association with certain life history characteristics, including discrete generations, a restricted breeding season and a limited period of female sexual receptivity (Wiklund and Fagerstrom 1977; Fagerstrom and Wiklund 1982; Bulmer 1983; Iwasa et al. 1983). By contrast, when generations overlap and/or occurrence of receptive females is staggered through time, the advantage of protandry may be outweighed, if males must compete for mates and prolonged development can confer greater competitive ability (see Trivers 1972; Warner 1984; Zeh and Smith 1985). In D. arizonensis breeding occurs throughout the year (Chapter 4). Colonization of ephemeral saguaro rots takes place through phoresy (Chapter 4) and the stochasticity of this dispersal mechanism contributes to asynchrony in generations and reproduction. Furthermore, under the high density conditions generated in patchy cactus rot habitats (Chapter 4), combat ability is a significant factor in D.

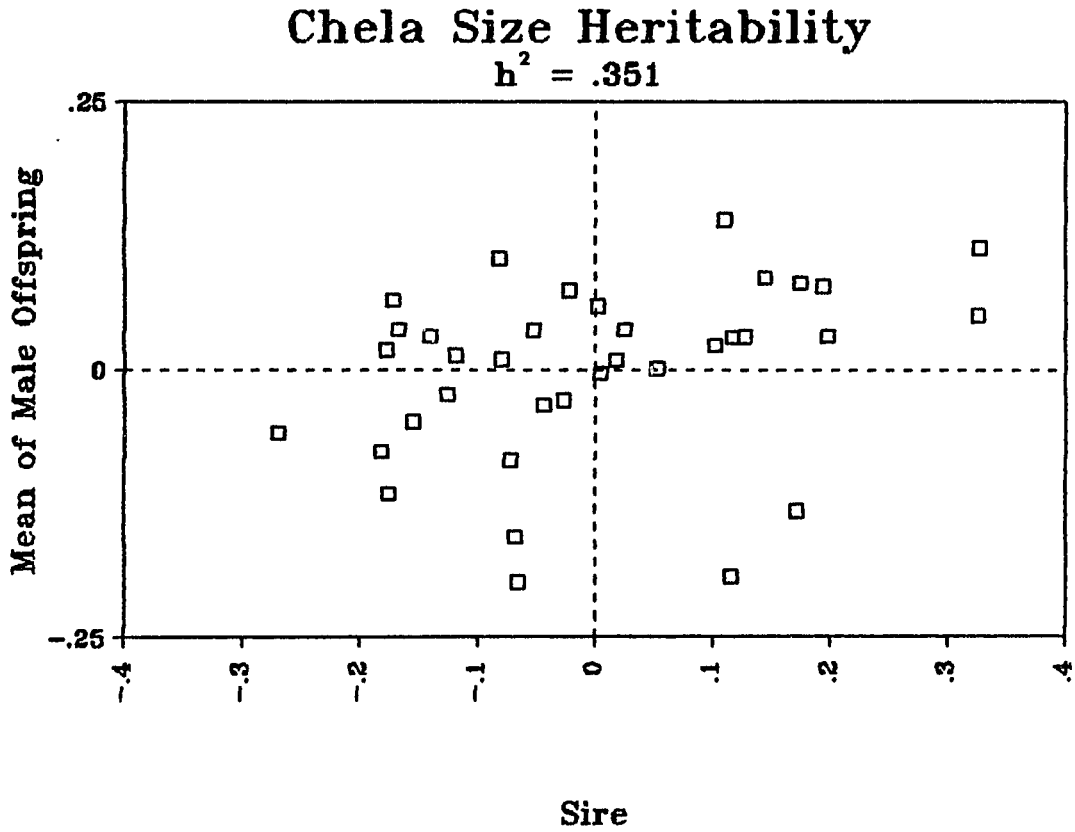


Fig. 29. Heritability of Male Chela Size. Values are graphed as deviations (in mm^e) from the mean in each generation.

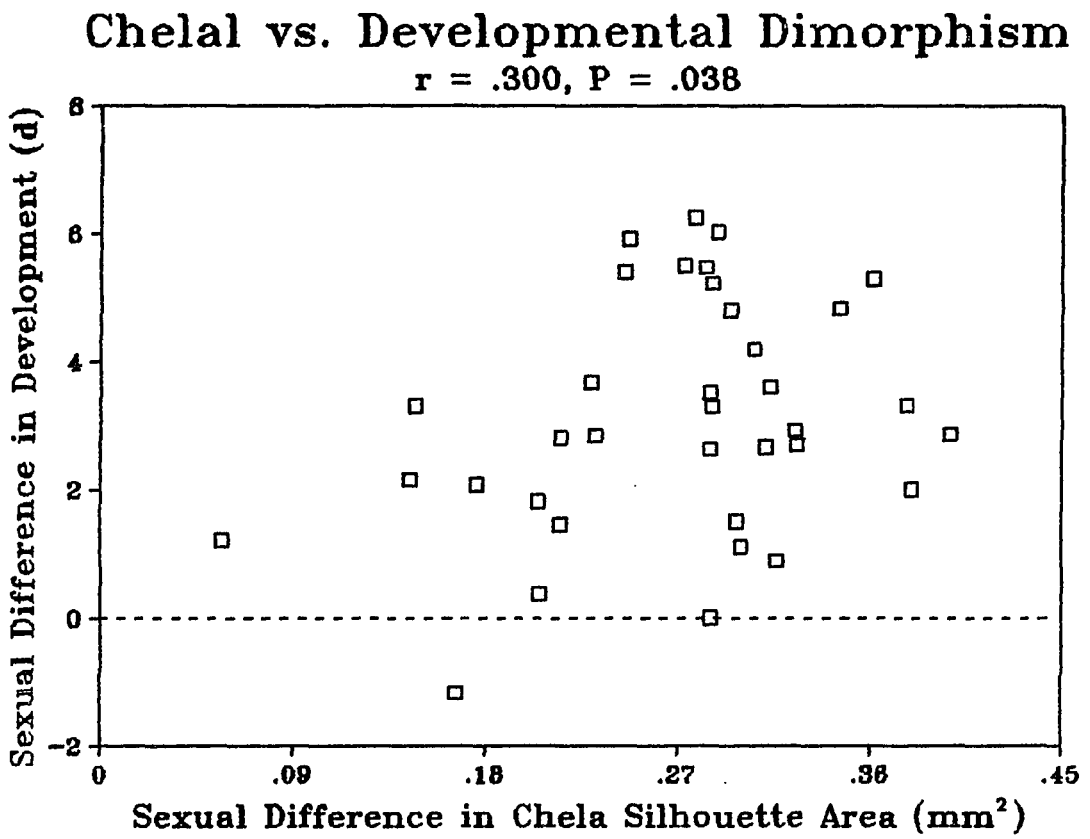


Fig. 30. Sexual Difference in Developmental Period versus Sexual Difference in Chela Silhouette Area.

arizonensis male mating success (Chapter 2).

Taken together, the results of these experiments on D. arizonensis and the correlative data on chernetid species (Chapter 2) suggest a plausible selectionist interpretation of the distribution of sexual dimorphism in the family Chernetidae. According to this hypothesis, population density and temporal patterns of female emergence/receptivity interact to determine the life history costs and benefits faced by a species, and thus influence the degree to which sexual dimorphism evolves. A test of this hypothesis requires quantitative studies of the life histories of non-sexually dimorphic chernetid species.

In order to demonstrate a connection between selection and evolution, the genetic basis of the traits involved must be determined (see Arnold 1983). This study represents the first phase in my investigation of the quantitative genetics of sexual dimorphism in chernetid pseudoscorpions. No previous work on pseudoscorpion development has entailed large-scale breeding programs, and considerable time was therefore expended in developing mass rearing techniques. As a result, the parental generation was established from field-collected nymphs, and data were limited to F_1 offspring. Due to the greater environmental variance

present in the parental generation, these results therefore probably provide minimum estimates of heritability. In addition, single generation mating designs may often fail to produce significantly non-zero estimates of quantitative genetic parameters (Mitchell-Olds 1986). Results must be interpreted cautiously, given the inherent imprecision and necessity for large sample sizes associated with such designs (Van Vleck and Henderson 1961; Falconer 1981; Mitchell-Olds and Rutledge 1986; Palmer and Dingle 1986). More precise estimates would be obtained from data on F_1 and F_2 generations of laboratory-reared populations. Nevertheless, the results reported here do provide some evidence of additive genetic variance underlying male chela size. However, they also indicate that sexual divergence in D. arizonensis may be constrained by genetic correlation between the sexes.

Sexual dimorphism in major phenotypic characters evolves through an interaction between genetic factors, life history trade-offs and selection. Life history compromises and selection may provide the impetus for enlarged male pedipalps in chernetid pseudoscorpions. However, the degree to which these factors result in sexual dimorphism may depend critically on the genetic structure of particular populations.

APPENDIX 1

LITERATURE DATA ON SEXUAL DIMORPHISM IN CHERNETIDAE

Abbreviations are as follows: Nm = number of males measured; Nf = number of females measured; MCSA = male chela silhouette area; FCSA = female chela silhouette area; Ref M = reference for morphometrics; Ref D = reference for density; ng = not given. Abbreviations for citations are as follows: B. = Banks; B.30 = Beier; BM. = Benedict and Malcolm; C. = Chamberlin; H. = Hoff; HB. = Hoff and Bolsterli; HC. = Hoff and Clawson; M. = Muchmore; MA. = Muchmore and Alteri; N. = Nelson; NM. = Nelson and Manley; Z. = Zeh.

Species	Nm	Nf	MCSA	FCSA	Ref M	Density	Ref D
Acuminochernes crassopalpus	11	11	.238	.207	H.45,49		
A. tacitus	2	3	.246	.184	H.61	4.00	H.61
Americhernes ellipticus	5	4	.220	.236	H.56	1.00	H.61
A. longimanus	1	4	.200	.172	M.76	1.33	M.76
A. oblongus	3	3	.114	.114	H.49	3.21	H.49,N.75,M76
A. reductus	7	4	.087	.096	M.76	7.00	M.76
Chernes ewingi	1	1	.128	.129	H.49	1.00	H.49,N.75
C. lyophatus	1	4	.188	.177	H.49	2.67	H.49,N.75
C. sanborni	4	1	.180	.205	H.46		
Dinocheirus aequalis	4	2	.638	.522	H.47,56	3.00	H.56
D. arizonensis	2	2	.774	.575	H.46	19.36	Z.86
D. astutus	5	14	.270	.213	H.56	5.57	H.56*
D. athleticus	4	4	.365	.252	H.56	8.40	H.56
D. horridus	4	5	.213	.249	NM.72	4.25	NM.72
D. imperiosus	3	5	.206	.174	H.56	24.00	H.56

Species	Nm	Nf	MCSA	FCSA	Ref M	Density	Ref D
D. pallidus	14	9	.294	.338	H.49,N.75	1.00	H.49
D. partitus	ng	2	.352	.330	H.47		
D. sicarius	7	7	.360	.308	C.52	8.65	C.52,BM82
D. solus	8	7	.157	.167	HB.56,H.49		
D. texanus	4	5	.288	.220	HC.52		
D. validus	6	5	.248	.190	H.47,56	2.92	H.56,61,BM.82
D. venustus	5	5	.324	.271	HC.52	41.00	HC.52*
Epactiochernes tristis	5	4	.122	.115	M.74	2.67	M.74
E. tumidus	9	5	.172	.138	M.74	8.86	M.74
Hesperochernes amoenus	10	10	.155	.185	H.62		
H. canadensis	4	5	.341	.281	H.61	6.00	H.61
H. laurae	4	2	.182	.197	M.74	7.50	C.24*
H. simulus	3	5	.259	.181	C.52	12.00	C.52*
H. mirabilis	1	1	.303	.353	H.46	3.00	B.1895
H. molestus	7	8	.300	.191	M.56	28.43	H.56*
H. occidentalis	1	0	.284	.27F	HB.56		
H. riograndensis	1	2	.157	.161	HC.52	8.00	HC.52*
H. tamiae	1	1	.413	.347	B.30	84.00	B.30*,HC.52*
H. thoracosus	4	2	.255	.235	H.48	11.00	H.48
H. unicolor	2	3	.152	.167	HC52,H47	1.00	HC.52*
H. utahensis	9	8	.175	.180	HC.52,H.56,61	5.00	HC.52*,H.56,H.61,BM.82
Illinichernes distinctus	3	3	.162	.165	H.49	5.50	H.49
I. stephensi	14	14	.194	.232	BM.82	19.84	BM.82

Species	Na	Nf	MCSA	FCSA	Ref M	Density	Ref D
Laeprochernes godfreyi	2	3	.089	.107	HB.56	2.50	HB.56
L. minor	1	2	.124	.134	H.49	2.20	H.49,H.61
Parachernes biseetus	5	15	.264	.282	MA.74	3.71	MA.74
P. diversus	2	1	.304	.332	MA.74	1.00	MA.74
P. latus	4	6	.571	.477	MA.74	4.00	H.47,MA.74
P. littoralis	14	8	.141	.166	MA.69	9.00	MA.69,74
P. nubilis	4	4	.163	.173	H.56	3.13	H.56,MA.74
P. pulchellus	3	4	.125	.169	MA.69	4.00	MA.69,74
P. rasilis	5	5	.218	.209	MA.74	7.50	MA.74
P. virginica	13	10	.155	.172	H.49,MA.74	8.88	H.49,MA.74
Paralaphochernes beckl	1	1	.084	.132	HC.52	1.00	HC.52*
P. parvus	4	3	.103	.128	H.45,49		
P. scorpioides	2	2	.084	.125	HB.56		

* Indicates collections from nests used in regression analysis (see text)

APPENDIX 2

LITERATURE DATA ON SEXUAL DIMORPHISM IN CHEIRIDIOIDEA

Abbreviations as in Appendix 1 except B. = Benedict.

Species	Nm	Nf	MCSA	FCSA	Ref M
Cheiridium insperatum	5	6	.027	.029	HC.52
C. firmum	1	11	.017	.019	H.52
Apocheiridium fergusoni	2	1	.023	.029	B.78
A. ferumoides	12	8	.032	.038	B.78
A. granochelum	3	4	.015	.019	B.78
A. inexpectum	5	8	.016	.017	B.78
A. mormon	3	3	.026	.032	B.78
A. stannardi	1	3	.025	.023	H.52
Garyops depressus*	12	11	.123	.143	H.63b
G. pumilus*	4	5	.104	.126	H.63b
Idiogaryops paludis	9	6	.049	.054	HB.56

* species names after Harvey (1985)

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