TAXONOMY, ETHOLOGY, AND ECOLOGY OF *Phidippus* (ARANEAE: SALTICIDAE) IN EASTERN NORTH AMERICA

BY

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A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL
OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1980

ACKNOWLEDGMENTS

In a work of this scope, it is impossible to individually thank every person who has contributed to its completion, but I do sincerely thank every one of you.

I would like to single out my committee members: Dr. W. H. Whitcomb, who tolerated the development of lines of research astray from his own; Dr. Jonathan Reiskind, for his positive reinforcement and assistance; and Dr. T. J. Walker, for demanding excellence.

Various types of technical assistance were provided by Mrs. Thelma C. Carlysle, Mr. P. M. Choate, Dr. Jonathan Reiskind, and Dr. Robert Paul. Special thanks are due Mrs. Katrina Vaughan for typing the manuscript and going to special effort to help make deadlines.

For identifications of prey and enemy records I thank Mrs. E. C. Beck, and Drs. W. F. Buren, R. J. Gagne, E. E. Grissell, D. H. Habeck, F. W. Harmston, L. A. Hetrick, K. W. Knopf, P. M. Marsh, F. W. Mead, E. L. Mockford, J. C. E. Nickerson, C. W. Sabrosky, R. I. Sailer, L. A. Stange, T. J. Walker, H. V. Weems, Jr., and R. E. Woodruff. Thanks are due the technical staff of the Bureau of Entomology, Division of Plant Industry, for their assistance and encouragement.

This list would not be complete without mentioning the dear friends who have put up with me and helped in so many ways: Ron and Peggy Williams, Earl Williams, Allen Mosler, Fred and Peggy Hansen, Anzle Mead, Wanda Weintraub, Ruth Schaeffer, Mary Warren; my parents, Glavis and Margaret Edwards, for their patient and continued support; and most of all, my wife, Sue, who has managed to keep both of us going.

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of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

TAXONOMY, ETHOLOGY, AND ECOLOGY OF Phidippus (ARANEAE: SALTICIDAE) IN EASTERN NORTH AMERICA

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December, 1980

Chairman: Dr. Willard H. Whitcomb
Major Department: Entomology and Nematology

The 16 species of Phidippus occurring in the eastern United States are redescribed and illustrated together for the first time. Thirteen of these species occur in Florida. First instars are briefly described for most of these species for the first time.

Both field and laboratory hybrids of P. regius x P. otiosus and F_1 backcrosses of hybrid females to males of both parent species are described. Hybrid males were sterile; hybrid females backcrossed to males of either parent species were significantly less fecund than either parent species. The two species are considered to be advanced sibling species which lack only the late stages of pre- and/or post zygotic isolating mechanisms (behavior and/or complete hybrid sterility) to completely separate each species.

The courtship behavior of 13 of the 16 eastern species, as well as the P. otiosus x P. regius hybrid, are described, 8 for the first time. A new method of communication for salticids, sound (made by a stridulatory mechanism on each palpus), is reported for P. mystaceus. A combined visual-vibratory display is reported for P. whitmani.

Differences in prey-capture behavior are noted for adult *Phidippus* proferred house flies and cabbage looper larvae. Cabbage looper larvae were captured by all species tested from an average distance of 5 - 6 mm, whereas average capture distances of house flies averaged 2 - 3.5 times this distance, depending upon the species of *Phidippus*. Prey-capture behavior was noticeably different depending upon the type of prey approached, with a much more stealthy approach used against house flies. Naive spiderlings, in similar prey-capture tests involving other types of prey, were shown to rely at least in part on experience after initial encounters with various prey types. In tests with small ants as the intended prey, the spiderlings initially attacked the ants, but were driven away by the ants. Spiderlings thereafter avoided ants for up to 4 days (the longest test), demonstrating learning of the basic trial-and-error type. That adult *Phidippus* generally avoid ants both in the field and laboratory is evidence that this type of learning is long-lasting.

Preliminary investigations with 2 lizard species indicated that *P. apacheanus* was a generalized Batesian mimic of red and black species of the velvet ant genus *Dasymutilla* (Hymenoptera: Mutillidae). Nearly all instars of *P. apacheanus* exhibited the red and black coloration; mimicry in adult males was most complete, as it included behavioral elements as well as color pattern similarity. Adult males of *P. cardinalis* are similar in color to males of *P. apacheanus*, and can probably also be considered Batesian mimics of *Dasymutilla*, although other possibilities are examined.

Most species were found to occur in several habitats, but dominant in only one, or never dominant. In habitats with more than one dominant, the phenology of the dominants was different. Some microhabitat separation was exhibited, both between species and between immatures and

adults of the same species. Prey included members of the orders Diptera, Hymenoptera, Lepidoptera, Coleoptera, Odonata, Orthoptera, Hemiptera, Homoptera and Araneae. Prey size was significantly correlated with spider size. Enemies included pompilid and sphecid wasps, acrocerid and mermithid parasitoids, mantispid and dipteran egg predators, hymenopteran egg parasites, predaceous fungi, frogs, lizards, birds, and other spiders. Mean reproductive rates correlated well with mean length of each species; _P_. _clarus_ was an exception. Niche breadth varied widely among species, and overall niche overlap was low among species. Temperature in peninsular Florida probably is less critical than in most temperate areas; however, at least one activity, hunting, ceased at temperatures below 15°C.

CHAPTER 1
GENERAL INTRODUCTION

The present research can be best described as a multi-discipline study of the biosystematics of members of the salticid genus _Phidippus_ in eastern North America, with emphasis on the species occurring in Florida. It is a natural extension and expansion of previous research (on the biology of _P. regius_; Edwards, 1975) and an offshoot of other research (e.g., Whitcomb et al., 1963) implicating species of _Phidippus_ and other salticids, as well as many other spiders, as important predators in agro-ecosystems. The final organization is in reverse order from how the research was initially conceived, from a study of the ecology of each species to a comparison of certain behaviors to the redescriptions and phylogenetic relationships of the species. The taxonomic section is presented first to introduce and describe the species. It is followed by ethological research, some of which (courtship behavior) is directly related to the phylogeny. The ecology section describes the phenology and both faunal and floral associations of the species. Finally, all three sections are interwoven to form an overview of the genus.

Adult _Phidippus_ are medium to large spiders (Figure 1-1) and often brightly colored. Generally they are docile spiders, which will attempt to hide or flee if threatened by the proximity of a human. Some can be easily handled; the specific epithet of one species (_audax_, meaning bold or audacious) was used to describe the manner of one of these spiders which would hop onto a person's hand if the hand was placed down carefully near the spider. That they can and will bite if carelessly handled is demonstrated by numerous reports in California of people bitten by P. formosus (=P. johnsoni). Elsewhere in the U. S., other species occasionally have been reported to bite humans, to which I can personally attest in the case of P. regius. The pain of the bite is light to moderate and of short duration, usually not lasting more than a few minutes. At least three species occur commonly about human dwellings: P. johnsoni along the west coast, P. audax throughout the eastern and central states, and P. regius in Florida.

Further introduction is best placed with the subject to which it appertains.

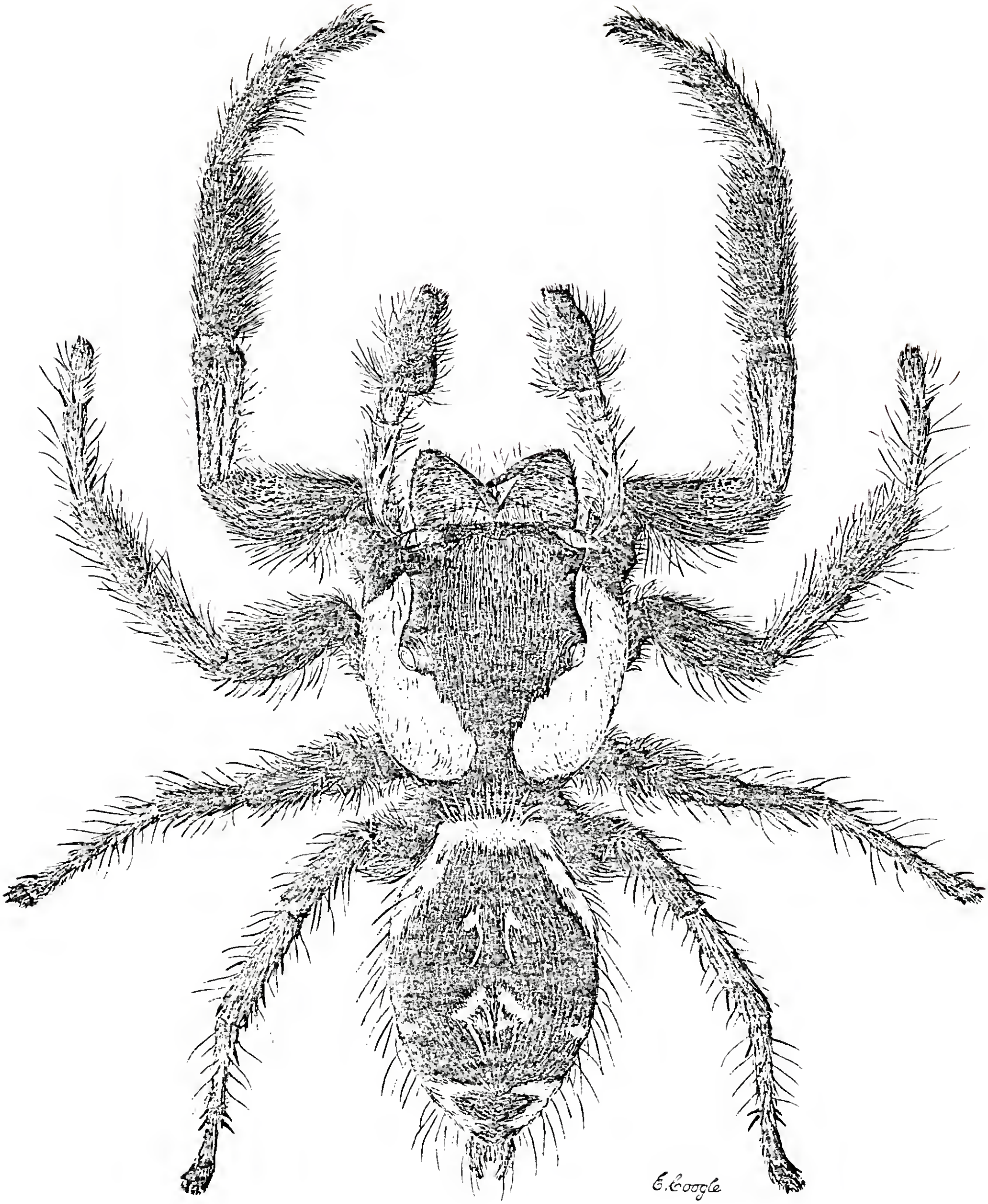


Figure 1-1. *Phidippus* habitus (dorsal view).

CHAPTER 2
TAXONOMY OF ADULT *Phidippus*

Introduction

The genus *Phidippus* has not been revised since the Peckhams' pioneering work (1901, 1909). Their 1909 paper, "Revision of the Attidae of North America," still stands as the definitive work on nearctic salticids, although numerous species and a few genera have been added subsequently to the faunal list. Little further work has been done on *Phidippus* other than new species descriptions, except for Bryant (1942), who attempted to redescribe several species; unfortunately, her paper contained several errors, and the single new species she described is placed into synonymy herein. The type species of *Phidippus* is *Salticus variegatus* Lucas = *Phidippus audax* (Hentz).

Genus *Phidippus* C. L. Koch, 1846

Attus Walckenaer (in part), 1805

Phidippus C. L. Koch, 1846

Phiale C. L. Koch (in part), 1846

Cyrtonota Simon (in part), 1864

Phidippia Simon, 1864

Megatimus Thorell, 1891

Dendryphantes (C. L. Koch, 1837) (in part), Peckham & Peckham, 1896

Synonymical listings indicate only the first use of a name prior to 1940. For complete listings before 1940 see Bonnet (1958). I have attempted to list all subsequent significant citations for species including those of Roewer (1954), which are more recent than those of Bonnet even though published earlier. For explanation of morphological structures and abbreviations, see Appendix A (Glossary). For explanation of name and place abbreviations, see Appendix B.

Medium to mostly large jumping spiders, 3.3 mm (small males) to 22 mm (large, gravid females). Integument of prosoma and prosomal appendages sclerotized, reddish brown; ocular quadrangle darker; venter often yellowish brown. Integumental surface highly reflective. Carapace width .75 to .90 length, height .50 (females) to .67 (males) width. Ocular quadrangle .40 to .50 carapace length, more coarsely reticulated than surrounding integument. PME .30 to .40 distance from ALE to PLE (nearer ALE). PLE row .75 to .90 carapace width. ALE row .56 to .85 carapace width. Clypeus radius or less of AME. Central short, longitudinal furrow within transverse depression just behind PLE row. Thoracic slope .33 carapace length, approximately 45°; cephalic area anterior to PLE slanted slightly downward.

Distinct setal tufts present in ocular area, usually 2 or 4 (0-6) situated one laterally below and lightly anterior to each PME, one halfway between each PME and PLE dorsally (always present in females), and/or a pair in the middle of the ocular quadrangle. Setal tufts are present in all free-living individuals of the genus except 1st instars, and, in several species, adult males. Scale-like setae ("scales") usually present on palpi, legs, clypeus (in females), and on various dorsal markings; sometimes covering most of dorsal surface and part of abdominal venter. Black vestitural setae more or less covering all of body surface, reduced on chelicerae and sometimes in ocular quadrangle. Elongate black setae also covering body to lesser extent, concentrated on lateral cephalic area and on anterior and lateral edges of ocular quadrangle.

Chelicerae rugose, robust, slightly porrect especially in males, and iridescent, usually gold-green-blue. Cheliceral promargin with 2 contiguous teeth (partially fused in male), retromargin with 1 tooth. Endites convergent in females, divergent and with anterolateral cusp in males. Labium longer than wide, 1/2 length of endites. Sternum slightly narrower to as wide as labium anteriorly, narrowed sharply posteriorly, 4th coxae nearly touching.

Abdomen ovoid, with dorsal pattern which varies from species to species, several variations on the presumed ancestral central dark stripe overlain by 4 pairs of light spots. In many species the 2nd spot pair is fused to form a central triangle. Usually with 2 pair of lateral bands and a basal (anterior) band, which may be fused together. The whole dorsum may be overlaid with red or gray scales which obscure the pattern, especially in males. Venter with 4 rows of dots between epigastric furrow and spinnerets; usually with light stripes bounding a dark central stripe.

The legs have a structure also occurring in Dendryphantes sensu latu that I have seen only in these 2 genera and in another dendryphantine genus, Rhetenor. On the dorsal surface of the femur, patella, and tibia are 2 longitudinal, subparallel depressions in the integument, most pronounced on the patella. These depressions are very slight in depth, but readily recognizable by the dense micro-reticulation of the integument within the depression, much denser and finer than on the surrounding integument. These depressions are also devoid of setae or scales. The depressions run nearly the entire length of each segment, except for the prolateral femoral one which is reduced to half the length of the femur. It is tempting to speculate a sensory function for this structure, but there appears to be no difference in sclerotization from the surrounding integument, nor do there appear to be any glandular structures associated with these depressions. They are even more reflective than the surrounding integument, and may function during inter-individual recognition (occurs in both sexes) somewhat like the chelicerae, which are much more coarsely reticulate over a larger surface. Another possible, passive, use is that these small reflective spots may contribute to an overall camouflage effect; they are more prominent on females which do not have as extensive leg fringes which tend to hide these structures.

Leg formula I, IV, II, III for males; IV, I, II, III (or IV, I, III, II) for females. First pair of legs half again as stout and 2nd legs slightly stouter than 3rd and 4th pairs. All legs fringed at least ventrally, especially the first pair, much more developed in males. Larger males may have proportionately larger and longer forelegs than smaller conspecific males; this appears to be an allometric growth phenomenon. Leg I of males usually fringed as follows: femur with black fringes dorsally, and on pro- and retrolateral edges of venter (area between ventral fringes glabrous and reflective distally); patella with white brush and tibia with black brush covering pro-, retrolateral, and ventral surfaces; metatarsus and tarsus with similar but reduced brushes, white on proximal half and black on distal half of each segment. White scales on prolateral surface on segments with white brushes (patella and proximal halves of metatarsus and tarsus).

Palpal femora have 1-3 dorsal macrosetae each. Leg macrosetation is restricted to the femur, patella, tibia, and metatarsus of each leg. Based on the spacing of macrosetae and the arrangement of macrosetae in other genera, the ancestral leg macrosetation is presumed to have been arranged in 4 sets on the femur and tibia and 3 sets on the patella and metatarsus. Otherwise the system of macroseta identification is similar to that used by Platnick & Shadab (1975). Ventral macrosetae are usually paired; dorsal and lateral macrosetae are single, with the dorsal macrosetae along the midline of the segment. Lateral macrosetae are sometimes marginal but are usually not identified as such unless confusion with another seta could occur. Marginal macrosetae, when necessary, are identified by the identification letters of both adjacent surfaces (e.g., DP = dorsoprolateral). If only one of a ventral pair is present, it is indicated as either pro- or retrolateral when distinguishable. Typical macrosetation is as follows: femur I*D 0-1-1-1, DP 0-0-0-2, tibia I*V 0-2-2-2, metatarsus I*V 0-2-2; femur II D*0-1-1-1, DP* 0-0-0-2, DR 0-0-0-1, tibia II V 0-1R-2-2, P*0-0-1-0, metatarsus II* V 0-2-2; femur III*D 0-1-1-1, DP 0-0-0-2, DR 0-0-0-1, patella III R 0-1-0, tibia III V 0-1P-0-2*, P 0-0-1-0, R 0-1-1*-0, metatarsus III V 0-2-2*, P 0-1-2*, R 0-1-2*, femur IV* D 0-1-1-1, DP 0-0-0-1, DR 0-0-0-1, patella IV R 0-1-0, tibia IV V 0-1P-0-2*, P 0-0-1-0, R 0-1-1*-0, metatarsus IV V 0-2-2*, P 0-1-2*, R 0-1-2*. Segments or individual sets of macrosetae marked with an asterisk (*) are invariable or nearly so. Those not so marked are more variable. Consistent differences from the above formula are noted with species descriptions. Larger specimens tend to have a fuller complement of macrosetae.

Scale-like setae, if present on legs, much denser on females and encompassing all but ventral surface of legs. Scales on legs of males predominantly on but not limited to legs I. Scales on palpi similar in females to leg scales, in males situated differently, apparently situated for display as it has evolved for each species.

Females have a well-sclerotized epigynum usually with well-developed anterolateral rims forming guides or shields over spermathecal duct openings, the latter usually bending away from each other. Males have palpi each with a simple embolus; the tegulum has an anterior rugose area (which I term the protegulum) associated with the embolus, and an external loop of the sperm duct; and usually a simple lateral (ectal) tibial apophysis.

The genus is most readily recognized by the possession of a dorsal pair of setal tufts, iridescent chelicerae, conspicuous leg fringes, and generally by their large size and dense vestitural setal covering. *Phidippus* is a typical genus of the Salticidae: Dendryphantinae and is most closely related to *Dendryphantes* *sensu* *latu* (i.e., including *Metaphidippus* and *Eris*).

Figures 2-1 and 2-2 illustrate the body parts used in the descriptions. Body measurements and ratios for the species under consideration in this study are given in Table 2-1. Characters on which hypothetical phylogeny are based are given in Table 2-2, and the resulting phylogeny is illustrated in Figure 2-3.

The following species included in *Phidippus* by Chamberlin and Ivie (1944), based on the descriptions by Walckenaer (1837) of Abbot's (1792) unpublished illustrations, are considered to be *nomena* *dubia*; their descriptions give little or no clue as to their specific identity, and the types are illustrations which contribute little to their identification. Also included here are species left in the genus *Attus* by Chamberlin & Ivie (ibid), but which are probably juvenile *Phidippus*; these latter are marked with an asterisk.

Table 2-1. Measurements and ratios of body parts of species of *Phidippus* occurring in the eastern U. S. See Glossary (Appendix A) for explanation of abbreviations. Ranges represent smallest (on left) and largest specimens examined.

Phidippus species,	sex	ALE-PME / ALE-PLE	ALE / CW	PLE / CW	CW
apacheanus	♂	.33-.31	.67-.65	.84-.81	2.8-3.9
	♀	.32-.31	.63-.61	.84-.83	4.4-4.5
audax	♂	.35-.32	.71-.59	.85-.75	2.9-5.5
	♀	.35-.30	.71-.56	.89-.78	3.4-5.4
borealis	♂	.40-.35	.66-.64	.77-.76	3.1-3.5
	♀	.36-.38	.63-.62	.78-.77	3.7-3.9
cardinalis	♂	.36-.31	.72-.64	.87-.82	3.0-3.9
	♀	.36-.32	.68-.62	.86-.85	3.6-4.2
clarus	♂	.42-.39	.79-.69	.87-.84	2.5-3.9
	♀	.40-.35	.73-.69	.83-.80	3.1-5.0
insignarius	♂	.42-.39	.74-.69	.82-.83	2.3-3.1
	♀	.43-.40	.83-.69	.97-.88	2.3-3.3
mystaceus	♂	.43-.41	.79-.71	.86-.84	2.7-3.4
	♀	.39-.36	.76-.71	.90-.89	3.4-4.2
otiosus	♂	.39-.32	.69-.58	.83-.74	3.9-5.6
	♀	.41-.30	.73-.54	.88-.71	3.5-7.0
pius	♂	.42-.37	.73-.70	.87-.84	2.6-3.2
	♀	.39-.38	.67-.68	.84-.86	2.8-3.1
princeps	♂	.39-.39	.75-.79	.87-.89	2.5-2.9
	♀	.41-.37	.68-.70	.83-.86	2.9-3.6
pulcherrimus	♂	.39-.40	.82-.72	.89-.86	2.6-3.5
	♀	.43-.36	.84-.70	.89-.87	3.1-3.9
purpuratus	♂	.36-.33	.70-.63	.89-.80	3.3-4.1
	♀	.34-.35	.72-.62	.90-.81	3.5-4.3
putnami	♂	.42-.42	.86-.76	.94-.89	2.5-3.4
	♀	.43-.42	.82-.76	.95-.91	2.9-3.8
regius	♂	.37-.31	.64-.49	.76-.63	4.2-7.5
	♀	.32-.36	.63-.55	.80-.72	4.9-6.7
whitmani	♂	.42-.39	.77-.71	.85-.85	2.7-3.4
	♀	.42-.40	.78-.74	.89-.85	2.5-3.5
xerus	♂	.37-.34	.75-.72	.89-.87	2.6-3.2
	♀	.38-.36	.76-.70	.90-.90	2.8-3.6

Table 2-1 - extended.

$\frac{CW}{CL}$	CL	$\frac{LOQ}{CL}$	BL	$\bar{X}$ BL
.74-.78	3.8-5.0	.47-.46	5.18-10.63	7.25
.76-.77	5.7-5.9	.46-.45	7.08-13.35	10.69
.81-.87	3.6-6.3	.51-.45	4.36-15.24	8.39
.77-.78	4.5-7.0	.49-.41	4.48-18.10	10.93
.80-.76	3.9-4.6	.47-.43	4.90- 9.05	7.58
.77-.80	4.9-4.9	.46-.43	8.45-13.81	10.96
.78-.83	3.8-4.7	.51-.49	4.36- 9.52	6.90
.79-.83	4.5-5.1	.48-.49	6.00-14.29	10.06
.79-.82	3.2-4.8	.54-.50	3.27-10.10	6.37
.81-.85	3.8-5.9	.51-.47	4.29-14.17	8.48
.83-.79	2.8-3.9	.51-.47	4.91- 7.81	6.32
.72-.81	3.1-4.0	.51-.50	5.45- 9.90	7.65
.81-.84	3.3-4.0	.52-.49	4.91- 8.57	6.96
.79-.81	4.3-5.2	.52-.46	6.81-13.33	9.84
.82-.88	4.8-6.4	.45-.43	6.27-13.65	10.04
.81-.93	4.3-7.8	.50-.46	7.63-17.10	13.10
.76-.78	3.5-4.1	.48-.51	4.91- 8.72	6.21
.81-.74	3.5-4.2	.49-.42	6.00-10.48	7.79
.79-.70	3.2-4.1	.47-.45	4.36- 8.54	6.75
.84-.78	3.4-4.7	.50-.46	6.00-11.46	8.34
.77-.77	3.3-4.5	.49-.47	6.25- 8.54	7.32
.76-.84	4.1-4.6	.47-.49	8.48-11.98	9.87
.76-.87	4.4-4.7	.48-.50	5.18-10.48	8.31
.81-.80	4.3-5.3	.51-.46	8.18-14.76	10.07
.78-.77	3.2-4.4	.54-.49	5.18- 9.06	6.94
.73-.81	4.0-4.4	.49-.50	6.00-11.88	8.98
.85-.90	4.8-8.3	.49-.42	6.00-17.78	11.78
.79-.80	6.2-8.3	.47-.38	6.63-21.88	14.80
.78-.79	3.5-4.3	.49-.49	4.09- 9.58	6.38
.74-.73	3.4-4.8	.50-.45	5.18-11.56	8.05
.81-.76	3.2-4.2	.50-.46	5.90-10.20	7.70
.75-.78	3.7-4.6	.50-.49	8.60-11.70	10.20

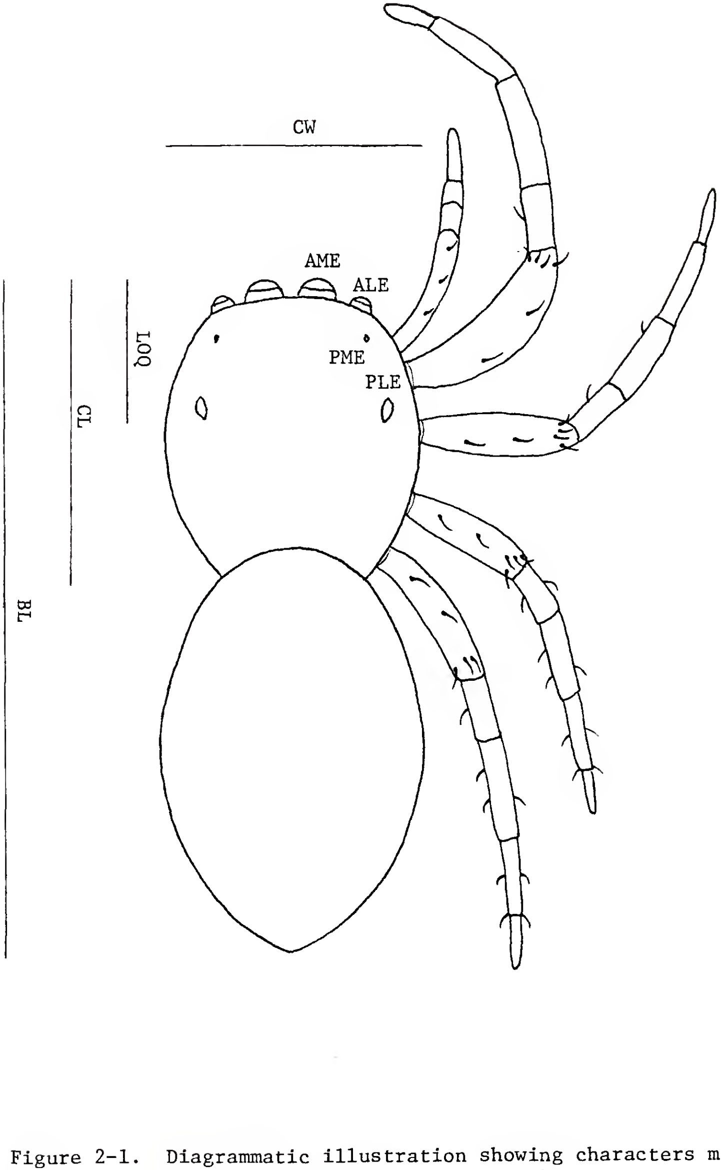


Figure 2-1. Diagrammatic illustration showing characters measured and macrosetae of legs of Phidippus (dorsal view).

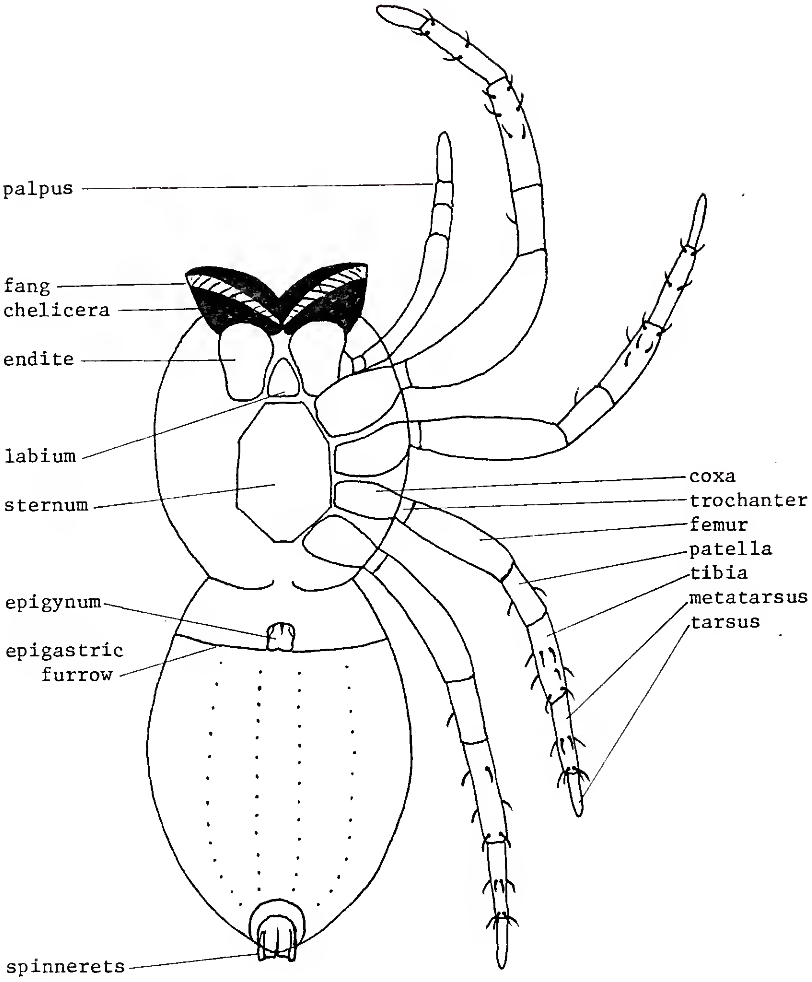


Figure 2-2. Diagrammatic illustration of Phidippus showing ventral characters and leg macrosetae.

Table 2-2. Characters used to construct hypothetical phylogeny of species of Phidippus in the eastern U. S. See Glossary (Appendix A) for definitions of terms. Characters are considered primitive or derived based on frequency of occurrence within Phidippus (more common are considered more primitive) or by comparison with sister group (Dendryphantes); characters shared between the two genera are considered more primitive.

	Character	Primitive	Derived
1.	Epigynum guides	absent	present
2.	Epigynum septum	absent	present
3.	Epigynum surface	smoothly sloping	depressed centrally
4.	Embolus shape	cylindrical	sickle-shaped
5.	Lateral tufts	absent	present
6.	Abdomen spotted	yes	no
7.	Chelicera tubercle	absent	present
8.	Carapace transverse bands	absent	present
9.	Leg I fringe	black & white	white only
10.	2nd Abdominal spots	separate	fused
11.	Epigynum surface	smoothly sloping	elevated centrally
12.	Leg I fringe	black & white	black & orange
13.	Ventral lateral stripes	white	black or gray
14.	Ventral stripes	2 white	3 light gray
15.	Ventral stripes	2 white	2 or 3 black
16.	Embolus tip	cylindrical	flared
17.	Central tufts	absent	present
18.	Tibial apophysis	simple	bifid at tip

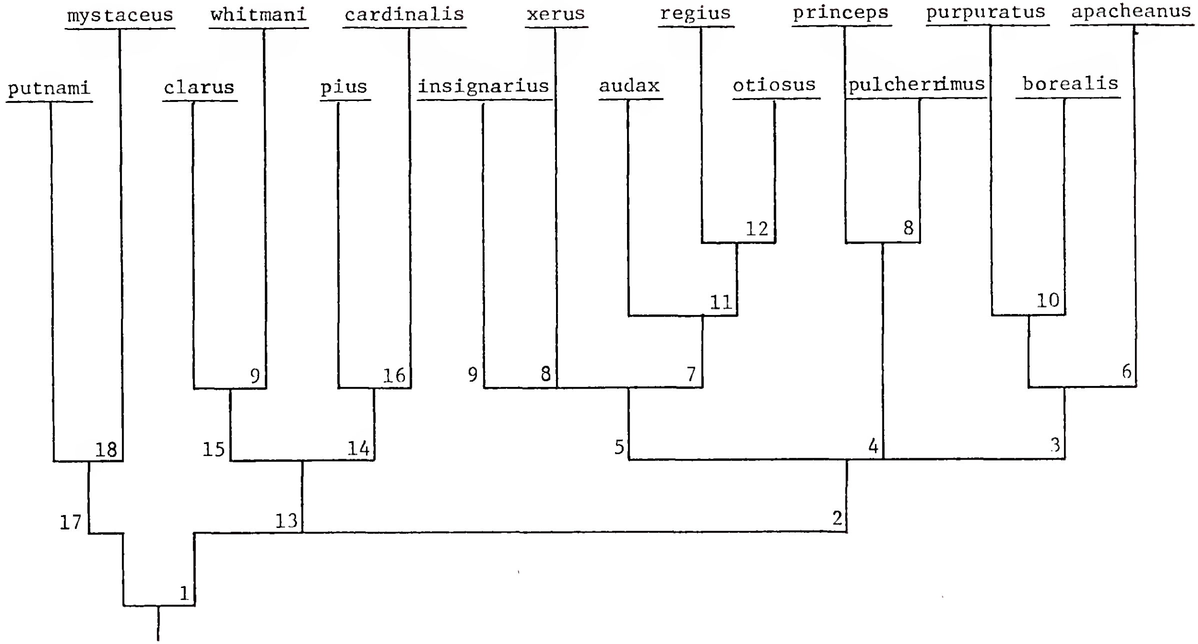


Figure 2-3. Cladogram of eastern species of Phidippus, based on characters listed in Table 2-2.

Attus cinereus Walckenaer, 1837

A. dissimulator Walckenaer, 1837

A. excubitor Walckenaer, 1837

A. explorater Walckenaer, 1837*

A. fraudulentus Walckenaer, 1837

A. infestus Walckenaer, 1837*

A. insidiosus Walckenaer, 1837

A. investigator Walckenaer, 1837

A. latus Walckenaer, 1837

A. multivagus Walckenaer, 1837*

A. pileatus Walckenaer, 1837

A. pilosus Walckenaer, 1837

A. purpurarius Walckenaer, 1837

A. rimator Walckenaer, 1837

A. sagax Walckenaer, 1837

A. scrutator Walckenaer, 1837*

A. signatus Walckenaer, 1837

A. tridentiger Walckenaer, 1837

The descriptions of the following species are also equivocal:

Phidippus carolinus C. L. Koch, 1846

P. testaceus C. L. Koch, 1846

Attus rupicola Hentz, 1846

Attus sinister Hentz, 1850

Other species considered *nomina dubia* are listed with their suspected synonyms.

Species misplaced in *Phidippus*

P. fasciatus Koch & Berendt = *Gorgopis fasciata* (Koch & Berendt)

P. formosus Koch & Berendt = *Gorgopis fasciata* (Koch & Berendt)

P. frenata Koch & Berendt = *Gorgopis frenata* (Koch & Berendt)

P. impressus Koch & Berendt = *Gorgopis melanocephala* (Koch & Berendt)

P. marginatus Koch & Berendt = *Gorgopis marginata* (Koch & Berendt)

P. melanocephalus Koch & Berendt = *Gorgopis melanocephala* (Koch & Berendt)

P. paululus Koch & Berendt = *Gorgopis frenata* (Koch & Berendt)

P. pusillus Koch & Berendt = *Gorgopis frenata* (Koch & Berendt)

P. bucculentus Gerstäcker = *Thyene bucculenta* (Gerstäcker)

P. inflatus Gerstäcker = *Thyene inflata* (Gerstäcker)

P. orbicularis Gerstäcker = *Thyene orbicularis* (Gerstäcker)

P. chrysis, Banks = *Dendryphantes aurantius* (Lucas)

P. disjunctus Banks = *Dendryphantes disjunctus* (Banks)

P. fartilis, Banks = *Dendryphantes fartilis* (Peckham & Peckham)

P. fraternus Banks = *Dendryphantes aurantius* (Lucas)

P. funebris Banks = *Dendryphantes funebris* (Banks)

P. luteus, Banks = *Dendryphantes luteus* (Peckham & Peckham)

P. marmoratus, Banks = *Dendryphantes fartilis* (Peckham & Peckham)

P. militaris, Peckham & Peckham = *Dendryphantes marginatus* (Walckenaer)

P. molinor Chamberlin = *Dendryphantes marginatus* (Walckenaer)

P. multicolor Banks = *Dendryphantes aurantius* (Lucas)

P. nigropilosus Banks = *Dendryphantes nigropilosus* (Banks)

P. orichalceus Peckham & Peckham = *Dendryphantes aurantius* (Lucas)

P. capitatus, Banks = *Dendryphantes galathea* (Walckenaer)

P. parvus F. O. P.-Cambridge = *Dendryphantes galathea* (Walckenaer)

P. cyanidens C. L. Koch = *Parnaenus cyanidens* (C. L. Koch)

P. keratodes Hasselt = *Hyllus keratodes* (Hasselt)

The several species described from India by Tikader (e.g., 1974) as *Phidippus* species do not belong in this genus; I am unable to place them at present.

I have included in the keys to species alternate characters for each species in cases where the destruction or absence of one character might cause confusion. The reader should be aware of populations variable in color pattern, especially of *P. audax*. I have attempted to use characters which would avoid problems in the keys caused by color pattern, although the latter character is used to some extent. Geographic area is included where it might be helpful. The term "semi-encircled" means that the periphery of the dorsum of the abdomen is covered with colored scales except for the posterior end, which is covered by part of the central black stripe. The dorsum of the carapace does not include the clypeus, sides or thoracic slope.

Key to Adult Male Phidippus of the Eastern U. S.

1. Ocular setal tufts or crests present 2

1'. Ocular setal tufts or crests absent 8

2. Ocular quadrangle with pair of setal crests and single white triangular spot, without setal tufts *putnami*

2'. Without crests or single spot, with 2 or 4 setal tufts 3

3. With 4 setal tufts, both dorsal and lateral 4

3'. With 2 dorsal setal tufts only 6

4. Ocular quadrangle with 3 red (rarely white or absent) spots arranged transversely, abdomen gray with white spots and very hirsute, palpal tibial apophysis bifid at tip *mystaceus*

4'. Ocular quadrangle without spots, abdomen not gray or exceptionally hirsute, palpal tibial apophysis simple 5

5. Leg I fringe white, abdomen orange to red; not in Florida *insignarius*

5'. Leg I fringe black and orange, abdomen black with yellow to orange spots; SE U. S., Atlantic coast to MD *otiosus*

6. Dorsum of carapace and abdomen red *apacheanus*

6'. Dorsum of carapace black, abdomen semi-encircled with tan or yellow to red 7

7. Embolus projecting distally post protegulum; Canada and adjacent states *borealis*

7'.	Embolus not projecting distally post protegulum	*purpuratus*
8.	Embolus sickle-shaped	9
8'.	Embolus not sickle-shaped	10
9.	Carapace unmarked, dorsum of abdomen completely red (rarely brown with white spots); not in Florida	*princeps*
9'.	Carapace with a short white band behind each PLE, abdomen semi-encircled with red; SE U. S.	*pulcherrimus*
10.	Dorsum of carapace and abdomen orange to red	11
10'.	Dorsum of carapace black, of abdomen variable	13
11.	Posterior half abdominal dorsum with 2 pair of white spots, venter with 3 black stripes, leg I fringe white	*whitmani*
11'.	Posterior half abdominal dorsun with 2 black stripes enclosing 2 pair white spots, venter otherwise, leg I fringe black and white	12
12.	Venter of abdomen with 3 gray stripes on pale background, embolus flared distally	*cardinalis*
12'.	Venter of abdomen black, embolus slender and hooked distally	*pius*
13.	Addomen with pair of red stripes, 2nd spot pair separate or no spots	*clarus*
13'.	Abdomen without stripes, 2nd spot pair fused	14
14.	White transverse bands behind PLE; small species, Florida endemic	*xerus*
14.'	White submarginal bands below PLE or usually carapace unmarked	15
15.	White posterior abdominal spots linear (all light spots may be fused and yellow to orange), abdomen dorsum with metallic black scales surrounding 8 quadrangular black spots	*audax*

15'. White posterior abdominal spots oval, black areas monotonous, without metallic scales; large species, SE U. S., Atlantic coast to VA regius

Key to Adult Female Phidippus of the Eastern U. S.

1. Epigynum without anterolateral guides 2
1'. Epigynum with anterolateral guides 3
2. Ocular area with 6 setal tufts, quadrangle with a white or tan triangular spot, abdomen brown with white spots putnami
2'. Ocular area with 4 or 6 setal tufts, quadrangle with 3 white spots arranged transversely, abdomen gray with white spots, hirsute mystaceus
3. Epigynum with deep transverse depression in middle third 4
3'. Epigynum without depression 6
4. Dorsum of carapace and abdomen yellow to red apacheanus
4'. Dorsum of carapace gray or black, of abdomen otherwise 5
5. Abdomen semi-encircled with tan to orange, 2nd spot pair fused; Canada and adjacent states. borealis
5'. Abdomen gray, sometimes semi-encircled with white, 2nd spot pair not fused purpuratus
6. Epigynum elevated immediately posterior to septum in center of epigynal plate 7
6'. Epigynum essentially flat or gradually sloping upward posteriorly, with or without distinct septum 8
7. Carapace with distinct submarginal bands, posterior abdominal spots enlarged and quadrangular; SE U. S., Atlantic coast to MD otiosus

7'. Carapace rarely with distinct bands, usually either without markings or covered with colored scales, posterior abdominal spots oval, not enlarged; large species, SE U. S., Atlantic coast to VA <u>regius</u>

8. Abdominal venter white with black or gray lateral stripes, usually with narrow median dark stipe; 2nd spot pair separate 9

8'. Abdominal venter black with or without lateral white stripes; 2nd spot pair fused or no dorsal pattern 12

9. Posterior abdomen with 2 pair white spots, dorsum of carapace and abdomen red to brown, 3 black ventral stripes <u>whitmani</u>

9'. Posterior abdomen with 2 black stripes enclosing 2-3 pair white spots, dorsum and venter variable 10

10. Two black ventral stripes (median stripe absent), abdomen dorsum gold to reddish-brown, usually darker in central stripe between spots <u>clarus</u>

10'. Three light gray ventral stripes, abdomen dorsum variable in color 11

11. Dorsum of carapace and abdomen red to brown, width of posterior epigynal notch 3 times its length, equal in width to distance between duct openings <u>cardinalis</u>

11'. Dorsum of carapace and abdomen yellow to orange, width of posterior epigynal notch 2 times its length, less in width than distance between duct openings <u>pius</u>

12. Dorsum of carapace and abdomen brown, without paired spots (rarely with fused 2nd pair and separate 3rd and 4th pairs, all white); not in Florida <u>princeps</u>

12'. Dorsum otherwise 13

13. Ocular area with 4 distinct setal tufts, abdomen semi-encircled with yellow to red 14

13'. Ocular area with 2 dorsal tufts only, the lateral setae not concentrated into a tuft, but spread out into a weak fringe, abdomen variable 15

14. Uniquely-shaped white spot in middle of ocular quadrangle, short yellow-orange transverse bands behind PLE or entire carapace encircled with gray and/or yellow-orange scales; Florida endemic *xerus*

14'. No spot in ocular quadrangle, carapace with white submarginal bands below PLE or carapace encircled with white scales; not in Florida *insignarius*

15. Short white to tan transverse bands behind PLE or entire carapace encircled with white or tan scales, abdomen semi-encircled with yellow to red, black quadrangular spots present but mostly covered by semi-encircling band of scales; SE U. S. *pulcherrimus*

15'. Carapace without markings or with white submarginal bands below PLE, never encircled by scales, abdomen rarely semi-encircled by white or orange, 2nd-4th pair spots rarely fused together and/or orange, black metallic scales encircling 8 black quadrangular spots. *audax*

Subgenus Anipalpus, new subgenus

The name of the subgenus is a contraction of "animated pedipalpus," referring to the unusual use of the palpi during courtship by males of the included species. I designate *Phidippus putnami* as the type species of this subgenus.

Two species in this subgenus occur in the eastern U.S., P. putnami and P. mystaceus. Females of both species have 6 ocular setal tufts (the central pair is occasionally missing). The epigyna of both species lack guides; the spermathecal duct openings are in a narrow slit. The emboli of the males have been modified (flattened) to fit into the slit. Males of P. putnami have a double setal crest in the ocular quadrangle, while males of P. mystaceus have a stridulatory organ on each palpus. Males of both species have yellow fringes on the legs I. The subgenus is characterized by the 6 tufts, the slit openings in the epigynum and the flattened embolus.

Phidippus putnami (Peckham & Peckham), 1883

Figures 2-4, 2-21

Attus putnamii Peckham & Peckham, 1883; type in MCZ, examined

Phidippus gracilis Keyserling, 1884 (synonymized by Peckham & Peckham, 1909)

Plexippus putnamii, Peckham & Peckham, 1888

Philaeus princeps (not Peckham & Peckham), Banks, 1892

Phidippus putnamii, Peckham & Peckham, 1901, 1909; Bryant 1942; Muma 1944, 1945; Bonnet, 1958; Richman & Cutler, 1978; Oehler, 1980

P. otiosus, Peckham & Peckham, 1909 (in part, ♀; Plate 34, fig. 6a, f)

Dendryphantes putnami, Petrunkevitch, 1911; Roewer, 1954

The female was illustrated as early as 1909 by the Peckhams, but thought to be a variety of P. otiosus.

Males have yellow leg fringes and light metallic blue femur in more northern specimens, mostly white leg fringes (with a few yellow setae) and dark metallic blue femur in more southern specimens.

MALE: integument dark; carapace with white bar just below and behind each PME, large white triangle between PLE, third white bar (often rubbed off) anteriorly at apex of triangle, short white stripe directly behind center of triangle; yellow fringe of setae over anterior eyes, dense cover of bluish gray setae across anterior dorsal ocular area; no ocular tufts, instead dorsal black setal crests originating from between PME and PLE extending forward ental to PME almost to level of ALE; chelicerae proximal half each side with scales in 3 vertical white and 2 vertical red stripes, with a red transverse bar below stripes, distal half iridescent blue covered with bluish-gray setae; clypeus covered with red scales, fringed with white setae; palpal femur covered dorsally with white scales, tibia with long ectal fringe of white-tipped black setae, cymbium fringed with black setae and covered dorsally with bluish-gray setae; leg I fringes all yellow or all white except black setae mixed in on prolateral tibia, covered dorsally with white scales; femur I dorsal fringe rudimentary, ventral setal fan pale yellow, distal prolateral and ventral surfaces covered densely with white scales and white or yellow prolateral setal fan, retrolatero-ventral edge with elongate tuft of pale yellow setae, swollen ventrally, light to dark metallic blue on pro-, retrolateral, and ventral surfaces; dorsal abdominal markings white; venter of abdomen blue-black or black bordered laterally by wide white stripes.

FEMALE: integument normal color; carapace with dorsal markings as in male or covered with white scales, chelicerae covered with white setae on proximal half, metallic green distal half; 6 ocular tufts, the midocular pair somewhat smaller than the other 2 pair, rarely lacking; clypeus, palpi, and legs with white setal fringes; abdominal integument brown, bronze, or black, dorsal abdominal spots white or tan.

LEG MACROSETATION: no consistent differences; sometimes metatarsi III & IV V 0-0-1 or 0-0-2.

Phidippus mystaceus (Hentz), 1846

Figures 2-5, 2-22

Attus mystaceus Hentz, 1846; type destroyed

Phidippus asinarius C. L. Koch, 1846; (synonymized by Marx, 1890)

Phidippus electus C. L. Koch, 1846; (synonymized by Marx, 1890)

Cyrtonota multivaga, Simon, 1864; not *Attus multivagus* Walckenaer, 1837, a NOMEN DUBIUM

Phidippus mystaceus, Emerton, 1877; Peckham & Peckham, 1909; Muma, 1944; Muma & Jeffers, 1945; Bonnet, 1958; Specht & Dondale, 1960; Whitcomb et al., 1963; Berry, 1970; Edwards, in Richman & Cutler, 1978; Oehler, 1980

Phidippus incertus Peckham & Peckham, 1901; type in MCZ, examined (synonymized by Peckham & Peckham, 1909)

Dendryphantes mystaceus, Petrunkevitch, 1911; Roewer, 1954

Phidippus hirsutus Barrows, 1919; type in OSU, examined (synonymized by Edwards, in Richman & Cutler, 1978)

P. incertus, Bryant, 1942; Warren et al., 1967

P. hirsutus, Bryant, 1942; Kaston, 1948; Whitcomb et al., 1963

Dendryphantes hirsutus, Roewer, 1954

Hentz's written description could fit either *P. mystaceus* or *P. purpuratus*, but his illustration of the extra long setal tufts on the carapace indicates that the species he was describing was *P. mystaceus*. Stability of nomenclature also favors retaining *P. mystaceus* for this species.

MALE: carapace integument with dark blue tinge, ocular area with 3 red-orange transverse spots; chelicerae iridescent green; 4 long ocular tufts; clypeus with mixed yellow and white fringe over-hanging proximal two-thirds of chelicerae; palpi with white lateral fringes on patella and tibia, dorsal cymbium with white and yellow setae and central spot of white and yellow scales; aplpi with short, blunt macrosetae encircling tip; leg I femur lacks dorsal fringe, with dorsal subproximal black setal tuft projecting anteriorly, venter with band of yellow scales, prolateroventral fringe lacking, prolateral surface metallic dark blue, dorsal distal edge of femur and all other segments covered with yellow scales, all fringes yellow; legs II-IV with yellow scales on distal segments and white scales on proximal segments; dorsum of abdomen with pattern like female overlain with long gray setae; venter of abdomen gray with 4 rows of pale dots.

A single dimorphic male of *P. mystaceus* is known. It is similar to the typical males with the following differences: carapace covered dorsally, laterally, and posteriorly with red scales, edged with yellow scales posteriorly; rounded transverse integumental ridge in ocular quadrangle (similar to *P. toro* Edwards); 4 typical setal tufts absent, instead 2 central tufts in ocular quadrangle.

FEMALE: similar to male with following differences: integument normal color, carapace covered with gray scales, ocular spots white outlined in black; third pair weak ocular tufts often present between ocular spots; clypeus covered with white scales, clypeus and palpi fringed with white setae, overhanging chelicerae as in male; legs covered with scales and having simple fringes, both white on females from eastern states, both yellow on females from midwestern states.

LEG MACROSETAE: metatarsus III & IV V 0-1-2.

Subgenus Phidippus

The remainder of the species of the eastern U. S. belong to the nominal subgenus. They are characterized by the usually cylindrical shape of the embolus and well developed anterolateral epigynal rims forming guides for the emboli. Most species have a longitudinal median septum dividing the anterior 1/3 to 1/2 of the spigynum. The purpuratus group has the protegulum extended ectanteriorly and the epigyna have a deep transverse depression across the central third.

cardinalis group

Four species in this group (P. cardinalis, P. pius, P. whitmani, P. clarus) occur in the eastern U. S. All are covered dorsally with yellow to red or brown scales and have a bilineate dark stripe pattern on the abdominal dorsum, and a trilineate dark stripe pattern on the abdominal venter (central stripe usually absent in P. clarus). The epigynum lacks a septum; the tegulum of the palpus is relatively narrow compared to other species groups.

Phidippus cardinalis (Hentz), 1845

Figures 2-6, 2-23

Attus rufus Hentz, 1835; NOMEN NUDUM

Attus cardinalis Hentz, 1845 (♂); type destroyed

Attus rufus Hentz, 1846 (♀); type destroyed; NEW SYNONYMY

Plexippus rufus C. L. Koch, 1846 (synonymized by Marx, 1890)

Plexippus bivittatus C. L. Koch, 1846 (synonymized by Marx, 1890)

Phiale modesta C. L. Koch, 1846 (synonymized by Banks, 1913)

Attus mccookii Peckham & Peckham, 1883; type in MCZ, examined; NEW SYNONYMY

Phidippus ruber Keyserling, 1884; type in BMNH, examined (synonymized with P. mccookii by Peckham & Peckham, 1909)

P. cardinalis, Peckham & Peckham, 1888; Wallace, 1950; Bonnet, 1958; Richman & Cutler, 1978; Gertsch, 1979

Dendryphantes cardinalis, Simon, 1901; Roewer, 1954

Phidippus oaklandensis Tullgren, 1901 (synonymized by Petrunkevitch, 1911)

P. mccooki, Muma, 1944; Kaston, 1948; Whitcomb et al., 1963

Much confusion about the identities of P. cardinalis and P. mccooki has existed since the Peckhams (1909) illustrated both species in consecutive figures. I have never seen a male palp as illustrated for P. mccooki. The drawing of the epigynum of this species appears to be a good rendition of P. whitmani, whereas the description of the female color pattern is that of P. pius. The type of P. mccooki is a female with a typical P. cardinalis epigynum. I can only speculate that the illustration of the P. mccooki male habitus is misplaced, and was meant to be the initial entry under P. cardinalis. Cheliceral color in the male of P. cardinalis agrees with Hentz's description and distinguishes this species from P. apacheanus.

Although the Peckhams (1909) were unable to recognize P. rufus, which they had previously attributed to what they renamed as P. whitmani, Hentz's description must be of the female of P. cardinalis. Only 3 eastern species (P. cardinalis, P. pius, P. whitmani) have 3 ventral, dark longitudinal stripes, and only 2 of these (P. cardinalis, P. pius) have 2 short dorsal, dark longitudinal stripes broken by 2 pairs of white spots. Since the type locality of P. rufus is Alabama, and the red form of P. pius occurs east of the Appalachians, P. rufus must be P. cardinalis.

MALE: integument reddish; carapace covered with red scales dorsally; chelicerae dark red proximal half, weakly iridescent blue distal half; no ocular setal tufts clypeus and palpi fringed with black setae; palpal femur with white or red scales on distal edge; leg I femur also with white or red scales on distal edge (white on legs II-IV), petellar brush black except white on proximal half of prolateral surface, white scales on proximal half patella; scales on proximal halves metatarsus and tarsus white to orange; dorsum of abdomen covered with red scales, with 2 black stripes in posterior half overlaid with 2 pair white spots, all of which may also be covered with red scales; venter of abdomen dark gray.

FEMALE: similar to male with following differences: 2 dorsal setal tufts; white scales below lateral eyes, across proximal edge of chelicerae, and on clypeus; clypeus also with dense fringe of white setae; palpi fringed with white-tipped black setae; dorsum red to brown, posterior stripes and spots not overlaid with red scales; venter of abdomen pale with 3 narrow gray stripes.

LEG MACROSETAE: femur II DR 0-0-0-0, tibia II V 0-1R-1R or 0-0-2; tibia III V 0-0-0-2, R 0-0-1-0; metatarsus III V 0-0-1 or 0-1-2, R 0-0-2; metatarsus IV V 0-0-1 or 0-0-2.

Phidippus pius Scheffer, 1906

Figures 2-7, 2-24

Phidippus pius Scheffer, 1906; type supposed to be in USNM, lost

P. pius, Peckham & Peckham, 1909; Bonnet, 1958; Edwards, 1977; Cutler, 1977; Richman & Cutler, 1978

Dendryphantes pius, Petrunkevitch, 1911; Roewer, 1954

Phidippus abboti Chamberlin & Ivie, 1944; type in AMNH, examined (synonymized by Edwards, 1977)

Dendryphantes abboti, Roewer, 1954

Phidippus abboti, Barnes & Barnes, 1955; Bonnet, 1958; Berry, 1970

Considerable variation in color pattern occurs in this species. In the typical form, females are yellow and males are orange; this color form holds throughout the northern range of the species and to the southwest (from the eastern plains to New Jersey and south to Texas). Southeast of the Appalachian Mountains, from Virginia to Florida, females are orange and males are red (P. *abboti* color form) and the amount of black on the legs and palpi is increased. Toward the southwestern portion of the range, in Texas, the black markings on the legs and palpi are only faintly indicated.

Although the type of *P. pius* is lost, Scheffer's description leaves no doubt as to which species he was describing.

MALE: integument yellow to red; carapace covered dorsally with yellow to red scales, lacking in ocular area in red males; no ocular setal tufts; clypeus with white setal fringe; palpi yellow to red, cymbium black, femur black in red males, white lateral fringes on patella, tibia, and cymbium; legs with black on ventral half of prolateral surface of all femora, distal third patella, distal half tibia, distal two-thirds metatarsus, distal half tarsus except for extreme distal edge which is pale (red males have femur, tibia and metatarsus all black), white scales sparsely on all legs and palpi; dorsum of abdomen covered with yellow to red scales; 2 posterior stripes similar to *P. cardinalis* and covered sparsely with metallic scales; venter pale (orange males) to black (red males).

FEMALE: similar to male with following differences: integument yellow to orange; 2 weak dorsal setal tufts; clypeus and palpi fringed with white setae; venter of abdomen with 3 narrow gray lines like P. cardinalis.

LEG MACROSETAE: femur II DR 0-0-0-0, tibia II V 0-1R-1R-2; patella III R 0-0-0, tibia III V 0-0-0-2, R 0-0-1-0, metatarsus III V 0-0-2; tibia IV R 0-0-1-0, metatarsus IV V 0-0-2.

Phidippus whitmani Peckham & Peckham, 1909

Figures 2-8, 2-25

Phidippus paludatus C. L. Koch, 1846; NOMEN OBLITUM

P. rufus (not Hentz), Peckham & Peckham, 1889 (in part, ♂)

Dendryphantes rufus, Simon, 1901

Phidippus whitmanii Peckham & Peckham, 1909

Dendryphantes whitmanii, Petrunkevitch, 1911; Roewer, 1954

P. whitmani, Comstock, 1912; Kaston, 1948; Bonnet, 1958; Berry, 1970; Cutler, 1977; Richman & Cutler, 1978; Gertsch, 1979

P. insolens (not Hentz), Kaston, 1938a, b

Banks' description (1913) of the pinned type of P. paludatus indicates it to be a specimen of P. whitmani. The latter name has been used for the species ever since the Peckhams' description (1909), over 50 years ago.

Females are brown in the northern states, red in the southern states. Southern males are more completely covered with red scales on anterior dorsum of carapace, only anterior half of distance from PME to AME exposed.

MALE: carapace covered with red scales dorsally except anterior to PME, where dark integument is exposed, laterally and on thoracic slope covered with white scales; chelicerae proximal half covered with white setae, especially medially, distal half faintly metallic blue; no ocular setal tufts; clypeus covered with white scales and setal fringe; palpi with white fringe entire length laterally and on cymbium dorsally, covered with white scales entire length dorsally; leg I-IV covered with white scales, all fringes white; integument of all femora black; dorsal abdomen covered with red scales, dorsal abdominal markings white; venter of abdomen gray laterally, with 3 narrow black stripes enclosing 2 submesal white stripes.

FEMALE: similar to male with following differences: carapace completely covered with red or brown scales dorsally; 2 weak dorsal setal tufts; palpi fringed with white setae but lacking scales; dorsal abdomen covered with red to brown scales except for white markings, rarely with 2 black lines posteriorly like *P. cardinalis* and *P. pius*.

LEG MACROSETAE: femur II DR 0-0-0-0, tibia II V 0-1R-1P or 0-0-2; patella III IV R 0-0-0, tibia III V 0-0-0-2, metatarsus III V 0-0-2, P 0-0-2, R 0-0-2; metatarsus IV V 0-0-2.

Phidippus clarus Keyserling, 1884

Figures 2-9, 2-26

Attus podagrosus Hentz, 1846; type destroyed; NOMEN DUBIUM, NOMEN OBLITUM

Phidippus auctus C. L. Koch, 1846; specimens from Keyserling coll., BMNH, examined; NOMEN OBLITUM

Phidippus castrensis C. L. Koch, 1846; NOMEN DUBIUM, NOMEN OBLITUM

Phidippus clarus Keyserling, 1884

P. clarus, Peckham & Peckham, 1909; Kaston, 1948; Wallace, 1950; Barnes & Barnes, 1955; Bonnet, 1958; Whitcomb & Tadic, 1963; Whitcomb, 1963; Berry, 1970; Richman & Cutler, 1978, Oehler, 1980

P. insolens (not Hentz), Peckham & Peckham, 1888

P. multiformis Emerton, 1891; type in MCZ, examined (synonymized by Peckham & Peckham, 1909)

P. minutus Banks, 1892; type in MCZ, examined (synonymized by Peckham & Peckham, 1909)

Philaeus princeps (not Peckham & Peckham), Banks, 1892

Phidippus bilineatus Tullgren, 1901 (synonymized by Roewer, 1954)

Phidippus clarconensis Tullgren, 1901 (synonymized by Wallace, 1950)

Dendryphantes insolens, Simon, 1901

D. multiformis, Simon, 1901

D. castrensis, Simon, 1901

Phidippus podagrosus, Banks, 1910

Dendryphantes clarus, Petrunkevitch, 1911; Roewer, 1954

P. rimator, Chamberlin & Ivie, 1944 (not *Attus rimator* Walckenaer, 1837 a NOMEN DUBIUM); Kaston, 1953, 1972, 1978; Snetsinger, 1954; Cutler, 1977

Numerous other references cited in behavior or ecology sections.

The usage of *P. rimator* (Walckenaer) for this species, a name which has become increasingly used for *P. clarus*, is completely unwarranted. The single illustration by Abbot (1792) given the name *Attus rimator* by Walckenaer (1837) was recognized as an immature by Chamberlin & Ivie (1944) when they resurrected the name. It is well know that immatures have been usually difficult, if not impossible given past techniques, to identify to species. Furthermore, I have examined a color reproduction of the copy of Abbot's drawing kept at the Museum of Comparative Zoology, and cannot positively identify the drawing to genus, much less to species; the dorsal pattern cannot be matched with any known species.

In saying this I might add that I have personally reared most of the species of Phidippus occurring in the eastern U. S., including P. clarus, and therefore have first hand acquaintance with their appearance as immatures.

MALE: integument dark; no dorsal ocular tufts; clypeus and lateral edges of palpi fringed with black setae; dorsum of palpal femur, patella, tibia, and cymbium covered with white scales and setae; leg I femur with dorsal fringe white, prolateroventral fringe absent, patella brush black, proximal fourth of tibial brush white; dorsum of abdomen with short white basal band, side stripe of red scales each side, dark metallic central stripe; venter of abdomen dark gray with 3 black stripes, the stripes sometimes enclosing a slight amount of white.

FEMALE: similar to male with following differences: integument normal color; 2 weak dorsal tufts; white scales below eyes laterally and densely covering clypeus, long white setal fringe on clypeus, palpi; abdomen with variable coloration, lateral wide stripes tan, yellow, or orange and median stripe tan, brown or black; venter of abdomen white enclosed by lateral black stripes which meet posteriorly, sometimes with faint median gray stripe.

LEG MACROSETAE: femur II DR 0-0-0-0; metatarsus IV V 0-0-1 or 0-0-2.

audax group

The 5 eastern species in this group (P. audax, P. otiosus, P. regius, P. xerus, P. insignarius) all have 4 setal tufts on the females as opposed to 6 or 2 tufts on females of other groups. Lumping these species together on the basis of number of setal tufts seems tenuous; P. insignarius and probably P. xerus will likely be shown to belong to other species groups when the fauna of the western U. S. becomes better known. Males of the 3 other species all have a cheliceral tubercle, which seems to be a shared, derived character. Behavioral data also seems to relate these 3 species (see chapter on courtship).

Phidippus audax (Hentz), 1845

Figures 2-10, 2-27

Attus morsitans Walckenaer, 1805; NOMEN NUDUM, NOMEN DUBIUM

Salticus variegatus Lucas, 1833; type lost; petition to suppress (Levi & Pinter, 1970) under consideration by the I.C.Z.N.

Attus audax Hentz, 1835; NOMEN NUDUM

A. tripunctatus Hentz, 1835; NOMEN NUDUM

A. morsitans Walckenaer 1837; NOMEN DUBIUM

A. audax Hentz, 1845; type destroyed; petition submitted to designate as type species of genus (Levi & Pinter, 1970)

A. tripunctatus Hentz, 1846 (synonymized by Banks, 1893)

A. fasciolatus, Hentz, 1846 (synonymized by Banks, 1910)

Phidippus togatus C. L. Koch, 1846; NEW SYNONYMY

Phidippus purpurifer C. L. Koch, 1846

P. smaragdifer C. L. Koch, 1846

P. alchymista C. L. Koch, 1846

P. rufimanus C. L. Koch, 1846

P. dubiosus C. L. Koch, 1846

P. mundulus C. L. Koch, 1846

P. personatus C. L. Koch, 1846

P. concinnatus C. L. Koch, 1846 (Koch names synonymized by Banks, 1910)

P. morsitans, Peckham & Peckham, 1888 (synonymized by Peckham & Peckham, 1909)

P. rauterbergii Peckham & Peckham, 1888 (synonymized by Banks, 1916)
P. tripunctatus, Emerton, 1891
P. audax, Banks, 1893; Peckham & Peckham, 1909; Bonnet, 1958; Kaston, 1948, 1953, 1972, 1978; Levi & Levi, 1968; Cutler, 1977; Richman & Cutler, 1978; Gertsch, 1979; Oehler, 1980
P. howardii Peckham & Peckham, 1896, NEW SYNONYMY
P. rauterbergii, Peckham & Peckham, 1901, 1909; Bonnet, 1958
P. howardi, Peckham & Peckham, 1901, 1909; Bonnet, 1958
P. variegatus, Peckham & Peckham, 1909 (the Peckhams considered *audax* and *variegatus* to be 2 separate species); Kaston, 1938; Bryant, 1942
Dendryphantes audax, Petrunkevitch, 1911; Roewer, 1954
D. howardi, Petrunkevitch, 1911; Roewer, 1954
D. rauterbergii, Petrunkevitch, 1911; Roewer, 1954
Phidippus bryantae Kaston, 1945 (synonymized by Kaston, 1948)
Also mentioned in numerous behavioral and ecological papers which are mentioned with their respective chapters.

Phidippus morsitans might also apply to *P. regius* C. L. Koch but would be unavailable for that species also.

This is an extremely common species over most of eastern and midwestern North America. It varies widely in both size and color pattern, although at least some individuals of a particular population retain the typical color pattern. Some individuals in Texas and Mexico reach nearly 20 mm in length, perhaps in part due to the lack of competition from a common, large species (like *P. regius* in Florida).

MALE: integument dark; carapace with or without lateral white submarginal band of variable size extending behind and below PLE; anterior face of each chelicera with subdistal tubercle; no ocular setal tufts;

clypeus fringed with black setae; palpal femur and patella with white scales and setae dorsally, black setae laterally and on dorsal cymbium; leg I with typical fringing; abdomen with spots white, yellow, or red, either distinct or coalesced with each other or with lateral bands, most of resulting patterns illustrated by Hill (1978); venter of abdomen with outer rows of dots often overlain with white scales which encroach to variable extent over median black stripe which is never completely covered.

FEMALE: similar to male with following differences: no cusp on chelicerae; 4 setal tufts; clypeus sparsely covered with white scales and white setae; palpi fringed with black setae, some of which have white tips.

LEG MACROSETAE: metatarsus III R 0-0-2; metatarsus IV V 0-0-2. Only species with an individual with femur I DR 0-0-0-1.

Phidippus otiosus (Hentz), 1846

Figures 2-11, 2-28

Attus pulcher Walckenaer, 1837, p. 439

A. pulcher pallida Walckenaer, 1837, p. 439

A. peregrinus Walckenaer, 1837, p. 445

A. otiosus Hentz, 1846; type destroyed; petition for retention submitted to I. C. Z. N. (see Appendix C)

Phidippus lunulatus C. L. Koch, 1846 (synonymized by Banks, 1910)

P. otiosus, Peckham & Peckham, 1888, 1901, 1909; Bryant, 1942; Murrill, 1942; Wallace, 1950, Bonnet, 1958; Anderson, 1966; Levi & Levi, 1968; Kaston, 1972, 1978; Edwards et al., 1974; Muma, 1975; Edwards, 1977; Richman, 1977; Hill, 1979; Gertsch, 1979

Dendryphantes otiosus, Petrunkevitch, 1911; Roewer, 1954

Phidippus dorsalis Bryant, 1942 (♂ holotype); holotype in MCZ, examined; NEW SYNONYMY

P. pulcher, Chamberlin & Ivie, 1944; Richman, 1978; Richman & Cutler, 1978

Dendryphantes pulcher, Roewer, 1954

Although *P. pulcher* (Walckenaer) has priority, the specific epithet *pulcher* in various generic combinations has only been used 6 times in the literature (3 in checklists), whereas *P. otiosus* (Hentz) has been used over 20 times (7 in checklists). Usage favors retention of *P. otiosus*.

MALE: carapace with very wide yellow to orange submarginal bands from PME to near posterior edge, not meeting behind but partially covering thoracic slope; chelicerae with tubercle like *P. audax*; 4 setal tufts; clypeus sparsely fringed with black setae; palpi covered with yellow to orange scales and setae on dorsal and lateral femur, ectal edge of patella; dorsal cymbium covered with black setae; leg I with typical fringes except yellow to orange where normally white, prolateroventral femur fringe lacks distal third, yellow setae and scales on distal femur; legs II-IV with yellow scales on dorsal distal femur and proximal patella; dorsal abdominal markings yellow, gold, or orange, center stripe metallic black, green, or blue; venter of abdomen black.

FEMALE: similar to male with following differences: carapace submarginal bands white to yellow; chelicerae without tubercle; ventral edge of clypeus to entire face covered with white scales, weakly fringed with yellow setae to strongly fringed with white overhanging proximal third of chelicerae; palpi densely fringed laterally with white or yellow setae; legs covered with white or yellow scales; abdomen integument gray, tan, or black, dorsal abdominal markings white to yellow-orange; venter of abdomen with broad black stripe with or without white border which may encroach on middle of black band.

LEG MACROSETAE: metatarsus IV V 0-1-2.

Phidippus regius C. L. Koch, 1846

Figures 2-12, 2-13, 2-29

Phidippus regius C. L. Koch, 1846, p. 146

Attus regius, Walckenaer, 1847

Salticus sagraeus Lucas, 1857

Attus miniatus Peckham & Peckham, 1883 (synonymized by Edwards, 1975, unpubl.; Richman & Cutler, 1978)

Phidippus miniatus, Peckham & Peckham, 1888, 1901, 1909

P. variegatus (not Lucas), Franganillo, 1930; Chamberlin & Ivie, 1944; Wallace, 1950

P. regius, Bryant, 1943; Bonnet, 1958; Levi & Levi, 1968; Levi & Pinter, 1970; Muma, 1975; Cutler, 1977; Hill, 1977; Kaston, 1978; Richman & Cutler, 1978; Edwards, 1975, 1979; Cutler, 1979; Gertsch, 1979

Dendryphantes regius, Simon, 1901; Roewer, 1954

D. miniatus, Petrunkevitch, 1911; Roewer, 1954

Phidippus tullgreni Wallace, 1950; NEW SYNONYMY (may be *P. otiosus* - *P. regius* hybrid)

Richman & Cutler (1978) synonymized *P. miniatus* with *P. regius* on the authority of the unpublished thesis of Edwards (1975). This species has been involved in considerable confusion with *P. audax* over use of the name *P. variegatus* and because of their similar appearance.

MALE: integument dark; carapace rarely with wide white submarginal bands (possibly hybrid); chelicerae with tubercle like *P. audax*; no ocular tufts; clypeus and palpi fringed with black setae; leg I femur with distal prolateral white setae and scales; dorsal abdomen black with white markings; venter of abdomen black.

FEMALE: carapace lacking scales or covered to variable extent with gray, tan and/or orange scales, ocular quadrangle never completely covered; chelicerae without tubercle, sometimes red-violet, may be covered proximally with white scales; 4 ocular setal tufts; clypeus and palpi with white fringes, clypeus covered with white scales; legs with or without gray, tan or orange scales; dorsal abdomen black or dark brown with or without covering of gray, tan, brown and/or orange scales; dorsal markings white or pale orange, sometimes overlaid with tan or orange scales, markings outlined with remnant of central dark band; venter of abdomen black, bordered with stripes of white scales when abdomen black dorsally.

LEG MACROSETAE: metatarsus IV V 0-1-2. P. regius, the largest species represented, was most likely to have more macrosetae than normal; especially the ventral subproximals on tibiae II-IV might be paired.

Phidippus xerus Edwards, 1978, emendation

Figures 2-14, 2-30

Phidippus xeros Edwards, 1978; holotype deposited in MCZ

P. xeros, Richman, 1979

A few specimens in collections were labeled P. workmani. The specific epithet was not latinized in the original description, and is here emended. All known specimens of this species have been collected in Florida.

MALE: integument dark; carapace with short white transverse bands behind PLE; no ocular tufts; clypeus and palpi fringed with black setae;

palpi with dorsal white scales on femur and patella; leg I like *P. regius*, except dorsal femur fringe of white-tipped black setae; dorsal abdomen black with white markings; venter of abdomen black with 4 rows pale dots.

FEMALE: integument normal color; carapace with markings like male (except they are yellow) or usually (including clypeus and over anterior eyes) covered with gray, yellow, and/or orange-yellow scales, except for lower thoracic slope and ocular quadrangle (which has white spot in center); 4 weak ocular setal tufts; clypeus and palpi fringed with white; tibia I reddish on proximal half with white fringe; dorsal abdominal markings orange-yellow to red-orange, or rarely lateral stripes lacking and yellow spots and basal band present; venter of abdomen like male.

LEG MACROSETAE: no consistent differences; ventral and lateral medians on metatarsi III & IV variable.

Phidippus insignarius C. L. Koch, 1846

Figures 2-15, 2-30

Phidippus insignarius C. L. Koch, 1846, 1851

Philaeus monticola Banks, 1896 (synonymized by Peckham & Peckham, 1909)

Phidippus comatus Peckham & Peckham, 1901 (in part, ♂) (recognized by Peckham & Peckham, 1909)

P. insignarius, Peckham & Peckham, 1909; Kaston, 1948; Muma, 1949; Whitcomb & Tadic, 1963; Cutler, 1977; Richman & Cutler, 1978

Dendryphantes insignarius, Petrunkevitch, 1911; Roewer, 1954

P. fraudulentus, Chamberlin & Ivie, 1944; not *Attus fraudulentus* Walckenaer, 1837, a NOMEN DUBIUM

P. insigniarius, Bonnet, 1958

Bonnet (1958) noted that the correct Latin spelling of the specific epithet is *insigniarius*. If Koch had misspelled the name unintentionally, this correction would be valid. However, Koch used the same spelling again in 1851, indicating he deliberately spelled the name without the extra "i", therefore the original spelling must stand.

There are no authenticated records of *P. insignarius* occurring anywhere in Georgia. If it does occur there, I would expect it to be in the mountains of the northwest part of the state, certainly not in the coastal plain of the southeast part from where Abbot made his drawings. *Attus fraudulentus* Walckenaer could be an immature of any of several southeastern species of *Phidippus*.

MALE: chelicerae weakly iridescent green; 4 ocular tufts, the dorsal pair longer and denser than usual; carapace with submarginal white band of scales extending well back on thoracic slope; clypeus densely covered with white scales and with long white fringe overhanging chelicerae; palpal femur, patella, tibia, and cymbium covered dorsally with white setae; leg I dense white scale cover on prolateroventral surface of femur, patella and tibia; leg I femur with weak dorsal fringe of mixed black and white setae, prolateroventral fringe white and short, retrolateroventral fringe white, very long and dense; all other leg I fringes white, dorsal stripe of white scales from distal tip patella to distal tip tarsus; legs II-IV similar but with progressively reduced fringes and scales, leg IV lacking most scales; dorsum of abdomen with pattern like female but overlain with orange scales; venter of abdomen with median black stripe that narrows toward spinnerets, white stripes on each side.

FEMALE: similar to male with following differences: 4 normal setal tufts; submarginal band less distinct than in male; white scales covering clypeus; clypeus and palpi fringed with white setae; legs with simple white fringes; abdomen with white basal band and lateral bands, tan to orange wide stripes laterally, white central triangular spot and white to orange posterior spots.

LEG MACROSETAE: femur II DR 0-0-0-0, tibia II 0-0-1R-1P or 0-0-1R-0; patella III R 0-0-0, tibia III 0-0-0-1P, metatarsus III P 0-0-2; metatarsus IV V 0-0-2.

princeps group

The 2 species in this group, P. princeps and P. pulcherrimus, are closely related allopatric species. Both have large, sickle-shaped emboli and a very long epigynal septum. Phidippus pulcherrimus is known from Florida and the southern parts of Alabama and Georgia. Phidippus princeps occurs from northeastern Texas and North Carolina north to Minnesota and New England. This group is probably related to the audax group, as evidenced by some similarities in color pattern.

Phidippus princeps (Peckham & Peckham), 1883

Figures 2-16, 2-31

Attus insolens Hentz, 1835; NOMEN NUDUM

A. insolens Hentz, 1845; type destroyed; NOMEN DUBIUM

Attus princeps Peckham & Peckham, 1883; type in MCZ, examined

Philaeus princeps, Peckham & Peckham, 1888

Phidippus brunneus Emerton, 1891; type in MCZ, examined (synonymized by Bryant, 1942)

P. princeps, Peckham & Peckham, 1901, 1909; Kaston, 1948; Barnes & Barnes, 1955; Bonnet, 1958; Berry, 1970; Cutler, 1977; Hill, 1977a, b; Richman & Cutler, 1978; Oehler, 1980

P. insolens, Peckham & Peckham, 1909 (in part, ♂); Muma & Jeffers, 1945;
?Muma & Muma, 1949

Dendryphantes princeps, Petrunkevitch, 1911; Roewer, 1954

P. dorsalis Bryant, 1942 (in part, ♀); paratypes in MCZ, examined

The only eastern species that comes close to resembling Hentz's description is the species now known as *P. princeps*. The name *P. insolens* has been misused for *P. apacheanus*, although a badly rubbed specimen of the latter species could fit the description.

MALE: integument nearly black; no ocular setal tufts; clypeus sparsely fringed with black setae; palpi fringed laterally with black setae, covered dorsally with white scales on femur and patella; leg I distal prolaterodorsal femur with white scales and setae, distal half patella with black fringe, all fringes unusually short; dorsum of abdomen completely covered with red scales, rarely brown with white or red central triangle and 2 pair posterior spots; venter of abdomen black bordered with row of pale dots.

FEMALE: sparse cover of white scales on carapace and legs; 4 ocular setal tufts; clypeus densely covered with white scales and setae especially along ventral edge; palpi fringed with white setae; dorsum of abdomen usually unmarked brown, occasionally with white median stripe running length of abdomen but not reaching either anterior or posterior ends of abdomen, rarely with white triangle followed by 2 pair posterior spots, or intermediate condition between central stripe and spots; venter of abdomen with broad black stripe bordered laterally and posteriorly by white.

LEG MACROSETAE: tibia II V 0-1R-1R-2; tibia III & IV V 0-0-0-2, metatarsus III & IV V 0-0-2.

Phidippus pulcherrimus Keyserling, 1884

Figures 2-17, 2-31

Phidippus pulcherrimus Keyserling, 1884; type in MCZ, examined

P. pulcherrimus, Marx, 1890; Banks, 1901, 1904, 1910; Peckham & Peckham 1909; Bonnet, 1958; Edwards, 1977; Richman & Cutler, 1978; Edwards & Hill, 1978

Dendryphantes pulcherrimus, Petrunkevitch, 1911; Roewer, 1954

The anecdote by Hill (Edwards & Hill, 1978), proclaiming to be the first description of the male of P. pulcherrimus, is incomplete.

MALE: carapace with short white transverse bands behind PLE; no ocular setal tufts; clypeus with sparse black fringe; palpi fringed with black setae, femur covered dorsally with white scales; dorsal leg I like P. princeps; dorsal abdominal semi-encircling band yellow (1 specimen) or red, spots white to red, metallic scales on black median stripe; venter of abdomen black.

FEMALE: similar to male with following differences: 2 dorsal setal tufts; carapace with bands like male or entire carapace sparsely covered with white to tan scales; clypeus with white scales and setae, especially along ventral edge; palpi with white setal fringe, white scales on tarsus and distal tibia; legs covered with white setae; dorsal abdominal spots usually white, rarely yellow to orange; venter of abdomen with wide black stripe with or without white borders laterally.

LEG MACROSETAE: femur II DR 0-0-0-0, tibia II V 0-1R-1R-2; tibia III V 0-0-0-2, R 0-0-1-0; tibia IV V 0-0-0-2; metatarsus III & IV V 0-0-2.

purpuratus group

Three species occurring in the eastern U. S. belong to the purpuratus group. One species, *P. borealis*, ranges across northern North America west from New Hampshire to Washington and Alaska. A primarily southwestern species, *P. apacheanus*, ranges east from California and Utah to North Carolina and Florida. The third species, *P. purpuratus*, is restricted to the eastern half of North America. All the species in this group can be readily recognized by the forms of the genitalia. In males, the protegulum is extended anteriorly on the ectal side. The embolus is a short, notched structure which arises anteriorly, but appears to be entally attached to the extension of the protegulum. The epigynum is like other members of the subgenus in the placement of anterior guides but differs in having a deep, rectangular, transverse depression across the central third.

The *johnsoni* group of western North America is intermediate between this group and the *audax* group. In the *johnsoni* group, the protegulum is less extended, the embolus longer, and the epigynum lacks the central depression.

Phidippus apacheanus Chamberlin & Gertsch, 1929

Figures 2-18, 2-32

Phidippus bardus Peckham & Peckham, 1901; type in MCZ, examined; NOMEN OBLITUM; NEW SYNONYMY

P. insolens (not Hentz), Peckham & Peckham, 1901, 1909 (in part♀)

Dendryphantes insolens, Simon, 1901; Roewer, 1954

Phidippus ferrugineous Scheffer, 1904; type in MCZ, examined; NOMEN OBLITUM; NEW SYNONYMY

Phidippus apacheanus Chamberlin & Gertsch, 1929; type in AMNH, examined

Phidippus nikites Chamberlin & Ivie, 1935; type in AMNH, examined; NEW SYNONYMY

P. nikites, Muma, 1949; Bonnet, 1958

Dendryphantes apacheanus, Roewer, 1954

D. nikites, Roewer, 1954

P. apacheanus, Bonnet, 1958; Gardner, 1965; Levi & Levi, 1968; Cutler, 1977; Richman & Cutler, 1978; Edwards & Hill, 1978; Kaston, 1978; Gertsch, 1979

P. paludatus (not C. L. Koch), Kaston, 1972

The Peckhams (1909) incorrectly synonymized *P. bardus* and *P. ferrugineous* with *P. insolens* (Hentz). This confusion resulted in a redescription of the species by Chamberlin & Gertsch (1929) as *P. apacheanus*, by which name it has been known since; the lone exception was Kaston (1972) who used *P. paludatus* C. L. Koch, but later recognized and corrected his error (Kaston, 1978).

The males of *P. apacheanus* (described from Utah) and *P. nikites* (described from California) are identical. The *P. nikites* type of epigynum differs from the typical *P. apacheanus* epigynum in that the central depression is shallow and not set off by a distinct rim. I consider this only a variation; a single female from Florida had a *P. nikites* type epigynum, but all other Florida specimens were typical. Other specimens from the type locality of *P. nikites* were typical of *P. apacheanus* (S. Johnson, personal communication, and specimens sent for confirmation). A similar type of variation occurs in females of *P. borealis*, and may represent a remnant recessive genetic representation of a less derived condition. The epigynum of the female allotype of *P. nikites* is somewhat shrivelled, which has changed the direction of the openings to the spermathecal ducts, accounting for this difference as noted in Chamberlin & Ivie's description.

MALE: integument dark; carapace covered with yellow to red scales dorsally in ocular quadrangle and above thoracic slope; 2 dorsal setal tufts; clypeus and palpi fringed with black setae; leg I patellar brush black except white on proximal half of prolateral surface, white scales on proximal half patella; scales on proximal halves metatarsus and tarsus white to orange; abdomen covered dorsally with yellow to red scales except for mid-dorsal black stripe, which may also be overlaid with scales; venter of abdomen black, outer rows of pale dots more conspicuous than inner rows.

FEMALE: similar to male with following differences: palpi with lateral yellow fringes; tibia I proximal half reddish, legs with scattered white scales; yellow to red dorsal scale cover may be reduced so that spider appears to be black with yellow or red abdominal stripes and a pale basal band; black central stripe may be indented by 0-3 pair of yellow or red spots.

LEG MACROSETAE: femur II DR 0-0-0-0; metatarsus III P 0-0-2, R 0-0-2; tibia IV P 0-0-0-0, metatarsus IV V 0-0-0 or 0-1-2.

Phidippus borealis Banks, 1895

Figures 2-19, 2-33

Phidippus borealis Banks, 1895; 2 syntypes supposed to be at MCZ, lost; Neotype designated, the larger of 2 specimens in a vial from the type locality

Phidippus altanus Gertsch, 1934 (synonymized by Edwards, 1977)

P. altanus, Gertsch & Jellison, 1939; Chickering, 1944; Levi & Levi, 1951

P. borealis, Edwards, 1977; Cutler, 1977; Richman & Cutler, 1978

Phidippus borealis was incorrectly synonymized with P. purpuratus Keyserling. The types are lost; since Banks' original description was somewhat equivocal, I have designated a neotype male from Crawford Notch, New Hampshire, the type locality; it is deposited in the Museum of Comparative Zoology.

MALE: 2 weak dorsal tufts; clypeus and palpi fringed with black setae; leg I patella and proximal half tibia reddish, both fringed with black setae; dorsal abdominal markings tan to orange; venter of abdomen black, inner rows of dots inconspicuous.

FEMALE: similar to male with following differences: 2 dorsal tufts; clypeus and palpi fringed with white setae; leg I unicolorous, not banded like male; dorsal abdominal markings white to orange.

LEG MACROSETAE: femur II DR 0-0-0-0; tibia III V 0-0-0-2, R 0-0-1-0; metatarsus III V 0-0-0 or 0-1-2, P 0-0-2, R 0-0-2; tibia IV R 0-0-1-0; metatarsus IV V 0-1-2, P 0-0-2, R 0-0-2.

Phidippus purpuratus Keyserling, 1884

Figures 2-20, 2-33

Phidippus purpuratus Keyserling, 1884 (p. 489)

Phidippus albomaculatus Keyserling, 1884 (p. 491); syntypes in MCZ, BMNH, examined; NEW SYNONYMY, Lectotype designated

P. galathea (not Walckenaer), Peckham & Peckham, 1888

P. mystaceus (not Hentz), Emerton, 1875, 1891

P. purpuratus, Peckham & Peckham, 1909; Kaston, 1948, 1978; Bonnet, 1958; Whitcomb et al., 1963; Cutler, 1977; Richman & Cutler, 1978

P. electus (not C. L. Koch), Banks, 1910, 1913; NOMEN DUBIUM

Dendryphantes purpuratus, Petrunkevitch, 1911; Roewer, 1954

Banks (1910) considered *P. electus* to be a synonym of *P. albomaculatus* (*purpuratus*). Later (1913) he examined the pinned type, found it to be a juvenile, and made no comment on its identity. Other authors have considered it a synonym of _P_. _mystaceus_. It probably cannot be recognized.

I examined specimens labelled "Type" of _P_. _albomaculatus_ from both the Museum of Comparative Zoology and from the British Museum (Natural History). A specimen at the MCZ has been labelled lectotype by L. Pinter, and I so designate it.

MALE: integument dark; 2 weak dorsal setal tufts; clypeus and palpi fringed with black setae; leg I all fringes black, with few white setae below normally placed white scales on proximal halves patella, metatarsus, and tarsus, femur prolateroventral fringe very short, prolateral surface of femur with metallic green or blue reflections; dorsal abdominal markings tan to red, spots usually less distinct than in female; venter dark edged with white laterally.

FEMALE: similar to male with following differences: 2 dorsal setal tufts; clypeus and palpi fringed with white setae; integument of abdomen dark gray, dorsal abdominal markings white or tan; venter of abdomen black with or without lateral white stripes, inner rows of dots conspicuous.

LEG MACROSETAE: femur II DR 0-0-0-0; patella III R 0-0-0, tibia III V 0-0-0-2, metatarsus III V 0-0-1 or 0-0-2, P 0-0-2, R 0-0-2; metatarsus IV V 0-0-1 or 0-0-2.

Figure 2-4. *Phidippus putnami*: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.

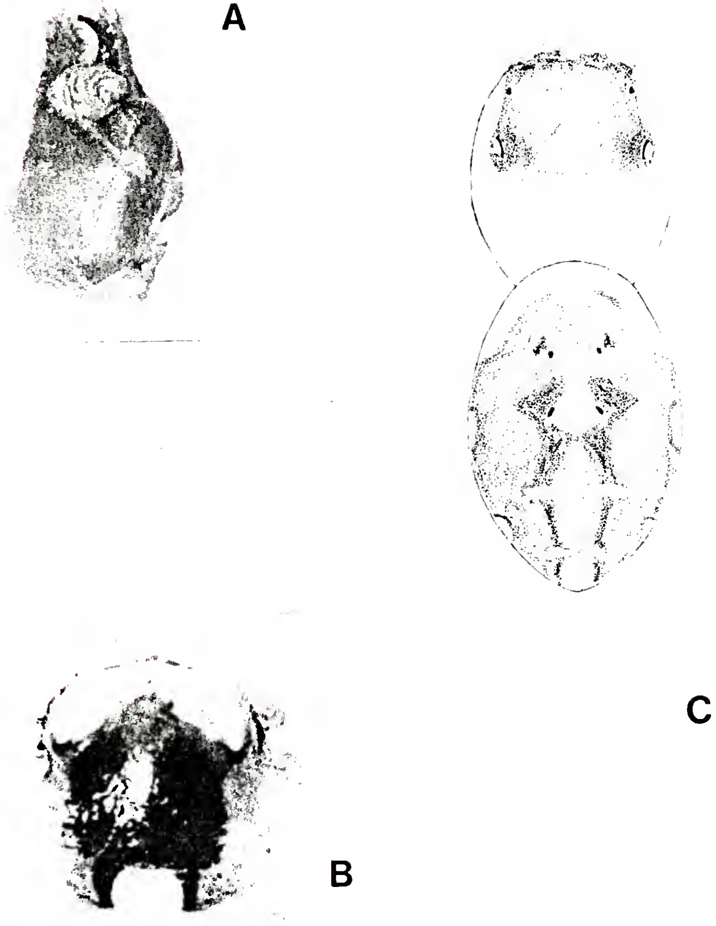

A
C
B

Figure 2-5. Phidippus mystaceus: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.

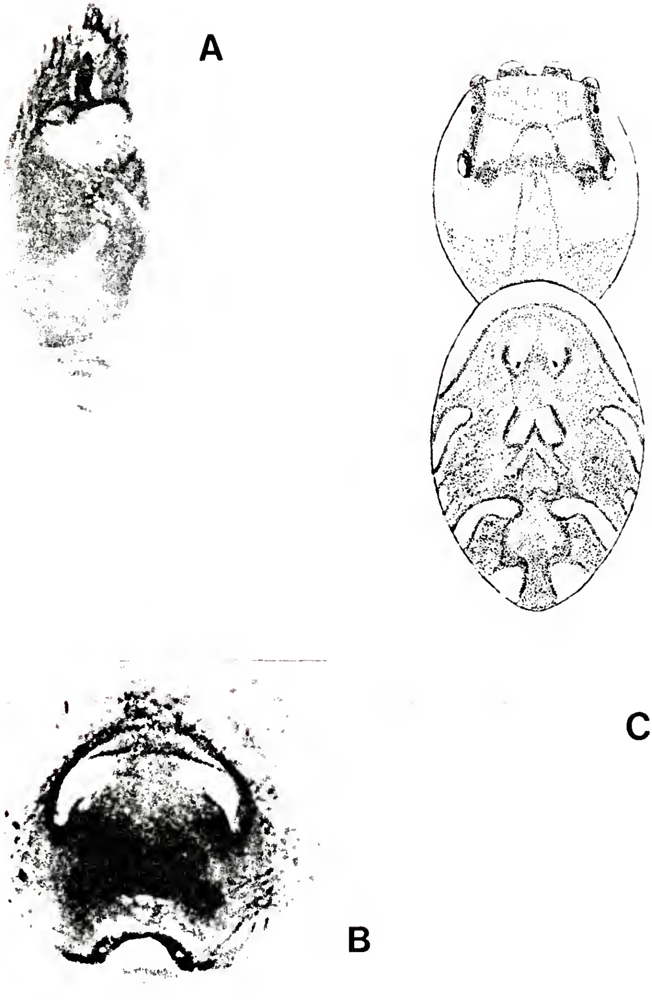
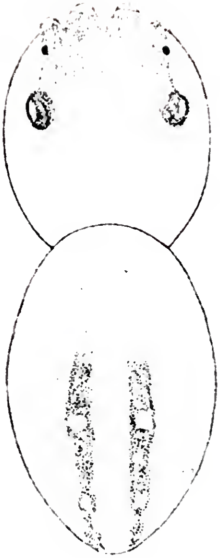

A
C
B

Figure 2-6. *Phidippus cardinalis*: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.

A



C

B

Figure 2-7. *Phidippus pius*: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.

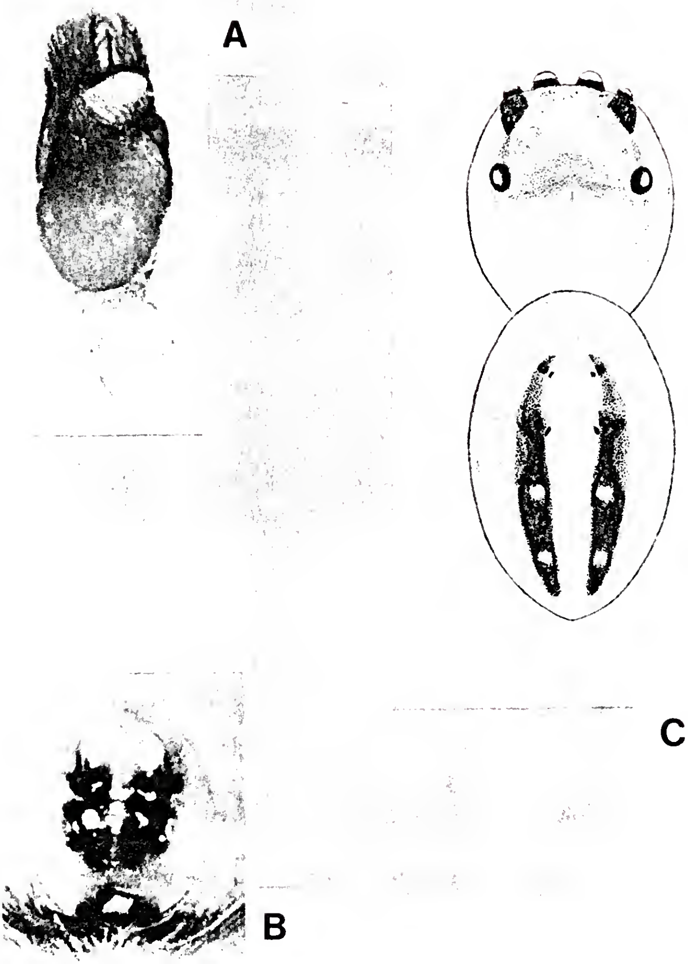
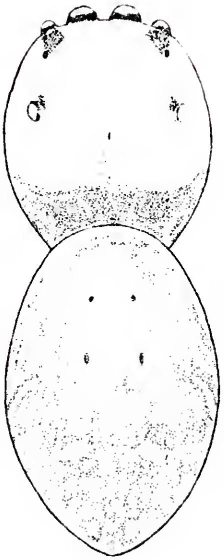

A
B
C

Figure 2-8. *Phidippus whitmani*: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.

A



C

B

Figure 2-9. _Phidippus clarus_: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female, D. Dorsal view of abdomen of male.

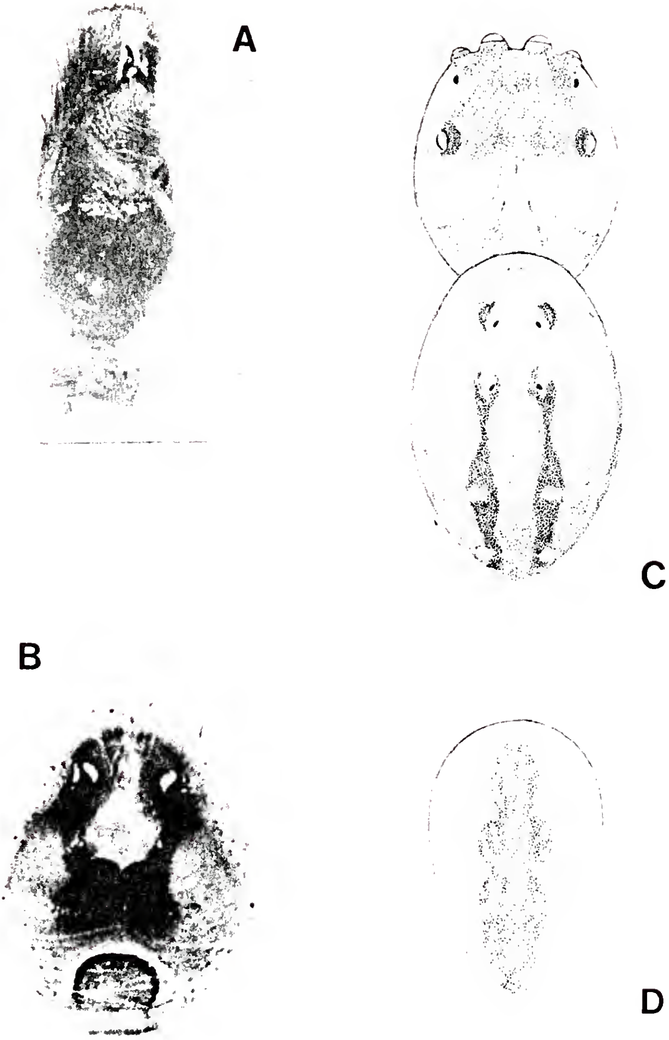
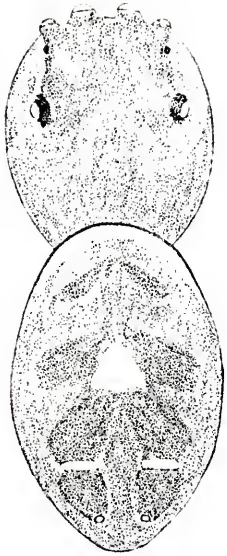

A
C
B
D

Figure 2-10. Phidippus audax: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.

A

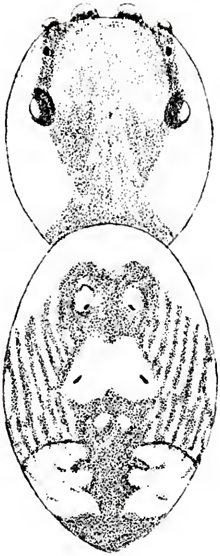
B



C

Figure 2-11. Phidippus otiosus: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.

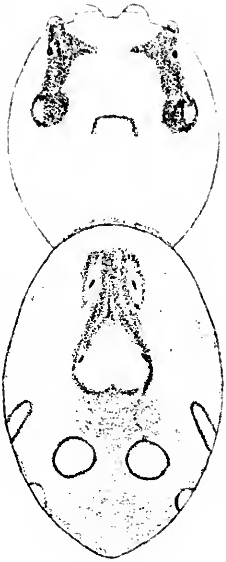
A



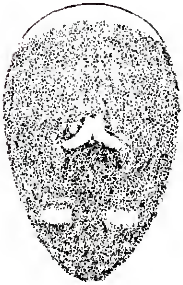
C

B

Figure 2-12. Phidippus regius: A. Dorsal view of female, B. Dorsal view of abdomen of male.



A



B

Figure 2-13. _Phidippus regius_: A. Ventral view of male palp, B. Ventral view of female epigynum.

A

B

Figure 2-14. *Phidippus xerus*: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female, D. Dorsal view of abdomen of male.

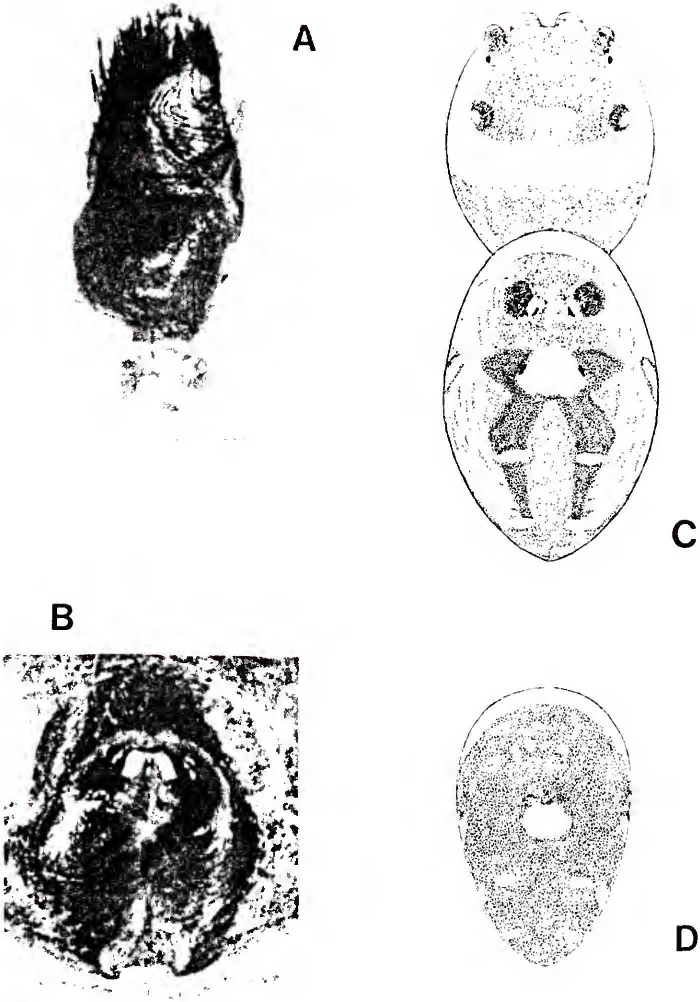
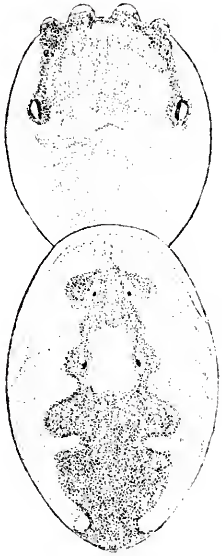

A
B
C
D

Figure 2-15. *Phidippus insignarius*: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.

A

B



C

Figure 2-16. Phidippus princeps: A. Ventral view of male palp, B. Ventral view of female epigynum.

A

B

Figure 2-17. *Phidippus pulcherrimus*: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.

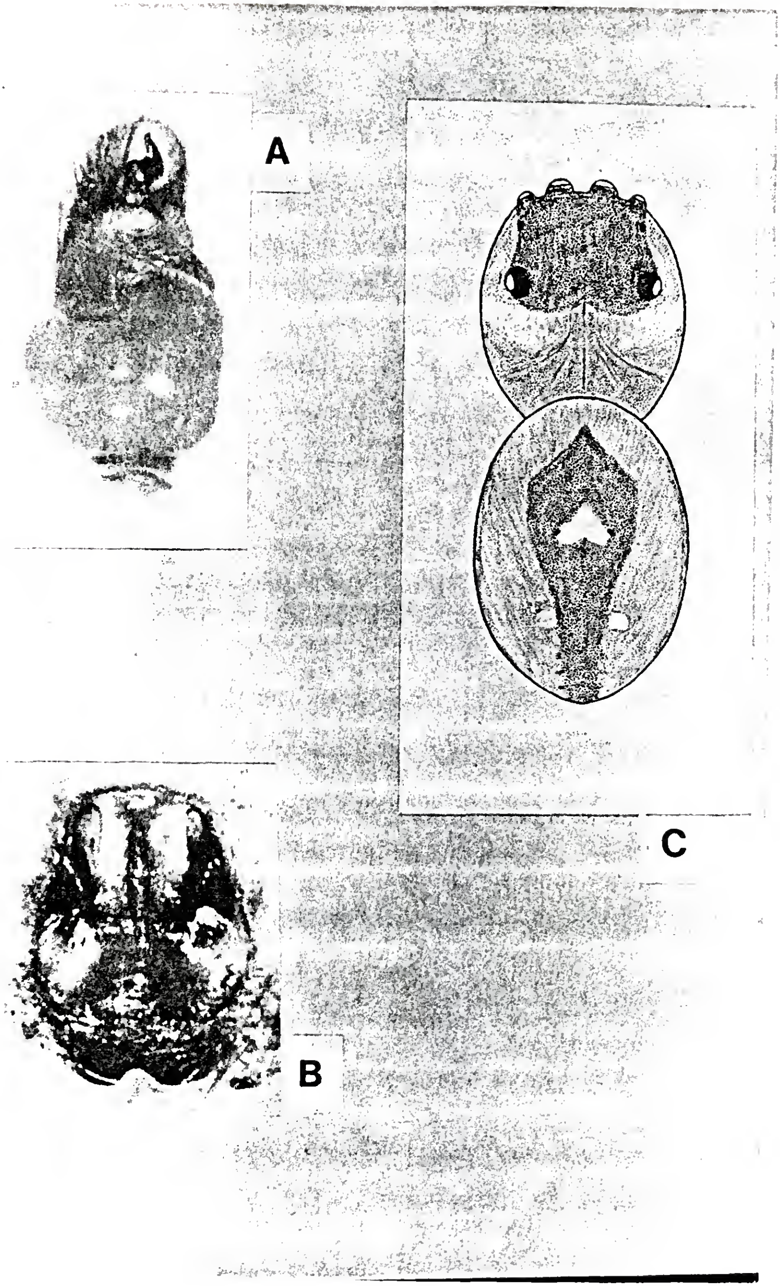
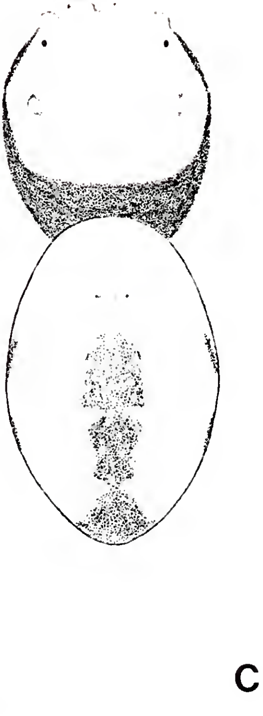

A
B
C

Figure 2-18. Phidippus apacheanus: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.


A


C

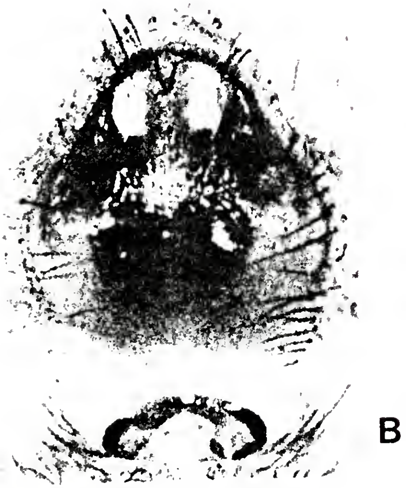

B

Figure 2-19. Phidippus borealis: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.

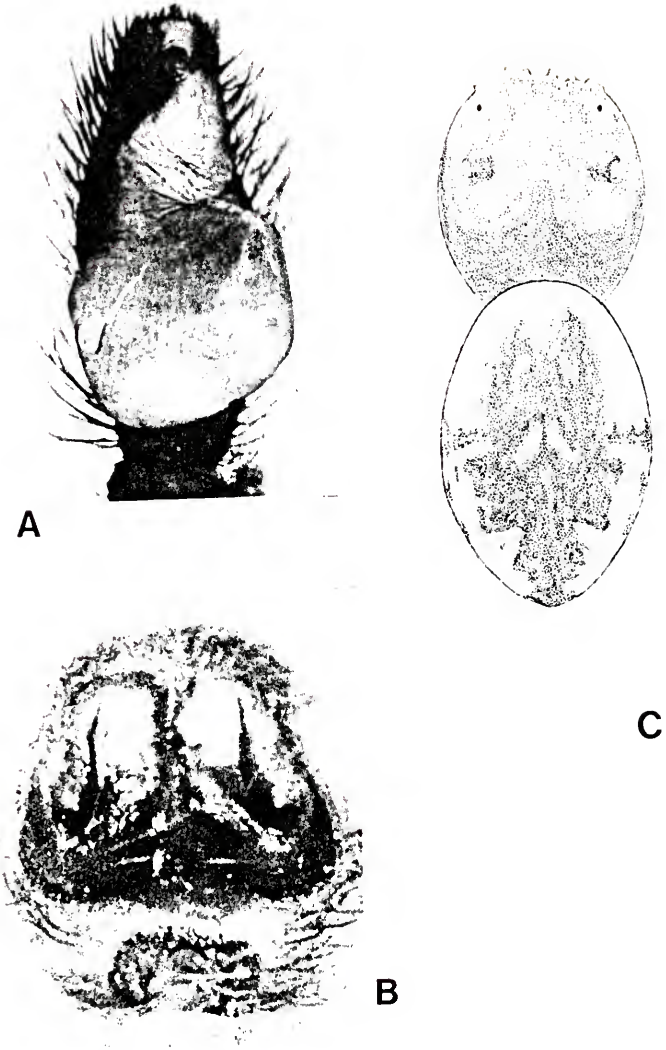
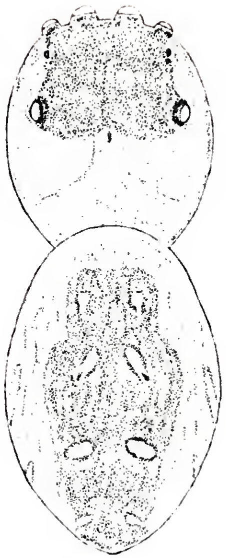

A
C
B

Figure 2-20. *Phidippus purpuratus*: A. Ventral view of male palp, B. Ventral view of female epigynum, C. Dorsal view of female.


A


C


B

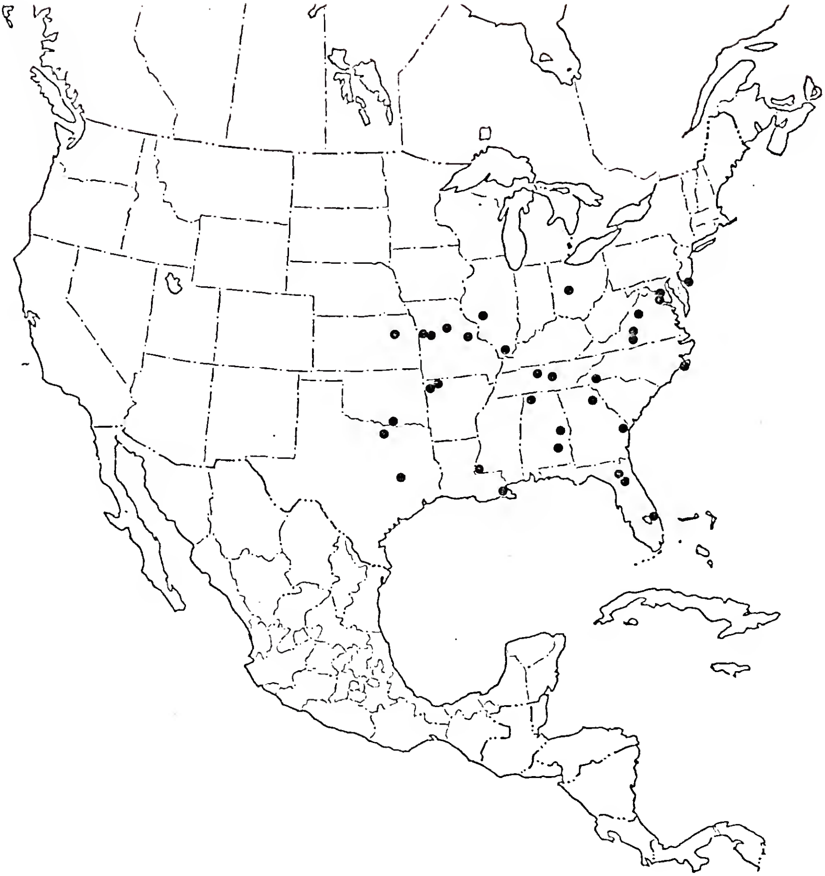


Figure 2-21. Distribution map of Phidippus putnami.

Figure 2-22. Distribution map of Phidippus mystaceus.

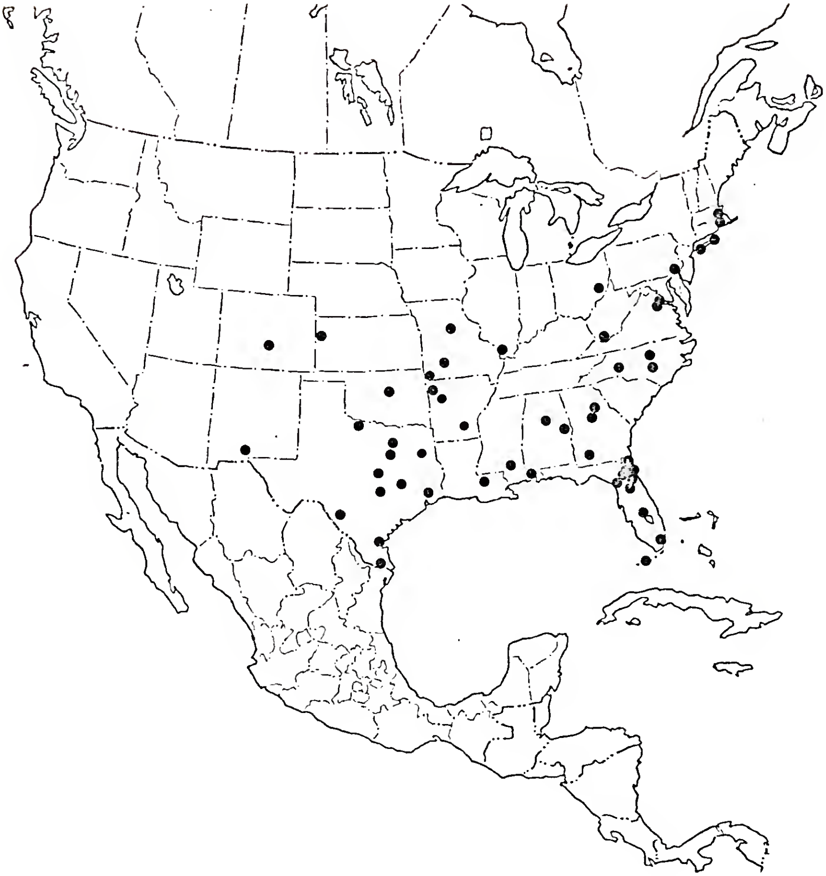


Figure 2-23. Distribution map of Phidippus cardinalis.

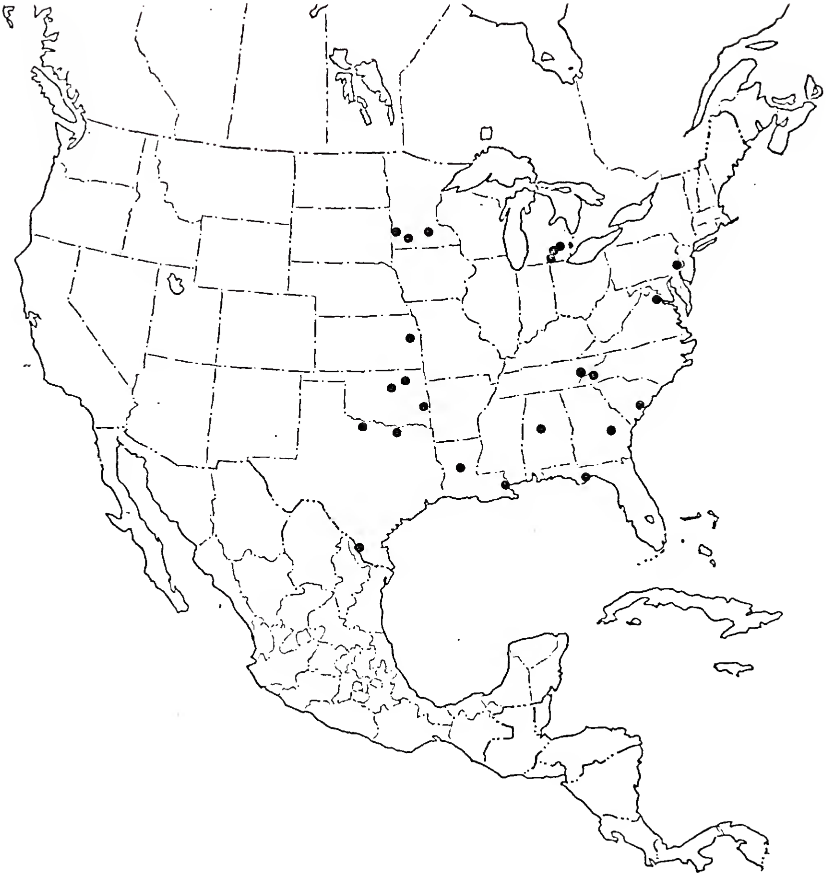


Figure 2-24. Distribution map of Phidippus pius.

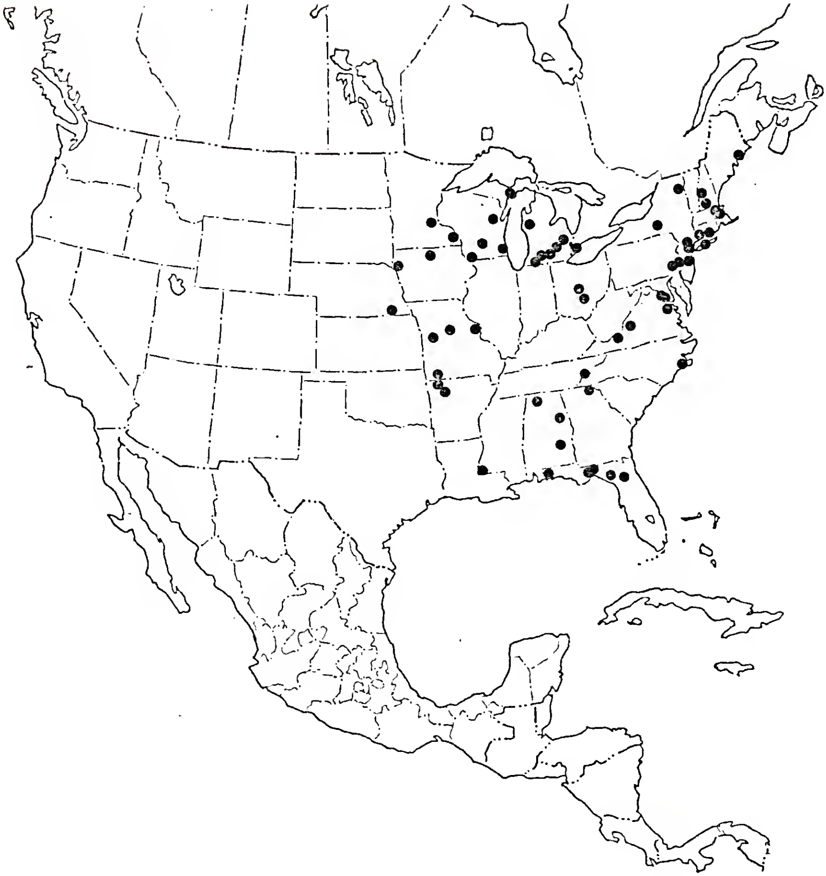


Figure 2-25. Distribution map of Phidippus whitmani.

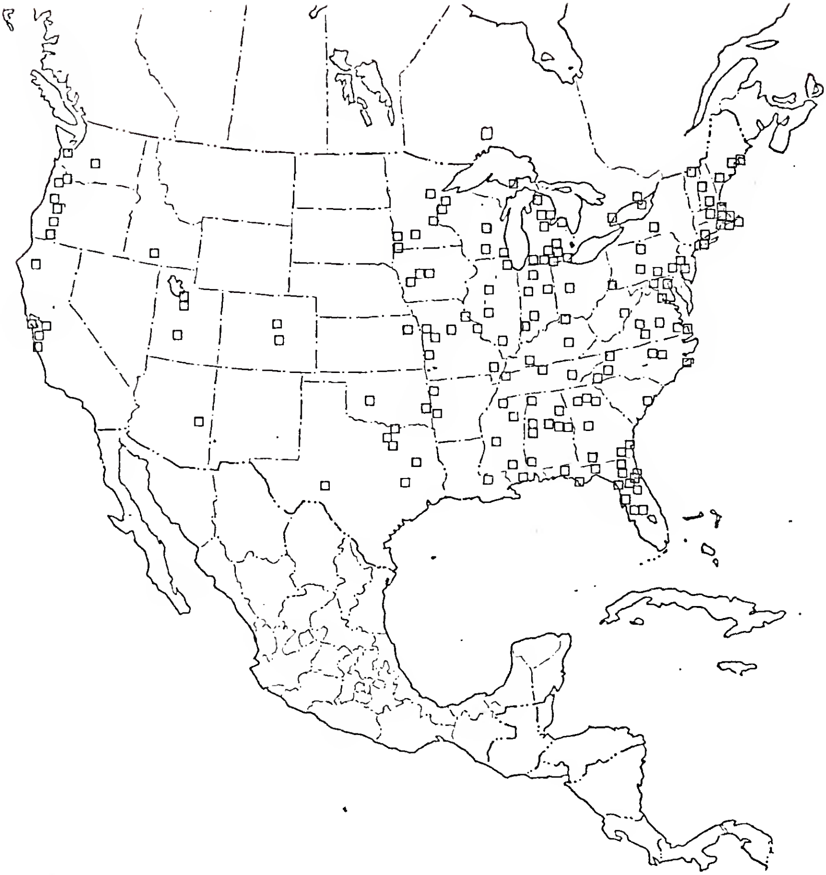


Figure 2-26. Distribution map of Phidippus clarus.

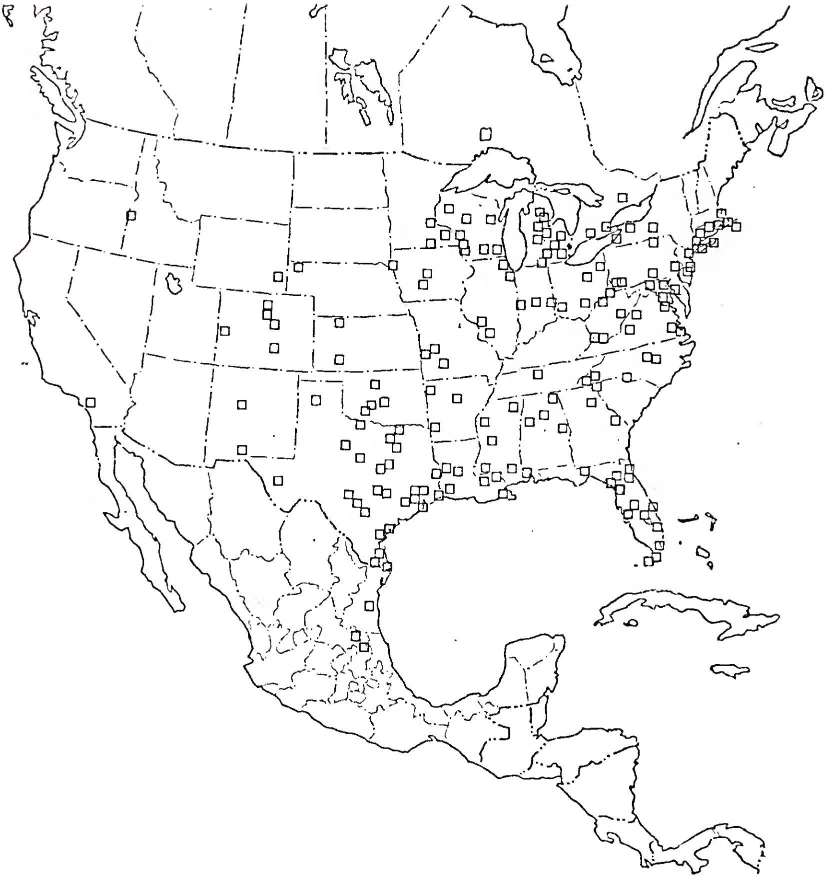


Figure 2-27. Distribution map of Phidippus audax.

Figure 2-28. Distribution map of Phidippus otiosus.

Figure 2-29. Distribution map of Phidippus regius.

Figure 2-30. Distribution maps of Phidippus insignarius (closed circles) and Phidippus xerus (open circles).

Figure 2-31. Distribution maps of Phidippus princeps (closed circles) and Phidippus pulcherrimus (open circles).

Figure 2-32. Distribution maps of Phidippus apacheanus (closed circles) and Phidippus borealis (open circles).

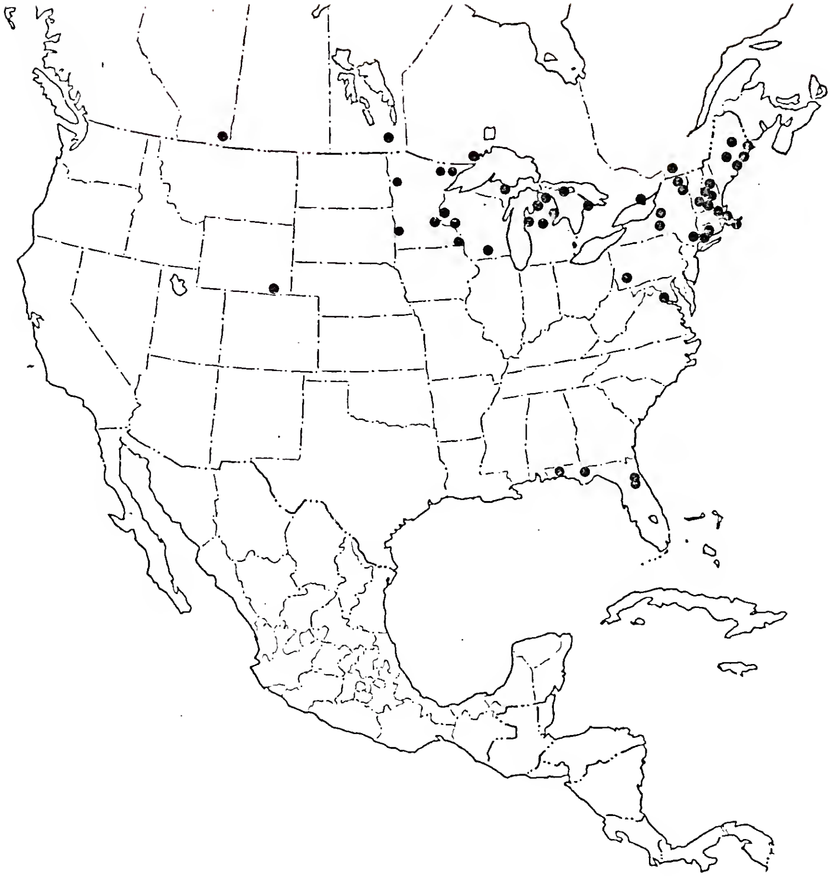


Figure 2-33. Distribution map of *Phidippus purpuratus*.

CHAPTER 3
IMMATURE STAGES OF *Phidippus* SPECIES

Peckham and Peckham (1909) and Kaston (1948) illustrated some of the immature stages of *P. clarus*, and Kaston (ibid) described some penultimate specimens of *P. cardinalis* (as *P. mccookii*) and *P. whitmani*. Bailey (1968) and Taylor and Peck (1975) measured carapace width for instars of *P. audax*, and the latter authors also illustrated some of the instars. Edwards (1975) measured carapace width for instars of *P. regius*. The lack of ability to identify immature stages of spiders has been a hindrance to workers attempting ecological studies (Turnbull, 1973) and for those working on the effects of spiders on pest populations in agro-ecosystems (e.g., Whitcomb et al., 1963).

For the most part, immatures have color patterns similar to adult females, and the pattern becomes more similar with each succeeding instar. The most difficult stage to determine to species is the first free-living instar, which in most species has a dark body with no scale pattern. The leg segments distal to the femur are usually much paler in color than the rest of the spiderling.

This report is preliminary in many ways, since characters of all instars of all species studied have not yet been quantified. Below I list known color patterns of first instars:

P. apacheanus - body black, distal leg segments black

P. audax, *P. pulcherrimus*, *P. regius* -

body black, distal leg segments red

P. clarus, *P. otiosus* - body brown, distal leg segments light brown

P. putnami - body brown, distal leg segments light brown, small white scale patches at back of ocular quadrangle and on each side of abdomen

P. whitmani - body black, distal leg segments pale yellow

P. xerus - body brown, distal leg segments distinctly orange

Those species with the same color pattern are usually separated either by season of occurrence, habitat, or microhabitat.

In a preliminary study of the leg macrosetae of successional instars of *P. regius*, definite differences between instars were noted for the first seven instars (Table 3-1). Macrosetae were added with each successive molt. Postembryos lacked macrosetae, and first instars had only a few macrosetae, establishing completely only the dorsal femoral sets and the ventral set of metatarsus I. The second instar added macrosetae to tibia II and metatarsus III, and increased the number on metatarsi II and IV. The third instar added a dorsoprolateral macroseta to all femora, and increased the number on tibia I and metatarsi II, III and IV, completing the set on metatarsus II. The fourth instar completed the full complement of macrosetae on the femora, added setae to all tibiae, and increased by one the number on metatarsus III. The fifth instar added the full complement of setae on patellae III and IV and tibia I, and increased the number on tibiae II, III, and IV and on metatarsi III and IV. The sixth instar completed sets of macrosetae on tibiae II and IV and metatarsi III and IV, while the seventh instar completed the macrosetal complement on tibia III, producing the adult macrosetation pattern.

Since most species of _Phidippus_ mature in 6-8 instars, and penultimate males can be distinguished by their swollen pedipalpi, this method of instar determination is likely to be a more accurate method than measurement of carapace width, since variable growth patterns of individuals result in a size range overlap in the later instars. Randall (1978) found that the macrosetal patterns of the femora of the green lynx spider, _Peucetia viridans_ (Hentz), were virtually 100% reliable for determining individuals of this species to instar.

Table 3-1. Leg macrosetae of instars 1-7 of *Phidippus regius*. Macrosetal codes are the same as those used for adult *Phidippus* (see Chapter 2). Values in parentheses indicate variation. Sample size was four individuals for each instar. Macrosetal additions to the previous instar are underlined.

First instar	femur I, II, III, IV D 0-1-1-1; tibia I V 0-0-2-0; metatarsus I V 0-2-2, II, IV V 0-1-1
Second instar	femora unchanged; tibia I V 0-0-2-0, II V 0-0-1R-0; metatarsus I V 0-2-2, II V 0-1-2, III V 0-0-1, IV V 0-0-1, R 0-0-1
Third instar	femur I, II, III, IV D 0-1-1-1, DP 0-0-0-1; tibia I V 0-1R(2)-2-1P, II V 0-0-1R-0; metatarsus I V 0-2-2, II V 0-2-2, III V 0-0-2, P 0-0-2, R 0-0-1, IV V 0-0-2, P 0-0-2, R 0-0-1
Fourth instar	femur I D 0-1-1-1, DR 0-0-0-2, II, III D 0-1-1-1, DP 0-0-0-2, DR 0-0-0-1, IV D 0-1-1-1, DP 0-0-0-1, DR 0-0-0-1; tibia I V 0-2(1R)-2-2, II V 0-0-1R-0, P 0-0-1-0, III P 0-0-1-0, R 0-0-1(0)-0, IV V 0-0-0-2(1R), R 0-0-1-0; metatarsus I, II V 0-2-2, III V 0-0-2, P 0-0-2, R-0-0-2, IV V 0-0-2, P 0-0-2, R 0-0-1
Fifth instar	femora unchanged; patella III, IV R 0-1-0; tibia I V 0-2-2-2, II V 0-0-(1R)-1R-2(1P), P 0-0-1-0, III V 0-0-0-2(1P), P 0-0-1-0, R 0-0(1)-1-0, IV V 0-0-0-2, P 0-0-1-0, R 0-1-1-0; metatarsus I, II V 0-2-2, III V 0-1-2, P 0-0-2, R 0-0-2, IV V 0-1-2, P 0-0-2, R 0-0(1)-2
Sixth instar	femora unchanged; patella unchanged; tibia I V 0-2-2-2, II V 0 1R(0)-2(1R)-2, P 0-0-;-0, III V 0-0-0-2, P 0-0-1-0. R 0-1(0)-1-0, IV V 0-1P-0-2, P 0-0-1-0, R 0-1-1-0; metatarsus I, II V 0-2-2, III V 0-2(1)-2, P 0-1(0)-2, R 0-0-2, IV V 0-1-2, P 0-1(0)-2, R 0-1-2
Seventh instar	femora unchanged; patellae unchanged; tibia I, II unchanged, tibia III V 0-0-0-2, P 0-0(1)-1-0, R 0-1-1-0, IV V 0-1P-0-2, P 0-0-1-0, R 0-1-1-0; metatarsus I, II unchanged, metatarsus III V 0-2-2, P 0-1(0)-2, R 0-1(0)-2, IV V 0-1-2, P 0-1-2, R 0-1(0)-2 (essentially adult macrosetae pattern established)

CHAPTER 4
HYBRIDIZATION IN *Phidippus* SPECIES

Introduction

Hybridization in arthropods has been known for several decades. Much of the early work on *Drosophila* by Dobzhansky and Patterson and their respective coworkers was reviewed by Patterson and Stone (1952). Clarke and Sheppard (1953) crossed four species of swallowtails (Papilionidae) in the laboratory. The contention of early taxonomists was that interspecies hybridization was unimportant to the evolution of species. This view was challenged by Sailer (1954), who, using his own data on crossing of 2 species of *Euschistus* (Pentatomidae) and reanalyzing data of earlier workers, demonstrated that hybridization could be a highly influential factor in affecting evolution of species, and even in creating new species.

Spider hybrids have been infrequently reported (Gerhardt, 1928; Bonnet, 1933; Locket, 1939). Dondale (1964, 1967) used hybridization experiments as an aid in species determinations in *Philodromus* (Philodromidae). Below I report on laboratory hybridization of *Phidippus otiosus* X *P. regius* and the subsequent discovery of hybridization under natural conditions between these two species. Speciation events are hypothesized based on geographic distribution of the two species. Laboratory crosses of other species of *Phidippus* are also noted and their significance discussed.

All laboratory crosses were obtained by the methods described under the courtship behaviors of other species (Chapter 5), and the descriptions of hybrid courtship are reported there. Rearing of hybrid offspring followed the procedure described by Edwards (1975). Maturation rates and sizes of F_1 crosses were compared with parent species. Matings were attempted between F_1 males and females, and F_1 individuals were backcrossed to both parent species. Fecundity of hybrids and backcrosses was compared to parent species.

Laboratory Results

Crosses

Three out of three attempted crosses of *P. otiosus* males X *P. regius* females from Alachua County were successful and produced viable offspring. Offspring from two of the crosses were reared; male hybrids were significantly smaller than males of *P. regius* and *P. otiosus* reared under similar conditions and the hybrid males matured in fewer instars than either of the parent species. Of 80 original offspring, 4 died as juveniles, 24 became males, and 52 became females. This sex ratio is approximately 1:2 in favor of females, whereas the sex ratio of *P. regius* is typically about 1:1.

Although Pinter and Walters (1971) reported the 2n chromosome complement of males of 3 species of *Phidippus* (*P. regius*, *P. audax*, and *P. johnsoni*) to be 20 autosomes + X_1X_2O, Wayne Maddison (personal communication) has found the chromosomes of *P. audax* and *P. purpuratus* to be 26 + X_1X_2O, as has been noted for most of the 35 species of salticids reported in the literature (e.g., Painter, 1914; Mittal, 1964). If the sex chromosomes were involved in the determination of the unusual sex ratio, one might have expected the females rather than the males to be the affected sex, due to the sex determining mechanism (males are X_1X_20, females are $X_1X_1X_2X_2$).

Although theoretically, hybrid males should be partially fertile when backcrossed to parent species, evidence presented below indicates that they were sterile or at least incapable of reproducing. This could be due to a number of factors: premature maturation could affect the number or viability of sperm, small size and/or hybrid courtship could cause rejection by females, and hybrid structure of embolus or palpal tibial apophysis could prevent successful copulation. The latter case was observed in the single successful courtship of a female *P. regius* by a hybrid male. The male was unable to engage the epigynum of the female, even after repeated attempts.

A single attempted cross of a *P. otiosus* male with a *P. regius* female from Palm Beach County was unsuccessful. This female accepted a *P. regius* male immediately prior to rejecting the *P. otiosus* male, and subsequently accepted an F_1 hybrid male (which was unable to copulate; see above) immediately after rejecting the *P. otiosus* male. *Phidippus otiosus* has not been reported from south of Lake Okeechobee; the southernmost record is a male from Archbold Biological Station near Lake Placid, Highlands County. Muma (1975) reported *P. otiosus* from Polk County. The geographic significance is discussed below.

Three attempted reciprocal crosses with *P. regius* males X *P. otiosus* females resulted in two successful matings but no offspring, and in the third encounter, the male killed the female.

Eight F_1 male X F_1 female crosses were attempted. On three occasions the females refused to mate, on four occasions females killed the male, and one male successfully copulated but no offspring were produced. The small size of the males apparently contributed both to their inability to defend themselves and to their rejection by females. Female predation on males prior to copulation is probably a strong selective pressure on males too small to defend themselves. In most cases, the large chelicerae and enlarged legs I of the male are used to repel a frontal attack by a female (Hill, 1977a); but small males do not have sufficient strength to fend off a female's attack. Supportive evidence is provided in later discussion of other attempted crosses.

Two hybrid F_1 females were backcrossed to parent species males, one each to a _P. regius_ male and to a _P. otiosus_ male. Total viable offspring (measured by number of eggs hatched) for the backcross to the _P. regius_ male was 8 in the first eggsac, and 42 in the second eggsac, a total of 50. The number of viable offspring for the backcross to the _P. otiosus_ male was 36, 16, and 8 in the first, second, and third eggsacs, respectively, a total of 60. Total infertile eggs were not counted, but few were noted.

Hybrids were described by Edwards (1975). To briefly summarize, F_1 females looked like _P. otiosus_ with dorsal abdominal spots like _P. regius_, whereas F_1 males looked like _P. regius_ with carapace bands and dorsal abdominal spots like _P. otiosus_; the markings of males were very pale orange, not white like _P. regius_ or deep orange like _P. otiosus_.

Results of F_1 backcrosses are incomplete as laboratory populations, reared in an outside insectary, were killed by exposure to the sun's rays as the angle of the sun changed in the fall. However, a few males did mature before the colonies were destroyed. Fourteen males and 4 males, as a result of F_1 backcrosses to *P. otiosus* and *P. regius* males, respectively, matured before destruction of the colony. Offspring of backcrosses to *P. otiosus* were evenly divided between males that looked like F_1 males and males that looked very much like *P. otiosus* males (the main difference in the latter males from *P. otiosus* males was the exaggerated color pattern which was more brightly orange and gold than a normal *P. otiosus* male). Offspring of backcrosses to *P. regius* resulted in 2 males that looked like an F_1 male, and 2 males that looked like *P. regius* males (except that the carapace bands were still present; all of the markings were pure white as in a normal *P. regius* male). This last mentioned form was of great interest, as it was essentially identical in pattern to the species described as *Phidippus tullgreni* by Wallace (1950), and was also the same as occasional males previously determined to be a rare color form of *P. regius*.

Field Records

As part of a rearing program designed to compare life histories of various species of *Phidippus* (not reported here), I began rearing offspring from 5 different females of *P. regius*, each collected from a different locality. After only a few instars, it became apparent that the offspring of the female from a very xeric habitat in Levy County (a turkey oak-rosemary area, just across the Alachua County line) were different in appearance than offspring of the other females, and were very similar to the F_1 hybrids I had reared earlier. When some of these offspring matured, they were determined probably to be the result of either a direct mating with a *P. otiosus* male, or of a male from a second or third generation removed backcross from an earlier hybridization. The latter situation was considered a possibility since most of the males resembled the F_1-backcross males more than they did F_1 males from the laboratory crosses, i.e., most of the males had white markings and only a few showed the pale orange tint present in the laboratory-reared F_1 males.

Since I began collecting P. regius 8 years ago, I have collected several dozen males and examined approximately 200 others in various collections. Of these specimens, 7 had white carapace bands. As mentioned above, F_1-backcross males were very similar to the field-collected males with white carapace bands. I therefore had to consider the possibility that these 7 males were exhibiting introgressive characters as a result of a previous hybridization in their ancestry.

I was able to collect one of these males in the xeric hammock which constituted one of the three primary study sites (see Chapter 10 and Appendix D). This male was crossed with a gray female also from Alachua County. The female made 2 eggsacs, neither of which was fertile (in fact, no distinct eggs were formed). This result seems to be additional evidence supporting the hypothesis that hybrid males are sterile.

The only field-collected female that I would consider a hybrid was a specimen collected in Ocala National Forest, Marion County. It essentially had the appearance of P. otiosus, but the posterior abdominal spots were intermediate in shape with P. regius. Females of P. regius almost always have either an unmarked carapace, or the carapace is almost completely covered with scales. Occasionally (in about the same proportion as males) females have pale yellowish or white carapace bands which are similar to those of P. otiosus. Possibly these females also represent earlier introgressive matings.

Much of the above was more or less speculative, since what occurs in nature does not necessarily follow what might be manipulated in the laboratory. It is possible that the variation apparently exhibited by _P_. _regius_ could be the result of true genetic polymorphism. A similar polymorphism in presence or absence of white carapace bands is well documented for the related _P_. _audax_ (Kaston, 1948). Strong evidence supporting the validity of the preceding discussion of hybridization in natural situations was provided by Dr. John F. Anderson, who collected a male _P_. _otiosus_ in copula with a female _P_. _regius_, 19 September 1980, on a small tree at the interface of a field and swamp forest at the south end of Newnan's Lake.

Ecological Factors Affecting Hybridization

My first hypothesis for hybridization between _P_. _otiosus_ and _P_. _regius_ was based on the fact that I had collected apparent hybrids in xeric woods habitats. Since the populations of the two species were likely to be and seemed to be at very low densities in xeric habitats, the chances of a female going unmated once maturity was reached were increased. A female should, eventually, rather mate with a related species and produce some viable offspring, than to not mate and be totally without offspring. Another factor is that a female is more likely to mate if it is in a nest when found by a male (Jackson, 1976); in Jackson's laboratory experiments, even already mated females occasionally remated under these circumstances. (I have on one occasion found a male _P_. _regius_ cohabiting with an obviously gravid conspecific female, lending support to the possibility that multiple matings of a single female occasionally occur under natural conditions.) Of course, the implication is that a male has an increased chance of mating with a non-specific female if he finds her in a nest. Other crosses between species under similar circumstances are reported below.

Using the clue provided by Anderson, who found a hybridizing pair in copula in an obviously non-xeric environment, I rechecked the habitat data for the seven white-banded males of *P. regius*. They were found in one of three situations: lake edge, xeric hammock, and open pine flatwoods. Because *P. otiosus* is a canopy species, while *P. regius* is an old field species that moves onto shrubs and palmettoes as an adult and then to various trees to reproduce, two types of opportunities are presented for interaction: 1) When *P. regius* females are searching for shelter under tree bark in which to lay their eggs, they may be encountered by *P. otiosus* males searching for conspecific females that are also searching for nesting sites in the smae situations at the same time; opportunity for this type of interaction would be most frequent at interfaces of fields and woods along lake shores, where *P. otiosus* is most abundant. 2) In open woodlands, young *P. regius* develop in the herb zone, but if there is no shrub or mature palmetto understory, the adult *P. regius* move directly to the trees instead. Here they are directly competing with *P. otiosus* for food and nesting sites for a longer period of time than in the first situation. In one such situation, a slash pine plantation in Duval County, *P. regius* has apparently completely displaced *P. otiosus* in the trees (R. A. Belmont, personal communication and specimens brought in for identification from the canopy of the pine plantation, obtained with the use of a cherry-picker at 50' height in the top of the canopy). *Phidippus regius* has been taken from the top of coconut palms by similar means in South Florida (J. A. Reinert, collector), where *P. otiosus* does not occur. Muma (1975) reports both species from citrus groves, another instance of a single-layered canopy.

It is perhaps in this second situation that my original hypothesis is partially valid, since conditions favorable to *P. regius* may permit it to exclude *P. otiosus*. In certain arid habitats, for example xeric hammock (which has little shrub understory), environmental factors may be stringent enough to keep populations of both species at low levels, allow them to coexist, and thus improve the chances for crossbreeding.

Sailer's (1954) contention that introgression may be important to the evolution of species seems to apply for one character of *P. otiosus*. This species increases in mean length from the northern part of its range to the southern part, which, considering its potential competitors, is just the reverse of what might be expected. In Maryland, *P. otiosus* is the same size as the synchronic *P. mystaceus*, the other primary canopy species in the region. Since both of these species are apparently uncommon in the region, perhaps the populations are small enough so that the resources are not limiting and therefore no competition is occurring. In the other situation, *P. otiosus* approaches the size of *P. regius* where the two species occur together. Since these two species are also synchronic, and *P. regius* can potentially displace *P. otiosus* in certain circumstances, one might expect that *P. otiosus* would evolve toward smaller size in order to reduce competition for food and nesting sites. Although other factors may be involved that are not readily apparent (such as competition with other medium-sized canopy salticids like *Dendryphantes pineus*, *Metacyrba undata*, or *Thiodina sylvana*), one feasible explanation of large size in *P. otiosus* is the introgression of genes for large size from *P. regius*. This would imply a massive period of interbreeding over one time period or frequent hybridization presently, discussed in the following section.

Species Relationships, Geologic History, and Speciation

Although I have emphasized in the above discussion the ability of *P. otiosus* and *P. regius* to hybridize, I have said nothing about their actual relationship. They in fact appear to be sister species, and a comparative examination of their genitalia (see Chapter 2) reveals a great deal of similarity between the two species. However, although the basic structures of the body markings are similar, the color patterns are quite different. In contrast, the color patterns of the sister species (?) *P. cardinalis* and *P. pius* are nearly identical, yet the male genitalia are quite different. These two opposite extremes seem to represent a principle that has not been commented on in the literature (P. Perkins, personal communication), but is apparently a widespread phenomenon. That is, closely related species differ greatly in the form of the genitalia or in their appearance. An example of the former is the species of *Mycotrupes* (Scarabeidae), which are similar metallic green or blue in appearance, but have amazingly complex genitalia which look completely different from species to species; an example of the latter is a species pair of *Cicindela* which have nearly identical genitalia, but one species is extremely hirsute, while the other species is nearly glabrous and highly iridescent (personal observation and P. M. Choate, personal communication). While the principle may be generally applicable, this particular interpretation seems to apply most readily to visually-oriented animals. It should be applicable to any two-dimensional system including genitalia as one dimension, e.g., cricket song similarities versus genitalic similarities, and therefore is a testable hypothesis.

The ranges of *P. otiosus* and *P. regius* overlap to great extent (see maps Chapter 2). *Phidippus otiosus* ranges a little farther north than P. regius, whereas the range of P. regius includes the southern tip of Florida, the Florida Keys, and the Greater Antilles. The geologic history of Florida has been one of alternate island formation and reconnection throughout the Cenozoic with little agreement as to whether or not the peninsula was totally submerged. At least there seems to be agreement that a peninsula existed in late Pliocene, and that four periods of island formation occurred during the Pleistocene, at least two of which caused major island formation (MacNeil, 1950). Certain groups of lizards (Carr, 1940), snakes (Highton, 1956), scarabs (Mycotrupes; also see above) (Hubbell, 1954), cicindelids (P. M. Choate, personal communicaton; one of the two species of Cicindela mentioned above has a distribution which corresponds with Red Hill Island of the Pleistocene Aftonian Interglacial stage), grasshoppers (Hubbell, 1956), and wolf spiders (Wallace, 1942; McCrone, 1963; Brady, 1972) have endemic Florida species with distributions roughly corresponding to the division of the Florida peninsula into islands during the Pleistocene. McCrone hypothesized that the Aftonian Interglacial isolated three populations of Geolycosa (Lycosidae), on the Trail Ridge, Lake Wales, and Red Hill island groups. Since these spiders are fossorial they probably dispersed little from their centers of origin during the subsequent Kansan Glacial stage. During the next Interglacial, the Yarmouth, the Trail Ridge islands were connected to the mainland, although extensive swamp prevented gene flow, and Lake Wales Ridge and Red Hill Island were connected, allowing gene flow between these populations. The net result was the formation of two new species from the parent Geolycosa pikei (Marx) of the mainland: G. patellonigra Wallace in north-central Florida, and G. xera McCrone; the latter species was further divided into subspecies corresponding morphologically with the initial geographic isolation of the Lake Wales island group from Red Hill Island.

Island formation can be used to hypothesize the speciation process separating P. regius from P. otiosus. A different interpretation of the significance of island formation from Geolycosa must be presented, since Phidippus species have much greater dispersal ability than species of Geolycosa, and only one new species evolved (actually three new species evolved, but P. xerus and P. pulcherrimus are not closely related to P. regius and are the result of isolation of parts of populations of different parent species).

Assuming P. otiosus to be the parent species, since it has the more northern distribution, it would have been isolated on the mainland during the Aftonian Interglacial, with isolated populations in the same three island groups mentioned above. But the distance of Red Hill Island from the Lake Wales island group, and the distance between the Lake Wales and western Tampa Bay island groups, was probably insufficient to maintain isolation of the populations in this region, since the ballooning early instars could easily travel this distance if the wind was favorable. Therefore, probably two populations were isolated, a northern and a southern. Edwards (1975) noted a marked delineation in color pattern of P. regius females which corresponds well with this hypothetical isolation pattern. Females from Alachua County north were either black or gray, whereas females from Marion County south were either orange or brown. The gray and brown forms may represent various intergrades of the black and orange populations which are nearly pure at the northern and southern extremes, respectively, of their ranges. This may be a relative function of actual gene distribution or selection for various colors. Evidence for the latter is found in various other animals. Animals in wet forested habitats tend to be darker than relatives in open arid habitats. Scarabs of the genus Phanaeus in Florida are dark in river swamp and metallic green and copper in xeric open woodlands (P. M. Choate, personal communication); Phidippus otiosus is darker in river swamp and cypress dome habitats than in xeric open woodlands (personal observation). Color selection in P. regius may be for darker females in the extensively forested north Florida area, and oranger females in the sandy open xeric scrub areas of central and south Florida. I have collected gray females from tropical forest in south Florida, which adds further support to the general observed pattern of color distribution with habitat association.

During the Kansan Glacial stage, when the populations were reconnected, gene flow on the sibling north-central population would come from both north and south. Some genetic isolation must have occurred prior to this time due to the gene complexes of the isolated populations adapting to the peripheral habitats in the absence of gene flow from the mainland population (genetic isolation of this type is discussed by Mayr, 1954). The more northern isolated population would be subject to greater hybridization pressure due to its proximity to the parent population. Also, the swamp barrier of the Yarmouth Interglacial would be ineffective in preventing gene flow between mainland and Trail Ridge populations. The southern population would again be isolated at this time. Presumably, the southern population was at one time connected to or was able to disperse to the Greater Antilles; females of P. regius in the Caribbean are generally orange.

Since the two populations of P. regius apparently interbred freely upon reuniting, it can be assumed that the conditions of their separate isolations and respective gene pools were so similar that reproductive isolation between the two populations was not achieved. Their rapid and extensive dispersal ability was probably also a factor in reuniting populations once the peninsula had reformed.

This pattern of isolation and speciation could explain why northern females of *P. regius*, which historically have more often been associated with *P. otiosus*, were more likely to mate with *P. otiosus* males than were the southern *P. regius* females which rejected a *P. otiosus* male, despite the fact that the reverse (behavior isolation in sympatric populations) would be expected. The amount of introgression of *P. otiosus* into *P. regius* is certainly like to be greater in the northern population of *P. regius*, perhaps enough so that pre-copulatory reproductive isolating mechanisms are broken down, at least under certain circumstances, e.g., low population densities. Southern females of *P. regius* would be far less likely to be affected by introgression, and might be expected to be more discriminating in choosing mates.

Hybridizations Between Other Species

P. regius X *P. audax*

A male of *P. audax* from Arkansas was placed in a petri dish with a nesting, virgin *P. regius* female from Alachua County (*P. regius* does not occur in Arkansas, but *P. audax* occurs in Florida). The *P. audax* male was able to enter the nest and attempt mating; however, he was apparently unable to copulate, i.e., he could not engage the epigynum with the palpal tibial apophysis. The female did not produce offspring.

P. princeps X *P. pulcherrimus*

Seven Type 1 (visual) courtships were observed between members of these sister species; three were *P. pulcherrimus* males X *P. princeps* females and four were *P. princeps* males X *P. pulcherrimus* females. Only one courtship was successful, between a *P. pulcherrimus* male and *P. princeps*

ceps female, and it culminated in a successful mating. This particular female was feeding during courtship, and did not successfully fend off the male as did the non-feeding females in the other pairings. The female that mated died 20 days after mating without making an eggsac, which is less than the average 30 days reported for *P. regius* to make an eggsac after mating (Edwards, 1975). Therefore the results of the mating were inconclusive.

Laboratory-reared males of *P. princeps* are usually small when compared with females and they are subject to intense predation by females during laboratory mating experiments. I have observed a single case of post-copulatory predation by a female of a male immediately following copulation after Type I (visual) courtship. Hill (1977a) noted several instances of post-copulatory predation after Type II (tactile) courtships; he also noted, however, that Type II courtship was a much more successful mating strategy than Type I courtship in terms of mating duration.

P. apacheanus X *P. cardinalis*

These two species are synchronic and syntopic, and both appear to mimic mutillids. The males also have similar courtships (see Chapter 5). On two occasions, I placed males of *P. cardinalis* with females of *P. apacheanus*. All were field collected, an adult and an immature of each species; the latter were reared to maturity in the laboratory. Both males of *P. cardinalis* were smaller than average.

Both males began courting the females. The females watched for a few seconds, then approached, attacked, and killed the males. In both instances it was clear that the males were too small to defend themselves.

CHAPTER 5
THE COURTSHIPS OF EASTERN Phidippus

Introduction

The known courtships of salticids have recently been reviewed by Jackson (1976) and Richman (1977). The courtships of only 9 species of Phidippus have been described (with a tenth in preparation; Jackson, in manuscript) (Peckham & Peckham, 1889; Kaston, 1936; Snetsinger, 1955; Gardner, 1965; Dewey, 1965; Bailey, 1968; Taylor and Peck, 1975; Edwards, 1975; Richman, 1977; Jackson, 1978b). Jackson (1977a, 1978a, b) described 2 types of courtship employed by male P. johnsoni under the following 3 conditions: Type I courtship with adult females outside nests, Type II courtship with adult females inside nests, and Type II courtship plus cohabitation with subadult females inside nests. These courtship strategies appear to be utilized throughout the genus, as several of the species in this study were found to cohabit in the field. The present work reviews and redescribes the courtships of 5 species, and describes for the first time the courtships of 8 additional species. Courtship of a hybrid (P. otiosus X P. regius) is also described. All eastern U. S. species of Phidippus are represented except P. borealis, P. insignarius, and P. pius, which were unavailable for study. The courtship of P. mystaceus, which includes a new method of communication for salticids, is dealt with in greater detail in the following chapter.

Methods, Materials and Terminology

Observations of courtship were made in one of two ways: Either a male and female were released onto a formica-covered table top about 10 cm apart, or a male was introduced into a petri dish containing a female and her nest. If in the former case the event was to be filmed, the table top was covered with a sheet of construction board marked with a grid containing 1 cm graticules. Timing of movements was made with the sweep hand of wrist watch for sequences of observed movements, or by counting frames in filmed courtships and converting to seconds.

The analyses of courtships for each species are composites of both observed and filmed courtships. Due to the fact that sample sizes for most species were small, only ranges are given for particular measures of positioning or movement, unless this figure is misleading, in which cases the means are also given. The mean was closely associated with the median (e.g., range 1-3, mean = 2 indicates that most of the time the measurement was 2; range 1-3, mean = 1.5 indicates measurements were usually 1 or 2). This is important to remember, since all measures of movement were integers except for the actual timing of events.

Femora I were either perpendicular to the substrate (90°) or angled forward (<90°); they were also held close to the body (0°) or held away from the body (45°+). The distal segments of leg I (patella, tibia, metatarsus, tarsus) were always at a different angle than the femur since the leg was bent at the femur-patella joint; usually the distal segments were in a straight line, but in a few species a second bend occurred at the tibia-metatarsus joint. In the latter cases, the figure for the metatarsus-tarsus angle is given in Table 1, and the patella-tibia (mid-leg) angle is discussed in the text. In most species, the distal leg was turned outward at the femur-patella joint; the amount of this positioning is measured in degrees from each leg I to the midline (sagittal plane) of the spider. A flick is defined as a sudden upward

Table 5-1. Courtships of eastern Phidippus species, describing major types of movements and positioning of appendages used by males to signal females. Details are described in the text. Asterisk indicates forward movement lacks a lateral component. Letter R indicates leg I is rotated.

	mystaceus	putnami	otiosus	regius
# filmed	2	4	5	5
# observed	1	1	3	12
femur I to substrate (°)	20	90	90	70-90
femur I to spider (°)	60	45	45	45
distal leg I to substrate (°)	0-40	45	30-35	45
distal leg I to spider midline (°)	10-20	0-5	30-40	45-85
peak of flick (°)	none	none	80	90
# leg movements/sequence	2-5	6-8R	1	1
# paired alternate palp movements/sequence	0	1/4sec	2-4 $\bar{x}$=3	2-6 $\bar{x}$=4.2
# lateral moves/sequence	1-4	1*	1	1
# sequences	1-8	4-5	6+	4-11
time of sequences (sec.)		4-7 $\bar{x}$=4.9	1-3.5 $\bar{x}$-2.5	2.5-6 $\bar{x}$=3.9
time of pause (sec.)		5-23 $\bar{x}$=10.8	2-7 $\bar{x}$=4	2-4 $\bar{x}$=3

Table 5-1 - extended.

hybrid	*audax*	*xerus*	*princeps*	*pulcherrimus*	*clarus*	*cardinalis*	*whitmani*	*apacheanus*	*purpuratus*
4	7	1	1	1	2	2	1	1	1
2	0	4	5	4	0	5	8	0	0
90	90	45-60	90	45	40	90	90	90	90
45	0	45	0	0	45	0	0	45	0
0	20	0	45	10	-10	75	45-50	30-70	30
45-85	30-40	0	0-40	15	45	0	0-10	0-25	0-5
90	35	20	70	25	70	90	90	50-90	45
1	2-4 $\bar{x}$=2.5	3-4 $\bar{x}$-3.2	1-3 $\bar{x}$=2	2	1	1-2	1-3 $\bar{x}$=1.5	?	1-2
4-7 $\bar{x}$=5	3-5	3-4	2	2-3	0	2?	0	2	0?
1	1	1	1	1	1	1	1*	1	1
6+	4-14 $\bar{x}$=7	9-10	6+	16	6+	13-15	3-20	4+	8
2.0	1-1.5	2.2	1-2.5	1-1.5	1-2.5	1-1.8 $\bar{x}$=1.5	.5-1.5	1.6-2	3-4.5
4.5-7	2	3-9 $\bar{x}$=3.6	1.5-6	1.0	3-6	4-15 $\bar{x}$=6.2	9-60 $\bar{x}$-21	4.5-6.5 $\bar{x}$=5.3	5-11 $\bar{x}$-8.8

movement of an appendage, which in most species is brought immediately back down to the original position of the appendage. The amplitude of a flick varies among species. A sequence of movement is defined as any actions occurring consecutively or simultaneously. Each sequence is separated by a pause in which no leg movement occurs.

Results

General Similarities

Males, even though they have several species-specific components to courtship, have certain components in common. The palpi are always held to the sides of the chelicerae, which exposes the iridescent surface of the chelicerae. Only in P. putnami, which has cheliceral scale and setal patterns, do the palpi cross in front of the chelicerae (also in the closely related P. femoratus; R. R. Jackson, personal communication). Stage II courtship (Crane, 1949) is also essentially the same among all species; P. mystaceus assumes a similar position early in Stage I. In Stage II courtship, the legs I are extended forward parallel to touch the female and the whole body is lowered close to the substrate, whereas in Stage I the prosoma is elevated and the legs I are positioned or moved otherwise in a species-specific manner. Although the abdomen may appear to be shifted from side-to-side during the zigzag approach of males of most species, this position appears to result from reattaching the dragline to the substrate at the end of each sequence of lateral stepping movements. When the spider changes direction, the release of silk for the dragline may not occur as fast as the spider is moving, resulting in the abdomen, which turns easily on the pedicel, being held back by the pull of the attached dragline. While this could be done deliberately, there do not appear to be any abdominal modifications intended for use in courtship. Likewise, abdomen bobbing by males did not appear to have any particular significance to courtship and usually occurred in an erratic fashion. It often occurred in conjunction with the specific sudden movement of an anterior appendage and may be an artifact of a sudden increase in hemolytic pressure intended to move the appendages, since spiders have an open circulatory system. Abdomen bobbing also occurs during mating, with each expansion and contraction of the hematodocha.

Males began courting from 3-6 cm from females, although Kaston (1936) reported three of the species reexamined here (P. audax, P. clarus, P. purpuratus) began courting as far away as 10 cm. Several species, during a lateral movement sequence which angled toward the female, partially retreated at the end of a sequence. The lateral movement was in the form of an asymmetrical arc.

The behavior of females during courtship consists of a set of actions, which, as they are not as directly involved in species specific recognition as are the movements performed by males, are essentially the same from species to species. Jackson (1978b) has described the set of behaviors used by female P. johnsoni during attempted courtship by males, and although all of the behaviors described by Jackson have not been observed for each species considered here, it seems likely that these behaviors will be found to apply generally throughout the genus. To briefly summarize these movements, adult females outside nests, upon the approach of a courting male, may strike at the male with fangs or forelegs, may raise the forelegs to block an attempted mount by the male, may remain motionless and allow mounting and mating, or may decamp (run away). Adult and subadult females inside nests have a similar repertoire of behaviors; additionally they have a variety of percussionary activities utilizing the legs and/or body, as well as the option of holding the entrance to the silken chamber closed with their forelegs.

Phidippus mystaceus

Anterior decorations of male. Chelicerae covered with white fringe proximally, iridescent green distally; clypeus fringe white and yellow; palpi with white fringes and dorsal cymbial spot of mixed yellow and white scales; legs I fringed with yellow ventrally, covered with yellow scales (especially venter of femur) except lateral sides of femur, and with black tuft on dorsum of femur; 4 dorsal setal tufts.

Type I courtship. Stage I courtship is divided into two stages; Ia, whish is similar to Stage I in other species, and Ib, which is a stage in which sound is produced. Stage Ib is elaborated on in the following chapter. Stage Ia is sometimes omitted altogether in the courtship sequence. In one instance (first courtship) the stages were alternated several times. When it occurs, Stage Ia is unusual in that the legs I are bobbed or rotated slightly (films are inconclusive) and continuously while lateral movement occurs. Lateral movements usually consists of one change of direction (0-3) with virtually no pause when changing direction during a sequence. Pauses between sequences were fairly long; the legs I continued to be bobbed and the palpi stridulated during pauses. Lateral movements were much wider than other species (2-2.5 cm vs 0.5-1 cm for other species).

Phidippus putnami

Anterior decorations of male. Chelicerae striped with red and white scales proximally, covered with blue-gray scales distally; clypeus with red scales and white fringe; palpi with blue-gray and white scales; legs I fringed ventrally with yellow or variegated with black, white and yellow, and venter of femur metallic blue, with ventral yellow tuft; dorsal setal crests.

Type I courtship. The courtship of this species is quite slow, equalled or surpassed in length only by that of *P. whitmani* and Stage Ib of *P. mystaceus*, both of which are otherwise quite different. At the beginning, both legs are bobbed alternately, then one begins rotating and the other stops. After a long pause, the other leg begins rotating. During each rotation of a leg I, the male advances directly toward the female, initially as much as 1.5 cm per move, later only a few mm as he nears the female. The palpi keep up a steady, alternate rotation, crossing in front of the chelicerae beginning with an upward, inward motion. One rotation occurs every 2 sec. and continues whether the male is moving or stationary; palpal movement continues until Stage II begins.

The courtship of *P. putnami* differs from other species in its long pauses, alternate rotation of legs, and rotation of palpi.

Phidippus otiosus

Anterior decorations of male. Chelicerae iridescent green-blue; clypeus fringe black; palpi black and orange, legs I fringed with black and orange; 4 ocular tufts. Female chelicerae are iridescent orange-gold-green, a unique color combination that may be important for recognition of the female by the male.

Type I courtship. The legs I are held away from the body and fairly high. The single flick per sequence occurs at the beginning of lateral movement; it is not quite vertical nor are the legs I quite parallel. The flick is relatively soft, i.e., is not a quick up-and-down jerky movement, but rather a smooth upward movement after which the legs I are gradually dropped back to their original position. The palpi are moved back-and-forth alternately just as the movement sequence ends. Some individual variation exists in timing of movement and pauses, but in all cases the pause is about twice the length of the movement sequence.

The courtship is similar to that of *P. regius*, except the flick is softer, the legs I are not spread as wide or brought as high, and the movement sequence faster. The anterior decorations also have different coloration than *P. regius*.

Phidippus regius

Anterior decorations of male. Chelicerae iridescent green-blue-violet; clypeus fringe black; palpi black and white; leg I fringed with black and white; no ocular tufts.

Type I courtship. The legs I are held wide and moderately high. The flick is a quick, strong up-and-down movement, bringing the legs I straight up and parallel, then quickly back to their original position. The flick occurs at the beginning of the lateral movement sequence, and palpal movement as in *P. otiosus* occurs at the end of the sequence. Some individual variation occurs in timing, but sequences averaged only slightly longer than pauses.

Although similar to *P. otiosus*, the courtship of *P. regius* was more extreme in its position and movements, and the timing of the lateral movement sequences was longer and similar in duration to the pauses between sequences. Large males, with their allometrically larger legs I, held the legs I closer together and lower than normal, and did not raise them as high during the flick.

Phidippus otiosus X *Phidippus regius* hybrid

Anterior decorations of male. Chelicerae iridescent green-blue; clypeus fringe black; palpi black and white; legs I fringed with black and white; no ocular tufts.

Type I courtship. Although parts of the courtships of both parent species were sometimes mixed in various ways, most often the courtship of the hybrids was as follows: The femora were held straight up and the distal part of the leg was spread very wide and parallel to the substrate. The flick was at the beginning of the lateral movement, and was very high and parallel, usually hard like *P. regius*, sometimes soft like *P. otiosus*. The palpi were moved at the end of the sequence as in both parent species. The pause was at least twice as long as the lateral movement sequence.

Overall, the position and movement of the legs I and the coloration was like *P. regius*, but the timing of movements and pauses was like *P. otiosus*.

Phidippus audax

Anterior decorations of male. Chelicerae iridescent gold-green-blue; clypeus fringe black; palpi black and white; legs I fringed with black and white, no ocular tufts.

Type I courtship. At the beginning of courtship the legs I are waved alternately; occasionally this type of movement is maintained throughout Stage I. Usually, however, the legs I become synchronized on the second or third lateral movement sequence. The legs I are held close to the body, moderately spread at the femur-patella joint, and distally held about 20° above parallel to the substrate. The flick is a short upward inward movement, bringing the tarsi halfway between parallel and touching one another. Usually two but up to four flicks may occur beginning as the lateral movement starts. The palpi move at the end of the movement sequence as in *P. otiosus*. The lateral movements and pauses are both quick, the pauses slightly longer.

The combination of femora held close to the body, moderate upward angle to the distal legs I (intermediate between *P. princeps* and *P. pulcherrimus*), and double flick are distinctive for *P. audax*.

Phidippus xerus

Anterior decorations of male. Chelicerae iridescent gold-green; clypeus fringe black; palpi black and white; leg I fringed with black and white, no ocular tufts.

Type I courtship. The legs I are held partially forward, away from the body; distally the legs I are parallel both to the substrate and to each other. Usually three quick upward inward flicks are done consecutively at the beginning of each lateral movement sequence; these are done so smoothly that they appear to be 3 consecutive rotations, and they may be, but the film is inconclusive on this point. The palpi are moved as in *P. otiosus*, but at the same time as the leg movements. The pause is nearly twice as long as the lateral movement sequence.

The relatively low position of the femur, the double parallel position of the distal leg segments, the triple smooth flick, and the timing of the palpal movements are diagnostic of the courtship of *P. xerus*.

Phidippus princeps

Anterior decorations of male. Chelicerae iridescent green; clypeus fringe black; palpi black and white; leg I fringed with black and white; no ocular tufts.

Type I courtship. The femora I are held straight up and close to the body. The legs I are held apart a variable distance, varying with individuals. The legs I are held moderately high; the usually double flick is upward and inward, so that the tarsi are halfway between parallel and touching, and occurs at the beginning of the lateral movement sequence. The palpi are moved twice each alternately at the end of the movement sequence. Pauses are 1.5-2 times longer than movement sequences; neither are particularly quick, although there is some individual variation.

The higher leg position and higher flick distinguish the courtship of *P. princeps* from those of the similar *P. pulcherrimus* and *P. audax*.

Phidippus pulcherrimus

Anterior decorations of male. Chelicerae iridescent green; clypeus fringe black; palpi black and white; leg I fringes black and white; no ocular tufts.

Type I courtship. The femora I are held partially forward, the distal segments of legs I only slightly apart and slightly angled away from the substrate. The double flick occurs at the beginning of each lateral movement sequence, and is short and straight up. Palpi are moved at the end of sequence as in *P. princeps*. Alternation of movement and pause is quick.

The courtship of *P. pulcherrimus* is very similar to the closely related *P. princeps*; the legs I are held much lower and the flick is of less amplitude and is straight upward, lacking the inward component of the flick of both *P. princeps* and *P. audax*.

Phidippus clarus

Anterior decorations of male. Chelicerae iridescent green; clypeus fringe black; palpi black and white; leg I fringe black and white; no ocular tufts.

Type I courtship. The femora I are held forward and away from the body. The distal segments of legs I are held wide at the femur-patella joint and slanted slightly toward the substrate (below parallel). A single flick occurs at the beginning of lateral movements sequence and covers 80° of arc (each leg). The legs I are straight up and parallel at the peak of the flick, then rapidly dropped back down. The palpi are held wide and downward without any movement. The timing varies with individuals, but generally the pause is about 3 times as long as the movement sequence.

The low, wide leg position and the quick, high amplitude flick easily distinguish the courtship of *P. clarus*.

Phidippus cardinalis

Anterior decorations of male. Chelicerae dull red proximally, slightly iridescent blue distally; clypeus fringe black; palpi black; legs fringed with black and white; no ocular tufts.

Type I courtship. The legs I are held high (the highest of any species studied), close to the body, and parallel to each other. The mid-leg is bent forward at a 60° angle from the substrate and 45° outward; the distal 2 segments are bent straight upward at a 70° angle. The single, sometimes double, flick at the beginning of a lateral movement sequence brings the legs I straight upward and inward so that the tarsi touch or cross. Palpal movement could not be confirmed by the films, but in one instance 2 alternate pair of palpal movements seemed to occur at the end of a movement sequence. Each lateral movement was quick, but the intervening pauses were much longer, usually 5-6 sec.

The courtship of *P. cardinalis* is similar to the related *P. whitmani*, but differs in holding the legs higher and lacking the vibratory component. Also similar is the courtship of *P. apacheanus*, but *P. cardinalis* holds the legs I close to the body, not away from the body as does *P. apacheanus*.

Type II courtship. On one occasion a male performed a vibratory courtship while entering a nest occupied by a female. I was unable to observe details of this courtship, and note here only that *P. cardinalis* does have a Type II courtship.

Phidippus whitmani

Anterior decorations of male. Chelicerae black, with proximal median white fringes, slightly iridescent blue distally; clypeus with white scales and fringes; palpi white; leg I fringes white; no ocular tufts.

Type I courtship. The legs I are held close to the body, the femora straight up. The distal segments of leg I are moderately high, angled outward slightly at the femur-patella joint. Usually 1 or 2 inward upward flicks bring the legs I parallel or rarely touching tarsi; the peak of the flick is held for 3-5 seconds, then the legs I are gradually returned to their original position. Simultaneous with each flick, the whole body is vibrated. The stance of the supporting 3 pairs of legs is exceptionally wide. The prosoma is held high and the abdomen angled downward. The palpi are angled outward about 30°, except the cymbia which were about 45° (in one instance the cymbia were bent upward 90°, parallel with the substrate). Movement time was very quick and consisted of the quick flicks and vibrations, and a shuffle forward straight at the female. Pause time varied considerably among individuals but was always quite long. Although there is no lateral movement in this courtship, one individual rocked back and forth in place several times at the beginning of the courtship, then commenced the usual flick and vibrate advance.

The courtship of *P. whitmani*, although showing some similarities to the related *P. cardinalis* in leg position and flicking, is very distinctive. The positioning of the palpi, the slow return of a high flick, and especially the vibrations are all unique. The positioning of the support legs and the vibrations seem remarkably similar to those reported for the courtship of a sparassid, *Heteropoda venatoria* (L.), by Rovner (1980). *Phidippus whitmani* is the only species which lives exclusively on forest leaf litter, a substrate that is used by lycosids to transmit and amplify vibrations during courtship (Rovner, 1967). There is considerable circumstantial evidence that the vibratory part of the courtship is a signal sent through the substrate to the female; it may be the single most important component of the courtship (since most of the male's courtship time is spent motionless) and merits further investigation.

Type II courtship. Five males were observed performing a vibratory courtship while attempting to enter nests of females (some were occupied, some were empty). The entire body was vibrated while the male was engaged with the silk. One male performed 9 consecutive vibrations, averaging about 1.2 vibrations per sec. A second male vibrated 3 times consecutively. The other males performed multiple sequences of vibrations (pauses between sequences averaged about 3 sec.), which I terminated after 6, 5, and 5 sequences, respectively. The ranges and mean number of vibrations per sequence were as follows: 9-12, $\bar{x}$=10; 2-4, $\bar{x}$=3; 6-12,

$\bar{x}=7.6$. See the end of the following chapter for further discussion of vibratory courtship.

Phidippus apacheanus

Anterior decorations of male. Chelicerae iridescent green; clypeus fringe black; palpi black; leg I fringe black and white; 2 dorsal tufts.

Type I courtship. During the single partial courtship I filmed, the legs I were held fairly low, the femora held away from the body. The single flick was upward and inward, the tarsi nearly touching. The palpi were moved twice each alternately at the end of a movement sequence. The pause was about 3 times as long as the movement sequence.

The courtship is similar to that of *P. cardinalis*, but the legs are held away from the body and usually not parallel to each other. The highly iridescent chelicerae are strikingly different from the dull chelicerae of *P. cardinalis*.

Possibly the part of the courtship I observed was a transitional stage between Stage I and Stage II, as the legs I were held much lower than described by Gardner (1965). Individual or geographic variations may also be the reason for the observed differences.

Phidippus purpuratus

Anterior decorations of male. Chelicerae iridescent gold-green-blue; clypeus fringe black; palpi black; leg I fringe black and white; 2 dorsal tufts.

Type I courtship. The legs I are held in an unusual fashion, the femora close to the body and straight up, the mid-legs parallel to the substrate and bent out 45°, and the distal segments straight forward and angled upward 30°. The flick is single or double, upward and inward and at the beginning of the lateral movement sequence. If double, the second flick is held up briefly before returning to original position.

The palpi did not appear to move, although the film did not show them well. Timing was a little slower than most of the quicker courtships; the pause was about twice as long as the movement sequence.

The peculiar angles of the leg segments are the most distinguishing feature of the courtship of *P. purpuratus*.

Discussion

The Type I courtships of *P. mystaceus* and *P. putnami* were clearly different in method (the types of movements of the legs I and palpi) from all of the other species observed, supporting their phylogenetic separation from the other species based on morphology (see Chapter 2). However, the courtships of *P. mystaceus* and *P. putnami* were as different from each other as they were from the other species, indicating that these two species may not belong to the same phylogenetic line. Further examination of related species will be necessary in order to determine the relationship of these two species. Jackson (in prep.) has found that the apparent sister species of *P. putnami* (*P. femoratus* Peckham & Peckham of western North America) has a courtship very similar to that of *P. putnami*.

In the subgenus *Phidippus*, similarities among courtships generally agreed with morphological groupings. The courtships of *P. audax*, *P. otiosus*, *P. regius*, *P. princeps*, *P. pulcherrimus*, *P. purpuratus*, and *P. xerus* differ only in details. The courtships of the related *P. cardinalis* and *P. whitmani* are very similar; *P. whitmani* appears to have evolved a vibratory component in connection with its leaf litter habitat. The courtship of *P. apacheanus* is more like the unrelated *P. cardinalis* than like the related *P. purpuratus*, and the courtship of *P. clarus* has more in common with those like *P. audax* than to its apparent morphological relatives, the *P. cardinalis* group (this latter group holds the legs I high, while the other species drop the legs I to a lower position after a high flick).

Overall, courtship behavior was a good indicator of phylogenetic relationship based on morphology. This finding agrees with that of Richman (1977), who examined one or a few representatives of several genera. The pitfalls of leaning too much on behavioral data are also pointed out; within a single genus, three phylogenetic lines of courtship development are apparent, two of which include components unknown for other salticids (stridulation and vibration), and the third line demonstrates a behavior (palpal rotation by *P. putnami*) which is known only from one species group of *Pellenes*, an unrelated genus also containing several lines of courtship development (Richman, 1977).

CHAPTER 6

SOUND PRODUCTION BY COURTING MALES OF *Phidippus mystaceus* (ARANEAE: SALTICIDAE)

The courtship rituals of male salticids generally are considered to be visually-oriented, despite the fact that a primarily tactile type of courtship has been demonstrated for 2 species of *Phidippus* (Edwards, 1975; Jackson, 1977a). In addition, chemotactic cues probably assist a male in locating a female in most species of jumping spiders (Richman, 1977). Males of *Phidippus mystaceus* (Hentz) produce sound as an integral part of their courtship. The sound, produced by means of a palpal stridulatory mechanism, is the first known case of this type for a salticid, although a similar stridulatory organ has been reported for lycosid spiders (Rovner, 1975).

The only other reports of a salticid producing sound were by Bristowe (1958), who reported that *Euophrys frontalis* (Walckenaer) made a "distinct sound as the tarsal claws (of the legs I of the male) hit the ground...," and by Bristowe and Locket (1926), who had reported earlier on the same species, but had implicated the legs II as the sound producers. In either case, it was not clear if the sound produced by *E. frontalis* was an integral part of the courtship or incidentally produced by the movement of the legs.

Experimental Procedure

Four females and 2 males, offspring of *P. mystaceus* female collected in Oklahoma, were reared to maturity from an eggsac containing 12 eggs.

The spiders were housed separately in 9 x 1 cm plastic petri dishes; twice a week they were provided with water by moistening a wad of cotton within the dish and were fed larvae of the cabbage looper, *Trichoplusia ni* (Hübner).

Two different techniques were used for observing courtships: 1) the male was placed directly into a female's petri dish, on the side opposite the female, or 2) the male and female were placed 5-15 cm apart on a 30 x 10 cm section of a live-oak branch, in order to simulate natural conditions. Temperature ranged from 24-26°C for all sessions.

Six separate filming and/or recording sessions lasted 10-90 min. each. Films were made using a Beaulieu Super-8-mm movie camera and an Auricon Pro 600 16-mm movie camera. Sound recordings were made with a Sony TC-756-2 reel-to-reel tape recorder and a Turner S22D microphone. The audiospectrogram was produced on a Kay 7029A Sound Spectrograph.

Results

Courtships were observed for one of the males (the second male was killed by the first female with which he was placed). Typically a male placed into the petri dish housing a female almost immediately begins palpating the female's draglines and her abandoned nests, continuing this palpal exploration until he detects the female visually.

If the female is not inside a nest when first seen by the male (usually from 3-6 cm), the male begins producing a soft, audible trill that is systematically repeated. By apparently engaging the substrate with enlarged setae (macrosetae) encircling apical, whorled setae on the tips of the palpal cymbia (similar to those observed on lycosids by Rovner, 1975; Figure 6-1), leverage is produced which enables a stridulatory mechanism on the palpus to be operated. This mechanism consists of a plectrum-like projection of the tibial apophysis which fits into a bowl-shaped area on the cymbium containing a complicated file system. The entire mechanism is located laterally (ectally); in lycosids it is located dorsally. Also, lycosids have the file on the tibia facing a cymbial plectrum, the reverse of the condition in *P. mystaceus*. The file system of *P. mystaceus* consists of 2 types of adjacent file fields which blend into one another. Within the concavity is a fan-shaped file, while along the distal edge of concavity is a linearly-arranged file similar to lycosid files. Neither file is as well-defined as the lycosid files. The individual ridges of *P. mystaceus*' files are rounded whereas those of lycosids have distinct edges; however, in *P. mystaceus*, both types of file are overlaid with numerous short ridges of variable length (Figure 6-2).

For each sound sequence, both palpi become engaged nearly simultaneously by a backward movement in which the palpi appear to be dragged along the surface of the substrate for a distance of about 1 mm. Halfway through the backward movement, the cymbia are bent backward at an angle to the palpal tibiae (Figure 6-3). At the end of the backward movement, the palpi remain stationary for a fraction of a sec. while the cymbia are rotated outward. The palpi may be returned to their most anterior position by reversing the sequence of backward movement. Only when the palpi are in their most anterior position are they clearly off the substrate. A single cycle of palpal movement is approximately 0.8 sec. (5 frames at 6 frames per sec.).

Audiospectrograms indicate that 13-20 ($\bar{x}$ = 17, n = 8) paired stridulations are made consecutively, separated by pauses subequal to the sound sequences (Figure 6-4). Alternation of stridulations and pauses occurs at the rate of 1.6 sound sequences per second.

Simultaneous with the initiation of sound production, the male extends his legs I forward, positioning them just above and parallel to the substrate, and spread approximately 40° apart. The tarsi and metatarsi are turned upward about 15° and occasionally flicked upward together. (On one occasion, at a distance of about 1 cm from the female, the tarsi and metatarsi were flicked continuously for several sec. at approximately 2 flicks per sec.).

The male's approach is usually direct, without the zigzag movement (lateral stepping movement) characteristic of some other *Phidippus* species and many other salticids. Forward movement is slow and halting, the male often remaining in one spot for several min. Total courtship time is long compared to the rapid advance of the males of some *Phidippus* species, on 3 occasions lasting approximately 8 min. before the female terminated the courtship by leaving the vicinity. These 3 longest courtships reached an advanced stage, wherein the male brought his legs I closer together, touched the female, and attempted to mount her; however, none of the 4 females allowed their male sibling to mate them. Instead, each raised her legs I to repel him, and, if the male was persistent, lunged sharply forward with open fangs, struck downward with the legs I, and forced him backward; the female then left the vicinity.

On two occasions, the male performed a zigzag display; once prior to assuming his stridulatory stance, and once in the middle of courtship after several sequences of stridulation. In the first instance, the zigzag display was brief, lasting less than 30 sec. and consisting of 4 changes of direction, with a pause between each lateral move. In the second instance, during mid-courtship, 7 multiple zigzags occurred which included 1-3 changes of direction during each lateral stepping sequence; total elapsed time was about 3 min.

If the female is initially in and remains in a nest when the male is introduced into the petri dish, the male continuously palpates the substrate, interspersing sequences of stridulation. Upon finding the nest sheltering the female, the male attempts to gain entrance by probing and pulling at the silk with his legs I, interspersing sequences of palpal vibration on the silk. (Note: other species known to use a tactile courtship vibrate their entire body). I could not determine the movement pattern of this palpal vibration, but the palpi were not in contact with the petri dish and no audible sound was produced.

After the preceding research was completed, I collected two antepenultimate *P. mystaceus* and reared them to maturity (October, 1979). A courtship and mating was observed for this pair, but it was neither filmed nor recorded. Courtship appeared in all respects to be identical to that of the Oklahoma male, including type of sound, stance, and the rapid upward flicking of the tarsi and metatarsi at less than 1 cm distance from the female. Mating occurred in the female's nest and lasted 87 min. until the female left the nest. Upon separating, the male renewed courtship, initially showing a single lateral stepping sequence as in the Oklahoma male. The female avoided the male, and the pair was separated.

Discussion

Known reproductive behavior of the males of species of *Phidippus* involves a male locating a female by visual or chemotactic means, a visually-oriented courtship by the male consisting of a series of movements with the legs I and palpi (usually while advancing in a zigzag path), mounting of the female by the male, and mating. Typically the male is conspicuously marked with bright and/or contrasting colors both anteriorly and dorsally; the anterior patterns are displayed during courtship. Unlike most other species, both males and females of P. mystaceus are cryptically-colored gray spiders that live in trees (Specht and Dondale, 1960; Warren et al., 1967, as P. incertus; see Edwards, 1977, for nomenclatorial comments); males have mostly anteriorly-oriented modifications (Figure 6-5). While anterior modifications are probably used by each sex to identify the other (especially the female recognizing the male as a conspecific and potential mate) from distances of a few centimeters, visual identification at longer distances would seem to be severely handicapped by cryptic coloration. A mechanism which increased the male's chances of locating a female could be selected for under these circumstances.

The role of acoustic or vibratory signals in the courtship of P. mystaceus probably evolved with cryptic coloration. As selection for cryptic coloration increased in association with exploitation of a new microhabitat (most Phidippus species live in the herb-shrub zone), the role of visual communication was in part supplanted by sound during courtship. The use of sound, whether airborne or substrate-borne, has several advantages over conventional visual courtship, because sound extends the male's communicatory distance from a few centimeters to over a meter (based on the audible component available to the human ear). Sound is transmitted well through solids, and considering that in this case sound is produced on the substrate, vibrations through this medium may be the most important sound component for female-to-male orientation (as Rovner, 1967, showed to be the case for wolf spiders). By orienting toward the male upon perception of the sound, the female might sooner visually detect and be able to evaluate the male as a prospective mate, and thus sooner choose to wait for or flee from him. The advantages gained by the male by increasing his communicatory distance might be: 1) alerting a receptive female to his presence at a greater distance, possibly causing her to remain in the vicinity for a longer period of time (and perhaps inhibiting her predatory instincts), so that the male has a greater chance of finding and courting her; 2) based on many observations of *P. mystaceus* and of other *Phidippus* species, non-receptive females usually avoid advancing males; thus, by alerting a female to his presence at a greater distance, a male would reduce the chance of triggering an aggressive response by a non-receptive female.

As evidence for these probable advantages, analysis of courtships showed that the male began courting a female from 2-4 times further away when unconfined (on the live-oak branch) than did other species of *Phidippus* when observed under unconfined experimental conditions (Edwards, 1975). At the greater distances, only sound was used initially by a *P. mystaceus* male upon sighting a female, indicating that this form of communication was important in alerting a female to his presence. Sound was also used alternately with palpal exploration of the silk when the male was in contact with the female's draglines in the petri dish, even though she was not visible. Under natural conditions, a male likely would often encounter a female's dragline prior to locating her; he could maximize his chances of mating by beginning to signal immediately, regardless of whether or not the female was visible to him.

The male's initial palpal exploration of the female's silk draglines and nests has been noted for other salticids (Richman, 1977). Hill (1977a,b) demonstrated the presence of whorled setae on the tarsi and palpal cymbia of other species of *Phidippus*, and, noting the similarity of these setae to insect pheromone receptors, hypothesized that those setae were contact chemoreceptors. Judging from the behavior of the male

P. mystaceus (which has the same type of whorled setae on its palpal cymbia; Figure 6-1), this hypothesis may well be correct; the presence of a contact pheromone on the silk could indicate to a male that a female was, or had been, in the vicinity.

The behavior in P. mystaceus of engaging the palpi against the substrate is probably derived from similar behavior among its relatives. Males of other species of Phidippus move their palpi up and down or back and forth during courtship. This behavior appears to preadapt them for engaging the substrate, since only a slight change in the amplitude and/or attitude of these movements would bring the palpi into contact with the substrate. The same movement occurs more intensely and rapidly when a male encounters silk made by a female, in association with chemotactile exploration; it is likely that this is the evolutionary pathway of the development of the use of sound in P. mystaceus.

The behavioral application of the palpi to the substrate by P. mystaceus appears to differ from lycosids in that P. mystaceus moves the tips of the palpi while stridulating during each brief sound sequence, whereas the lycosids apparently remain attached in one place to the substrate for a prolonged sequence of sound production.

The presence of a linearly-arranged file on the distal edge of the cymbial bowl was indicated by a few large ridges (at 75X). Subsequent S.E.M. photomicrographs showed a fan-shaped file system which was barely discernible at 100X. As noted earlier, both files were overlaid with minute ridges. It is possible that the larger ridges are responsible for the lower frequencies observed on the audiospectrogram, and the smaller ridges produce the higher frequency wavelengths.

By simulating the direction of palpal movement with a model, it is apparent that the backward movement would cause the fan-shaped file to be drawn across the plectrum, while the rotary movement would bring the linear file into contact with the plectrum. The fan shape of the proximal file would accomodate the arc-shaped movement as the palpus is bent on the backward stroke. Despite the differences in arrangement and shape of the larger ridges, the ultrastructure of the two files is similar and they seem to produce the same sound. The entire sequence appears to be reversible; in fact, the timing of a complete palpal movement (approximately 0.8 sec.) is remarkably close to half the number of sound sequences per sec. (1.6), suggesting that two stridulatory actions are made with each palpus, one on the back stroke, and a second by reversing the action on the return stroke. The files appear to be oriented so that they could be stroked from either direction. Examination of Figure 6-4 will show one sound sequence is exactly 0.8 sec., equally divided between sound and pause.

The shape and arrangement of the macrosetae at the tip of the cymbium are such that a downward, forward pressure would engage them with the substrate. By dragging the palpus backward, enough leverage is apparently produced to move the fan-shaped file across the relatively stationary plectrum; however, the backward movement and bend of the palpus also may be a prerequisite to positioning the macrosetae into the substrate. Once the palpus is anchored in the substrate, the cymbium is rotated laterally outward, then the direction of movement is reversed. The structure involved in sound production by rotating is the linear file; the cymbium must be rotated sideways due to the lateral position of the file. The mechanics of sound production with the linear file are similar to those of the lycosids with respect to the palpus anchored by macrosetae and the similar file structure, by P. mystaceus differs from the lycosids in the location of the stridulatory organ, the type of movement needed to engage the file, and the reversed positions of the file and plectrum.

The stridulatory mechanisms known in other spiders incorporate plectrum and file systems on opposing faces of the chelicerae and palpi, legs I and II, carapace and legs I, carapace and abdomen (Gertsch, 1979), or between palpal tibia and tarsus (Rovner, 1975). In each of these cases, either the plectrum is moved across a stationary file, or both plectrum and file are moved together. The stridulatory mechanism of P. mystaceus differs from all of these in that the primary moving part is the file. Although the plectrum is passively moved in space during the movement of the palpus to engage the substrate, the cymbium containing the files is actively moved against the plectrum on the tibia. When the palpus is fixed on the substrate with the macrosetae, again it is the cymbium that is moved against the stationary plectrum.

Conclusion

The use of stridulation to produce sound by P. mystaceus appears to represent a third method of communication for salticids (a fourth method if the tarsal percussion of Euophrys frontalis is a valid communicatory process). Despite the fact that females used for the present research failed to respond favorably to courtship by their sibling male, the behavioral and morphological evidence in the male of a functional role for sound production during courtship is substantial.

Additional Observations

A third method of sound production in spiders, vibration (producing a "buzz" similar to that of a fly), has been demonstrated for the sparassid spider, *Heteropoda venatoria* (L.) (Rovner, 1980). In the same paper, low amplitude appendage oscillations resulting in a faint whirring sound were reported for *Lycosa rabida* Walckenaer. *Phidippus whitmani* Peckham and Peckham employs entire-body (?) vibration (lacking an audible component, but with a widely-spaced stance similar to *H. venatoria*) during its Type I visual courtship (Edwards, unpublished). This is probably an adaptation to its microhabitat (mesophytic leaf litter), the same substrate used for vibratory signalling by many lycosids. I have noted another vibratory behavior that also seems similar to that of *H. venatoria* during the Type II tactile courtship of *Phidippus regius* C. L. Koch, while the male is contacting the nest of the female (Edwards, 1975). Subsequent laboratory observation showed a similar behavior for *P. whitmani*, although the timing of vibratory sequences was different than those of *P. regius*, probably a species-specific difference. Jackson (1977) reported a similar behavior for *P. johnsoni* (Peckham and Peckham) and suggested a similarity in some respects to the vibratory courtships of web-building spiders. I suspect that the vibratory courtships of *Phidippus* species, although not producing an audible component that I could detect, may be more like the courtships of *H. venatoria* than like web-builders (perhaps these latter two are similar?) and should be further investigated. It is curious that all known forms of non-tactile direct inter-individual communication not involving vision in salticids involve the production of acoustic or vibratory signals. In the case of *P. mystaceus* and *P. whitmani*, both types of communication are used simultaneously, although the two species produce vibrations in different ways.

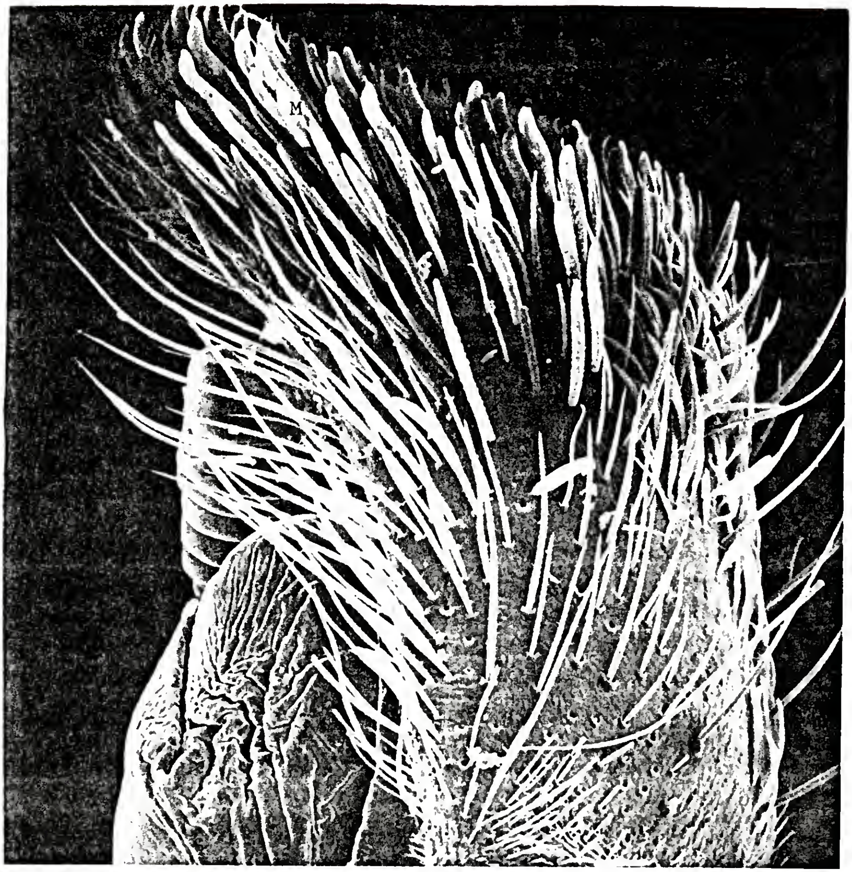


Figure 6-1. Distal ectal view of palpus of P. mystaceus, showing macrosetae (M) used to engage substrate (100X).

Figure 6-2. Stridulatory organ of male P. mystaceus, showing fan-shaped file (F), linear file (L), and plectrum (P).

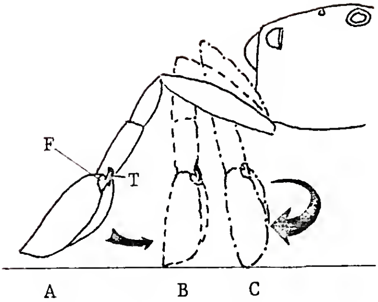


Figure 6-3. Diagrammatic illustration of movement of left palpus by male P. mystaceus during stridulation. A. Anterior position. B. Backward movement, during which cymbium is bent backward, moving fan-shaped file across plectrum. C. Rotary movement, during which macrosetae are engaged in substrate and cymbium is rotated outward. F = File cavity, T = Tibial apophysis.

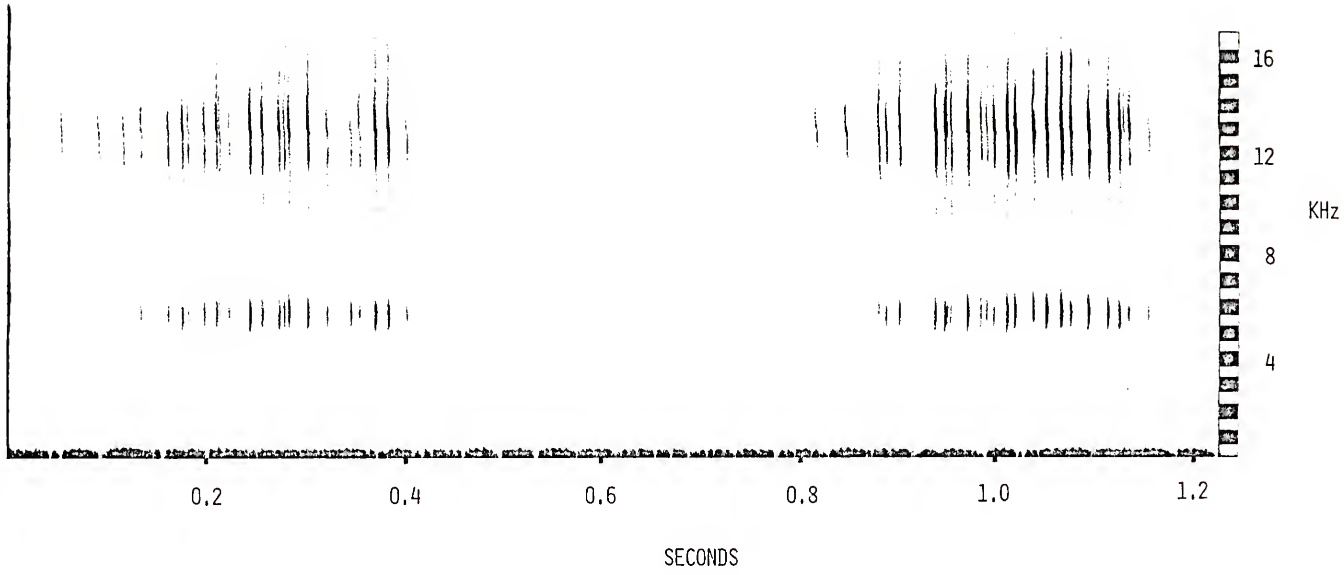


Figure 6-4. Audiospectrogram of male _P_. _mystaceus_ stridulating on live-oak bark at 25 ± 1^{o}C.

Figure 6-5. Anterior view of male P. mystaceus.

CHAPTER 7
DIFFERENTIAL ATTACK RESPONSES BY *Phidippus* SPP. (ARANEAE: SALTICIDAE) TO CONTRASTING PREY TYPES

Hollis and Branson (1964) first recorded differential responses by a salticid to different types of live prey. They observed *Phidippus audax* (Hentz) attempting to capture the salticid *Metacyrba undata* (DeGeer) by jumping at the intended prey, but not jumping when capturing *Tenebrio* larvae. Gardner (1965) noted slight differences in the approach of juvenile *P. coccineus* Peckham & Peckham to *Drosophila* and *Calliphora*. Edwards et al. (1974) described different attack methods used by the salticid *Corythalia canosa* (Walckenaer) (= *Stoidis aurata* (Hentz)) when attacking various ant species. Field and laboratory observations of prey capture by *Phidippus regius* C. L. Koch (Edwards 1975) indicated that this salticid utilized different methods of approach and capture for larval Lepidoptera and adult Diptera. These 2 prey types have frequently been reported in the natural diet of foliage-dwelling species of *Phidippus* (Whitcomb et al. 1963, Warren et al. 1967, Jackson 1977). In the present research, 7 species of *Phidippus* were analyzed for differences in attack behavior due to these 2 types of prey and to the species of spider.

Materials and Methods

Adult and subadult *Phidippus* (Fig. 7-1) were obtained from their natural habitats in Florida, except for 6 *P. clarus* and 2 *P. putnami* (captured in Missouri); some adults of *P. regius*, *P. otiosus*, and *P.*

apacheanus were laboratory-reared from eggsacs of females captured in Florida. The spiders were individually housed in 90 X 10 mm plastic petri dishes and were provided with fresh water by means of a small, moist wad of cotton in the dish. Only adult spiders were tested. Proffered prey were 4th and 5th instar larvae of the cabbage looper, *Trichoplusia ni* (Hübner), and adults of the house fly, *Musca domestica* (L.).

Individual tests were conducted in the following manner: 1) a single cabbage looper (hereafter referred to as looper) was placed directly into the petri dish housing a spider, or 2) first a spider and then a house fly (hereafter referred to as fly) were placed in a 90 X 20 mm glass petri dish (because the 10-mm-deep petri dishes overly restricted the flies' flight). I measured the distance the spider jumped to capture its prey by refering to a sheet of graph paper lined with 1 mm graticules positioned under the petri dish. Measurements were made from the point where the chelicerae of the spider had been located just prior to a jump to the part of the prey nearest the spider. I estimated my accuracy of measurement to be ± 1 mm for the capture of loopers and ± 2 mm for flies. The position of the spider in respect to the prey at the time of attack was also recorded. The spider was considered to be anterior to a looper if the spider's sagittal plane was in front of the 3rd pair of true legs, posterior to the looper if behind the mid-abdominal prolegs, and lateral if in-between. Similarly, the spider was considered to be anterior to the fly if in front of the cervix, posterior to the fly if behind the pedicel, and lateral if in-between. Most spiders were offered both types of prey, but the number of times each type of prey was tested for each spider varied. Capture distances were compared for the 2 types of prey using Students' t test; differences among species of Phidippus were examined by using a 1-way analysis of variance, Duncan's Multiple Range Test for unequal sample size, and Chi-square ($p<0.05$ for all tests unless otherwise indicated).

Results

Spiders attacked loopers from significantly shorter distances than they attacked flies (Fig. 7-1). Typically, upon seeing a moving looper, a spider would rapidly approach to within 10-12 mm, then pause and watch the intended prey. If the looper continued to move, the spider would circle until it was directly in the looper's path, stalk forward a few mm, leap, and then bite the looper in the dorsum of the thorax. If the looper changed its direction of movement as the spider was preparing to jump, the spider would reposition itself. If the looper stopped moving after the spider had already seen it but before the spider approached it, the spider might approach and attack the posterior or the anterior end while the looper was stationary, or might attack any part of the looper that moved. On 5 occasions (out of 225) involving 3 species (P. regius (3), P. otiosus, P. audax), a spider walked directly to a looper and captured it without jumping (0 mm).

In contrast to captures of loopers, which were predominantly made from anterior to a looper, captures of flies by most species of Phidippus tested occurred with similar frequencies from all directions (Fig. 7-2). Upon seeing the fly (mean distance approx. 60 mm), the spider would move stealthily, although rapidly (approx. 1-2 cm/sec) to within 25-30 mm of the fly. Regardless of the direction of attack, the spider almost always captured the fly by biting it in the thorax near the wing bases. Over 50% of successful attacks on flies were initiated from directions other than anterior to the flies for all Phidippus species tested.

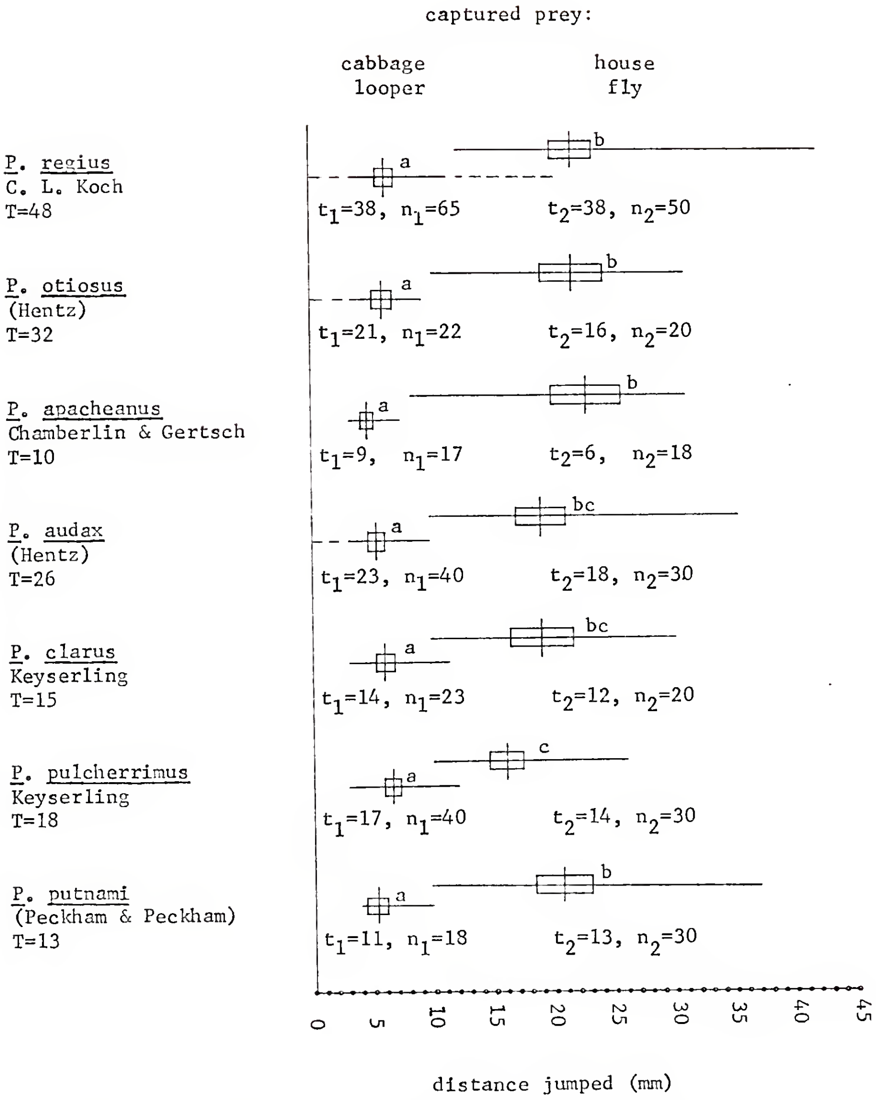


Figure 7-1. Comparison of capture of cabbage looper and house fly by _Phidippus_ species. Diagram consists of mean, 95% confidence interval, and range. Diagrams accompanied by the same letter (a,b,c) are not significantly different (Duncan's Multiple Rnage Test, p 0.01). T = total # of spiders of that species tested, t_1 and t_2 = total spiders of that species tested for cabbage looper and house fly, respectively. Likewise, n_1 and n_2 = total captures of cabbage looper and house fly, respectively. Spider species listed by descending mean length; only _P. regius_ and _P. otiosus_ are significantly larger than the other species.

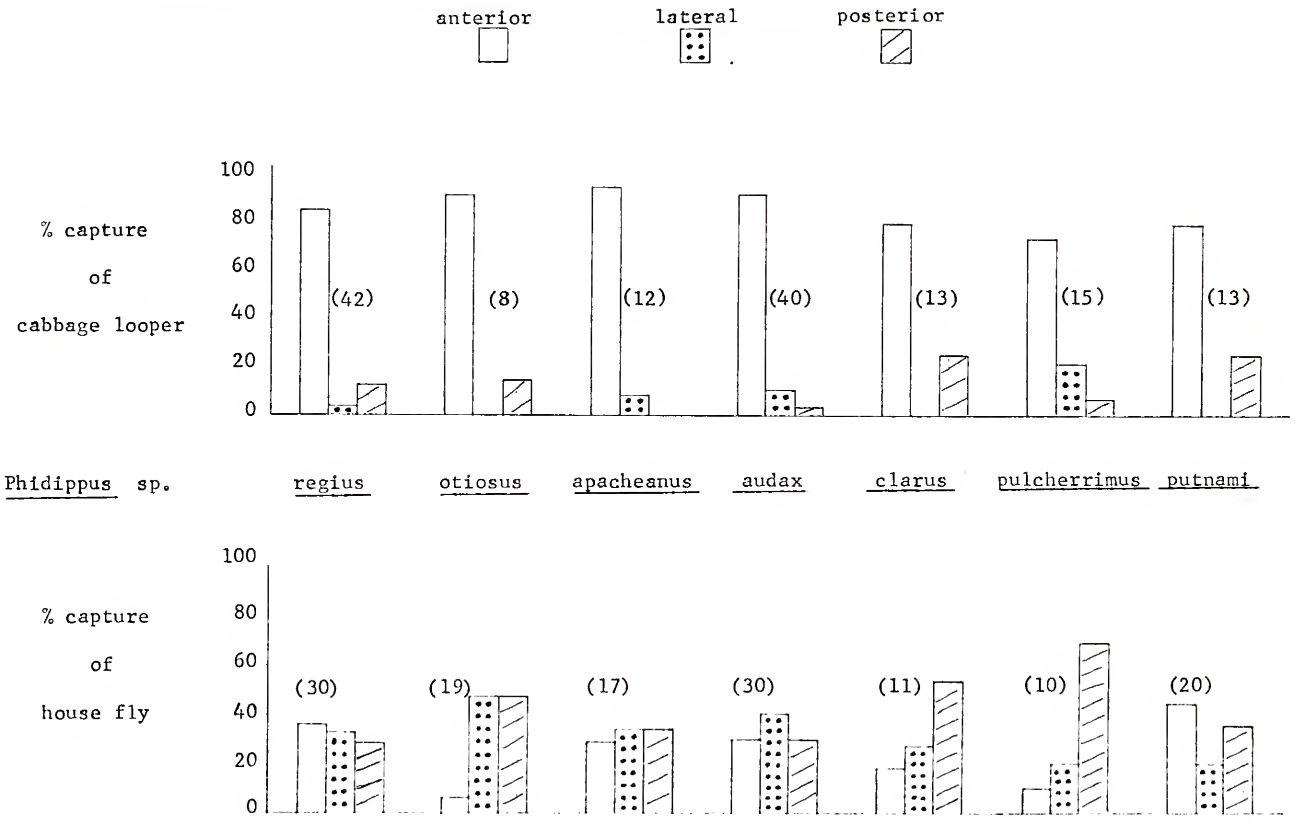


Figure 7-2. Percentage of attacks by direction of attack in respect to prey for *Phidippus* species attacking cabbage looper and house fly. Numbers in parentheses indicate number of observed captures recorded for direction of capture.

		P. regius	P. otiosus	P. apacheanus	P. audax	P. clarus	P. pulcherrimus	P. putnami
P. regius	62%	--	ns	<.10	<.05	ns	ns	ns
P. otiosus	55%		--	<.10	<.05	ns	ns	ns
P. apacheanus	83%			--	ns	ns	<.05	ns
P. audax	83%				--	ns	<.05	<.10
P. clarus	65%					--	ns	ns
P. pulcherrimus	47%						--	ns
P. putnami	63%							--

Table 7-1. Comparison among *Phidippus* species of success in capture of house flies on the first attempt. Percentages given are actual success rates. Sample sizes are the same as n_2 for each species in Figure 7-1.

Four species (P. regius, P. otiosus, P. apacheanus, P. putnami) captured flies from distances significantly greater than P. pulcherrimus; P. audax and P. clarus were intermediate in capture distance. On 2 occasions, individuals of P. putnami refused to attack loopers offered to them, but subsequently captured flies.

Loopers were always captured on the first attempt, but flies were often successful in evading a spider 1 or more times. I observed that some unsuccessful attacks were caused by the collision of the spider with the lid of the glass petri dish in mid-jump. This happened when the fly was on the side or top of the petri dish and the spider jumped from the bottom of the dish. Misses caused by collision with the glass were detected in 17% of all capture attempts in which one or more misses occurred. Phidippus audax and P. apacheanus appeared to be more successful than most other species at capturing flies on their first try (Table 7-1).

Although female Phidippus were slightly larger than males, there were no significant differences between sexes within a species for prey-capture distance.

Discussion

All species of Phidippus tested appeared to be highly capable of distinguishing between loopers and flies. It seemed that the size, shape, and/or speed of movement of the intended prey influenced the method of approach and capture utilized by a spider; this observation agrees with those reported by Gardner (1964) of P. clarus and Drees (1952) and Land (1972) for other salticids. It is not known whether this distinction between types of prey is an innate response or is a result of trial-and-error conditioning; however, judging by the markedly different approaches used, the spiders had in some manner evaluated the motility of the prey prior to attacking it. Usually a spider would watch the potential prey for a few seconds before approaching it, but a spider alternately might begin its approach as soon as a moving prey attacted its attention. In these instances, perhaps the prey was evaluated during the early, rapid stage of approach. In either case, apparently the spider can quickly recognize a generalized shape, associate it with motile ability, and then initiate its own appropriate response.

Not only does a spider's attack sequence adjust for prey motility, but it is also deftly accomplished so as to minimize the prey's defenses. When attacked from the posterior, a looper strikes hard with its head capsule and also attempts to smear saliva on its attacker, but adult spiders simply use their forelegs to fend away the looper's head until the spider's venom takes effect (however, I have observed this defensive maneuver on the part of the looper to be sometimes effective against young _P. regius_). A spider's normal attack immobilizes the looper's head, preventing the looper from utilizing any defense except writhing (which I have observed to also be occasionally effective against young _P. regius_ when the mass of the looper was considerably greater than that of the spiderling). Under natural conditions, a writhing looper that was released would escape by dropping from the foliage. In addition, the petri dish deprives the looper of a similar defensive maneuver, that of dropping from the plant on a silken thread. The early instars of the cabbage looper are known to use this method of escape effectively when approached within 2-3 mm by the small salticid _Hentzia palmarum_ (Hentz) (R. B. Skinner, personal communication). Since mean capture distances of loopers for each species of _Phidippus_ were greater than 5 mm, it would seem that individual adult Phidippus normally circumvent this last defensive maneuver by jumping from a distance farther away than the looper's "early warning system" can detect.

Flies are notorious for their quick escape flight. Spiders attacked flies by moving in a straight line directly toward the fly, regardless of the orientation of the fly in respect to the spider. Adjustments in direction were made only if the fly changed position. (In respect to changing position, I suspect that Gardner's (1965) observations of difference in the attack of P. coccineus on Drosophila and Calliphora are due to the fact that Calliphora move faster across the field of vision of the spiders, therefore more often exposing their posterior to attack.) Spiders made no attempt to orient toward the anterior of the flies; to do so would probably have alerted a fly.

Phidippus pulcherrimus, which had the shortest mean capture distance for flies, also had the poorest success at capturing flies on the first try. This contrast may be related to the spider's relatively small size, and the difficulty in its closer approach resulting in its greater tendency to attack from posterior to the fly. The little evidence available indicates that P. putnami may prefer fly-like prey, perhaps in part explaining why the mean capture distance for flies of this species was significantly greater than the comparably-sized P. pulcherrimus.

Considering the relatively low expenditure of energy used in the pursuit of a lepidopterous larva (and sometimes in addition the availability of a considerable amount of biomass relative to the spider), it would seem to be a good strategy to specialize on lepidopterous larvae; in fact, some Phidippus may actively seek out this type of prey in preference to others, although this has yet to be demonstrated. One disadvantage of this feeding strategem would be increased competition with more specialized predators, e.g., nabids, some reduviids, of this particular type of prey. Another disadvantage is that lepidopterous larvae do not normally occur in a regular distribution, so that search time would be increased for a specialist (especially a non-winged specialist) on this prey type. On the other hand, Diptera, Hymenoptera, Hemiptera, and other smaller, winged and wingless prey are usually more numerous. A spider would be more likely to encounter prey in one of these latter categories. Although its pursuit time would be increased, its search time probably would be drastically reduced if it could capture many smaller prey. While many web-weaving spiders probably specialize to some extent on prey capture (e.g., Eberhard, 1975), the optimum strategy for a vagrant spider would be to take advantage of whatever prey was most available. In the case of a visual hunter like a *Phidippus*, modifications in its own behavior which would allow the hunter to recognize and circumvent different defensive behaviors by different prey types would certainly seem beneficial to the predator's survival. The demonstration here of different attack responses to contrasting types of prey indicates that species of *Phidippus*, probably in conjunction with their visual mode of hunting, have evolved the ability to discriminate between various potential prey organisms, and are able to modify their own attack behaviors to maximize the success of an attack on any particular prey individual.

CHAPTER 8

INSTINCT AND CONDITIONED LEARNING AS FACTORS IN THE PREY-CAPTURE BEHAVIOR OF NAIVE SPIDERLINGS (ARANEAE: SALTICIDAE)

As shown previously (Chapter 7), adult Phidippus demonstrated behaviors when attacking adult Musca domestica (L.) that were quite different from their attack behaviors against larval Trichoplusia ni (Hübner). In an effort to determine whether or not these differences were instinctive, a result of conditioned learning, or a combination of both, naive Phidippus regius C. L. Koch first instar spiderlings (first free-living instar, after Vachon, 1957; Galiano, 1967; second instar of other authors) were tested against prey classes comparable to those used for adult Phidippus, as well as aphids and ants. Ants are known to be consistently fed upon by relatively few spiders (Levi, 1957; Hoelldobler, 1969; Edwards et al., 1974).

Methods and Materials

Individual spiderlings of P. regius were isolated and provided with water in individual petri dishes as described for adult Phidippus. Spiderlings were fed only during test situations. All were assumed to never have captured free-living prey, although some may have fed on infertile eggs (Valerio, 1974; Edwards, 1975). Spiderlings do not generally feed on each other while associated with the eggsac. Tests ranged over a period of 7 days, with no more than 1 prey offered per group per day. Spiderlings from 3 eggsacs were tested on 3 different occasions.

Groups of 10 or more spiderlings from eggsacs A and B were tested against 3 of the following types of prey: 1) 2nd instar cabbage loopers, *Trichoplusia ni* (Hübner), 2) winged or vestigial-winged *Drosophila melanogaster* Meigen, 3) minor workers of the ants *Pheidole metallescens* Emery and *Pheidole dentata* Mayr, 4) robust, powdery-blue aphids of an undetermined species. Prey size ranged approximately from 0.25 the mass of the spiderlings in the case of the smaller ants to 1.5 times the spiderling's mass in the case of the aphids and loopers. Spiderlings from eggsac C were tested only with vestigial-winged *Drosophila* and loopers.

Single prey individuals were placed into a 90 x 10 mm plastic petri dish. A spiderling was placed into the same dish immediately after (when *Drosophila* were prey) or before (all other prey) the introduction of the prey. Each test lasted at least 30 min. (unless the prey was captured sooner), during which time all interactions of the spiderling and prey were recorded. Distances of attempted captures were measured as described for adult *Phidippus*. All other test conditions were as described for adult *Phidippus*.

Each group of spiderlings from a specific eggsac was subjected to a different type of initial prey. The second prey offered to a group was always different than the first prey. The third prey offered was either unlike any previous prey, or the same as the first. For one group (A), a fourth prey was tested (loopers) which was the same as the second prey. No group was tested twice on the same day.

Prey categories were tested with the following groups of spiderlings: 1) winged *Drosophila* - A_1; 2) vestigial-winged *Drosophila* - B, C_1^1, C_1^2, C_2, C_3; 3) aphids - A_1; 4) ants - A_1, A_2, A_3, B; 5) loopers - A_2, A_3, A_4, B, C_1^1, C_1^2, C_2, C_3. Subscripts indicate successive tests, superscripts indicate successive tests with same group of spiderlings.

Spiderlings from eggsac A were divided into 3 initial groups for the first prey. Subsequent prey were not offered to specific groups due to within-group mortality, but were instead offered to composite groups made up of spiderlings from groups which had been given a different type of prey in an immediately preceding test. The only exception was the fourth prey offered (A_4) which was the same as the second prey (loopers) for all individuals tested.

Spiderlings from eggsac B were divided into three groups and only tested once. Spiderlings from eggsacs A and B were between 21 and 28 days old.

Spiderlings from eggsac C were tested in an effort to determine the effects of age, since spiderlings upon emerging from an eggsac normally disperse by ballooning as their first activity. These spiderlings emerged at day 9 and were divided into 3 groups which were tested with first prey as follows: 10 days (C_1), 12 days (C_2), and 14 days (C_3). Subgroups of C_1 were given a second prey on day 12 (C_1^2; day 10 denoted by C_1^1), but they prey were reversed.

Student's t test was used to evaluate each pair-wise group comparison of prey-capture distances. Prey categories were then lumped regardless of group or sequence and tested in the same manner. Success of first attempt against different prey was compared with Chi-square. Direction of capture was recorded and compared with data for adult _P. regius_. Level of significance was considered to be 0.05. Since there were no significant within-group differences in distance jumped between capture attempts and actual captures, the former category was used so as to enlarge the sample size.

The most meaningful comparisons due to reasons discussed in the results were the following: comparison of first prey of groups C_1^1 (10-

day-old), C_2 (12-day-old), C_3 (14-day-old), and second prey of C_1 (C_1^2); comparison of inexperienced and experienced spiders with various prey; and comparison of lumped prey groups, regardless of sequence offered to spiderlings.

Results and Discussion

Effects of Age

Early instars of many spiders, including immatures of species of *Phidippus* (Glick, 1939, 1960; Horner, 1974) are known to disperse by ballooning. Dispersal occurs within a few days after leaving the eggsac and has been reported on numerous occasions, following a period of communal gregariousness which is presumed to be a period of acclimatization to the environment (Burch, 1979). The potential functions of dispersal are well-known, yet results of dispersal, such as the actual distance dispersed or even the nature of ballooning (whether it is obligatory or facultative) are poorly known (Crosby and Bishop, 1936; Kaston, 1948).

In order to assess the effects of age on hunting behavior, 3 groups of 20 spiderlings each from eggsac C were offered prey during a period of time in which they would normally be dispersing. The results are presented in Table 8-1. Spiderlings normally attempt to balloon as soon as they leave the eggsac (personal observation).

The response of *P. regius* naive spiderlings was initially good (15/20 attempted prey capture; 11 successful) when the first prey was offered on day 1 after emergence from the eggsac; only 7/20 attempted prey capture when the first prey was offered on day 3 (with only 3 successes), and 17/20 (with 16 successes) attempted prey capture when the first prey was offered on day 5 (Table 8-1). This trend is opposite that found by Forster (1977b), who found a peak in pursuit and captures between days 2-3 after emergence for a New Zealand salticid, Trite auricoma (Urquhart), which was continuously presented with prey. It agrees with her observation of one group of spiderlings not fed until the third day, few of which showed hunting responses; however, in another group she observed, 80% of the spiderlings caught prey on either the third or fourth day, and she noted considerable variation between broods.

The apparent age effect on attempted prey capture is modified when the time of capture is considered. Only 2 of the 20 spiderlings of group C_1^1 (10-day-old) attempted to attack prey in less than 10 minutes from introduction of the prey. Five spiderlings made no attempts, and the 15 spiderlings which did attack did so an average of 42.7 min. (SE=9.5) for the 7 spiderlings attacking loopers, and an average of 16.9 min. (SE=2.6) for the 8 spiderlings attacking Drosophila (flies). These times were significantly different between types of prey ($p<.02$). Probably the more rapid movement of the flies caused a significantly sooner response by the spiderlings; yet, unlike older spiderlings or adults tested which usually responded in less than a minute to a prey stimulus, these spiderlings continuously wandered about the petri dish until eventually regarding a fly or looper as prey. During the wandering stage, the spiderlings would sometimes encounter the intended prey, but would either avoid contact or react defensively by raising the legs I and backing away (especially if the fly or looper was moving directly toward the spiderling). The same group (C_1^2) offered prey 2 days later (on day 12) was less likely to attack prey, and another group (C_2) offered first prey on day 12 was the least likely to attack prey. Group C_3, offered first prey on day 14, was both most likely to attack prey and most successful at capturing prey.

Five of the 8 spiderlings that had attacked loopers (C_1^1) also attacked flies (C_1^2; 2 successes). Four of the 8 spiderlings that had attacked flies (C_1^1) later attacked loopers; in addition, 2 spiderlings which did not attack flies (C_1^1) attacked loopers (C_1^2; all 6 attacks successful). In some instances where the spiderlings pursued flies in either C_1^1 or C_1^2, it was clear the spiderlings could not complete the hunting sequence because the flies moved too fast or too erratically. This observation agrees with Forster's (1977b).

For those spiderlings which attacked prey, C_1^2 and C_2 were not significantly different than C_1^1 in the time taken for the first attack for either flies or loopers, respectively (C_2 could not be compared for loopers).

I cannot explain why C_1^1 spiderlings were successful at switching from dispersal behavior, whereas the same group 2 days later (C_1^2) and another group (C_2) were less inclined to hunt and even less successful, given the same opportunity. But it was clear that the initial reaction from emergence from the eggsac through day 12 was of dispersal. I confirmed this by using spiderlings of the same age from another eggsac as a control: when set free, these spiderlings at once began climbing various plants and released silk in ballooning attempts.

Attempted capture by C_3 spiderlings were significantly sooner than C_1^1 and C_2 for loopers ($\bar{X}$=4.9 min., SE=2.1). Attempted captures of flies by C_3 were not significantly different in average time of first attack than any of the other groups in this test sequence. Two conclusions are suggested by these results: 1) by day 14, spiderlings normally have already completed dispersal and are more attentive to slower prey, and 2) the faster movement of flies is more likely to attract the attention of spiderlings, regardless of their age or dispersal tendencies. This latter conclusion might in part explain Forster's (1977b) findings with Trite using Drosophila as prey; however, a more likely explanation is that since Trite are restricted in habitat, their dispersal is limited to leaving the immediate vicinity of the eggsac, and they begin to hunt sooner.

Successful capture of loopers on the first attempt (81%) was significantly greater than for flies (41%) ($p<.01$). This result is the same found for adult Phidippus tested with similar prey, and reflects the relative ease of capture of slower prey. Forster (1977b) found that Trite were more successful at capturing Drosophila when the flies were less active.

Effects of Type of Prey

Groups from eggsacs A and B were between 21 and 28 days old when tests began. Presumably they were past the primary dispersal stage. I did not keep records of times of attack for these groups, but I did note that attack responses were generally less than 3 min., often less than 30 sec., and therefore generally much sooner than spiderlings from eggsac C, supporting the contention that dispersal behavior is strongest soon after leaving the eggsac. Results from A and B were compared with C_3, since this group of spiderlings was also considered to be in a post-dispersive stage.

Comparative results are presented in Table 8-2, and sizes of prey and spiderlings are compared in Figure 8-1. As with the experiments with spiderlings from eggsac C and with adults, captures of loopers were significantly more likely than captures of flies, or any other prey, on the first attempt. Success of capture of both categories of flies and of aphids was at or near 40% on the first attempt, similar to capture of flies by spiderlings from eggsac C (41% initial success). Difficulty with flies was due to their speed of movement, but difficulty with the slow-moving aphids (Table 8-4) was because the aphids used their long legs to kick away attacking spiderlings. Only 4 of 10 aphids were captured during the initial 30 min. of the test, but 3 other aphids were eventually captured within 4 hr.

Results for prey categories lumped together regardless of group or sequence are presented in Table 8-3. Almost all categories of prey were significantly different from one another for mean distance jumped by spiderlings during capture attempts when the prey categories were lumped together. The only exception was between vestigial-winged Drosophila and aphids, which were similar in size and general configuration.

While comparison of lumped categories was overall an excellent representation of attack distances by spiderlings for particular prey species, certain effects of offering sequential prey and between-group variability were masked. Aphids were attacked from significantly greater distances than loopers in all comparisons except with A_3 and A_4. Ants were attacked by group A_1 from significantly greater distances than loopers except when compared with A_3 and A_4; group B did not attack ants from significantly greater distances than any group attacking loopers. Group A_1 attacked ants from significantly greater distances than group B, a case of between-group variability. Capture of aphids by group A_1 was also significantly greater than attacks of ants by group B, but not significantly greater than attacks of ants by A_1. Flies were attacked from significantly greater distances than loopers for all comparisons except B-A_3 and C_3-A_3. All flies were attacked from significantly greater distances than ants. Aphids were not attacked from significantly different distances than vestigial-winged flies. Loopers were not attacked from significantly different distances between any groups except C_3-A_3. Vestigial-winged flies were not attacked from significantly different distances between groups. Winged flies were attacked from significantly greater distances than any other type of prey.

Analyzing the above comparisons gives the following conclusions: 1) group B tended to attack from closer distances than other groups; between-group variability was noted by Forster (1977b); 2) winged flies present a stimulus that causes spiderlings to increase their attack distance when compared to similar wingless prey; recent evidence suggests that some property of the wings themselves is the stimulus (Edwards, 1980); 3) previous experience with other types of more mobile prey (A_3) significantly increases the attack distance of spiderlings when given loopers as prey; when loopers were one of the previous prey categories along with other types of prey, attack distances were increased when loopers were given as prey, but to a lesser extent (A_4). Previous experience, therefore, does seem to affect capture distance. This result agrees with the findings of Forster (1977b), who states, "it must be concluded that jumping spiders become progressively more adept (at hunting)."

One aspect of gaining experience with prey is that of encountering noxious prey. A predator would waste less time and risk less injury if it could remember previous encounters with particular types of prey and avoid those which had been noxious or difficult to subdue. To test the ability of spiderlings to remember noxious prey, I tested them using ants as prey. Ants are generally avoided by spiders except for spiders which specialize in capturing ants (Levy, 1957; Hoelldobler, 1969). Species of Phidippus as a rule do not attack ants (Edwards et al., 1974; see Chapter 10 for exceptions).

Most (16/20) spiderlings (A_1 and B) attacked ants when the ants were first offered as prey, averaging 2 attacks per spiderling (range 0-5). Often a spiderling's first attack would be short (this was also observed when flies were prey); it appeared to underestimate the ant's (and flies') speed of movement. When an attack was successful in contacting the ant, the ant defended itself with its mandibles and sting, and probably also gave off an alarm odor. Spiderlings would immediately release the ants and back away; there were only 2 exceptions, when spiderlings caught ants by the dorsum of the abdomen, rendering the ants helpless. Usually the spiderling would attempt one or two more captures, which were unsuccessful, then it would watch the ant for several sec. without further attacks. Sometimes a spiderling would touch an ant with the legs I, then back away. Many spiderlings struck at approaching ants with the legs I to drive the ants away, but the ants usually attacked in response. The spiderlings would run away and avoid further contact.

On 3 occasions, ants were able to retaliate to such an extent that the spiderlings were forced to defend themselves. One P. metallescens bit the spiderling on the right leg I, but released its hold when the spiderling let go of the ant. A second P. metallescens bit the right palp of a spiderling and attempted to sting; the fighting pair rolled over so that the spiderling was on its back; the spiderling pulled its palp free and attempted to escape, but the ant bit the right tarsus III and held on; a tug-of-war ensued, during which the spiderling attempted to bite the ant, then finally pulled its leg free and escaped; the spiderling turned and watched the ant for several sec., and subsequently strongly avoided all contact. In a third such encounter, a *P. dentata* worker (*P. dentata* are larger than *P. metallescens* but smaller than the spiderlings) bit and held onto the right leg I of an attacking spiderling; the spiderling was unable to pull free and instead autotomized its own leg to escape. The loss of a leg did not seem to seriously hamper the spider's mobility, and a short time later it captured a looper.

The last encounter occurred during a pilot experiment to see if spiderlings were less likely to attack the larger *P. dentata*. Two of 3 spiderlings attacked *P. dentata* when this ant was offered as first prey. It seemed unlikely that the species of ant made any difference since the 2 species were related, so *P. dentata* was used in subsequent tests for groups which had been offered *P. metallescens* as the first prey, since the latter species was unavailable for further tests.

None of the 8 spiderlings offered ants on 2 consecutive days (A_2) attacked the ants on the second day. All exhibited strong avoidance responses and, when confronted by an ant, struck at it with the legs I, then ran away. Spiderlings of group A_3 were offered loopers as second prey, ants as first and third prey. All had the same response to ants on their second encounter with ants (3 days after the first encounter) as did the spiderlings from group A_2; the one exception was a spiderling that made a single attack, but immediately released the ant and thereafter behaved like the other spiderlings. One spiderling avoided the ant when its second encounter with an ant was on the fourth day after the first encounter.

These results show that the spiderlings: 1) will initially attack any suitably-sized prey, 2) will remember unfavorable encounters with certain types of potential prey, and 3) will remember which potential prey caused these unfavorable encounters, subsequently avoiding encounters with this type of organism. Chemotactic as well as visual cues may be utilized, as evidenced by the tapping of the ants by the legs I of the spiderlings. The salticid *Corythalia canosa* (Walckenaer) can even distinguish between different types of ants of similar size (*Prenolepsis* and *Crematogaster*) which belong to different subfamilies (Edwards et al., 1974). Chemotactic cues or perhaps even odor may have been important in the differentiation of these 2 ants, as the different subfamilies they belong to use different chemicals for defense and alarm (Hermann, 1969).

The experiments with ants show that not only do spiderlings become more proficient at capturing prey, but they also become more discriminating in what they will attack.

Table 8-1. Comparison of hunting behavior of 3 different age groups (10-day, 12-day, and 14-day) of Phidippus regius spiderlings when presented with first (C_1^1, C_2, C_3) or second prey. Prey reversed for subgroups of C_1 between first and second prey presentations. Directions of capture: A=anterior, L=lateral, P=posterior. Distance of attack given as number of attacks, mean distance (in mm), standard error of the mean. There were no significant differences between groups for attack distances for a particular type of prey. All comparisons of attack distances between Drosophila and loopers (except C_1^1 - C_1^1) were significant at $p<.05$.

Group	C_1^1	C_1^2	C_2	C_3
Age (days)	10	12	12	14
Days after leaving eggsac	1	3	3	5
Prey:				
Drosophila				
# spiders tested	10	10	10	10
# flies attacked	8	5	6	10
# captures	6	2	3	9
capture direction	1L,5P	2A	1A,1P	1A,4L,4P
# of attacks	n=11	n=9	n=14	n=22
distance of attack	$\bar{X}$=3.18 ± 0.32	$\bar{X}$=3.50 ± 0.35	$\bar{X}$=4.86 ± 0.92	$\bar{X}$=3.82 ± 0.48
Looper				
# spiders tested	10	10	10	10
# loopers attacked	7	6	1	7
# captures	5	6	1	7
capture direction	4A,1P	5A,1P	1A	7A
# of attacks	n=10	n=7	n=1	n=7
distance of attack	$\bar{X}$=2.05 ± 0.53	$\bar{X}$=1.36 ± 0.09	$\bar{X}$=2.50 ± 0	$\bar{X}$=1.57 ± 0.13

Table 8-2. Comparison of attacks by *Phidippus regius* spiderlings to different types of prey. Groups of spiderlings are identified along the left margin, prey along the top margin. Statistics given are number of attacks, mean distance of attack (in mm), standard error of the mean. Statistics followed by the same letter (a, b, etc.) are not significantly different ($p<.05$).

	Aphids	Ants	Winged flies	Vestigial-winged flies	Loopers
A_1	n=9 $\bar{X}=3.44 \pm 0.65$, bc	n=24 $\bar{X}=2.58 \pm 0.22$, c	n=25 $\bar{X}=6.32 \pm 0.43$, a	---	---
B	---	n=14 $\bar{X}=1.89 \pm 0.19$, de	---	n=32 $\bar{X}= 3.17 \pm 0.20$, b	n=21 1.79 ± 0.14, de
C_3	---	---	---	n=22 $\bar{X}= 3.82 \pm 0.48$, b	n=7 1.57 ± 0.13, e
A_2	---	0	---	---	n=23 1.76 ± 0.19, de
A_3	---	n=1 $\bar{X}= 5.00 \pm 0$ (not comparable)	---	---	n=5 2.20 ± 0.20, bcd
A_4	---	---	---	---	n=11 2.14 ± 0.38, cde

Table 8-3. Prey offered to Phidippus regius spiderlings, comparing lumped responses of spiderlings to prey regardless of sequence or group prey was offered to. Prey are ranked by size and motility (see Figure 8-1). Statistics are total number of attacks, mean distance of attack (in mm), and standard error of the mean; statistics followed by the same letter are not significantly different.

	Distance Attacked	Motility Rank	Size Rank
Winged flies	n=25 $\bar{X}$= 6.32 ± 0.43, a	1	3
Vestigial-winged flies	n=54 $\bar{X}$= 3.43 ± 0.23, b	2	4
Ants	n=38 $\bar{X}$= 2.33 ± 0.17, c	3	5
Loopers	n=67 $\bar{X}$= 1.84 ± 0.18, d	4	1
Aphids	n=9 $\bar{X}$= 3.44 ± 0.65, b	5	2

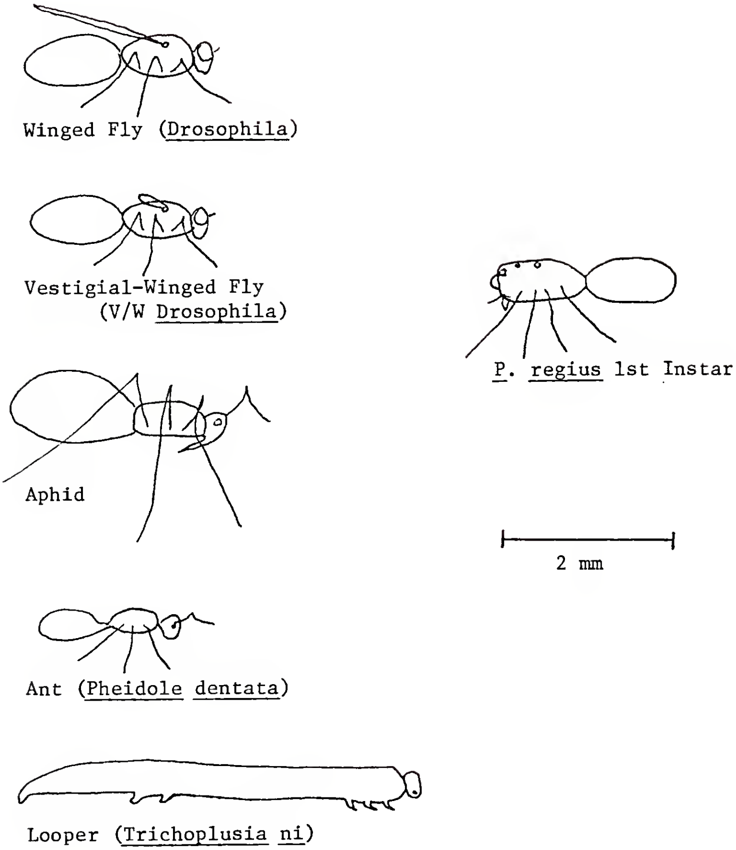


Figure 8-1. Diagrammatic illustrations of prey offered to naive *P. regius* first instars, showing size relative to spiderling.

CHAPTER 9
MIMICRY IN Phidippus

Introduction

Many animals are known to use mimicry in a number of ways (Wickler, 1968). Although numerous spiders are cryptically-colored and resemble inanimate objects or part of the substrate they inhabit (Kaston, 1948), few are known to specifically mimic other organisms. A few salticids mimic beetles (Kaston, 1948), especially of the family Chrysomelidae. Members of at least 8 spider families mimic ants (Reiskind and Levi, 1967); especially numerous in this respect are members of the families Clubionidae and Salticidae. Males of the mygalomorph family Atypidae appear to mimic pompilid wasps. No specific spider mimics of velvet ants (Mutillidae) have been reported, although Reiskind (1969) implicated some species of *Castianeira* (Clubionidae). Mutillid females would seem to be ideal models with their potent sting and aposematic coloration. Here I present evidence that certain species of *Phidippus*, perhaps most of the species in the genus, mimic mutillid wasps. The spider stage most often implicated as a mimic is the adult male, although juveniles and females appear also to be mimics in some species.

Methods

A preliminary experiment to test the value of aposematic coloration in *Phidippus apacheanus* was conducted with two lizard species, *Anolis carolinensis* Voight and *Sceloporus undulatus* (Latreille). The lizards were of mixed age groups, but all except one *Sceloporus* male appeared to be either juvenile or young adult. Each day in captivity the lizards were fed 1 cabbage looper larva, *Trichoplusia ni* (Hübner), in order to ascertain that they were feeding and in reasonably good condition.

A wooden frame box 25 x 31 x 40 cm with 5 hardware cloth sides was used. Three lizards were placed in the box (2 *A. carolinensis*, 1 *S. undulatus*) in one of three test situations. The lizards fed freely on cabbage loopers under such conditions; it was therefore concluded that testing of multiple individuals simultaneously in one cage was a valid procedure. The lizards used for each test were different individuals, and there was only 1 replicate of each test. The 3 groups of lizards were offered one of the following: a female *Dasymutilla mutata* (Blake), a penultimate male *Phidippus apacheanus*, or both simultaneously. I made periodic observations of encounters. Each test lasted 24 hours, after which the prospective prey was removed and the lizards released.

Results and Discussion

No predation occurred in any of the above tests. The lizards largely remained stationary on the sides of the cage. The mutillid would alternate between walking around the bottom of the cage and not moving. The spider would walk anywhere in the cage or remain still in an edge or corner.

The lizards would sometimes watch the moving mutillid, but made no attempt to approach it. Sometimes the lizards would approach the spider, but they made no attempt to capture it, even when the spider assumed a defensive stance, thus betraying its identity as a non-mutillid.

Perhaps the lizards already had experience with mutillids, although mostly young individuals were used to reduce the chance of this possibility. If they were inexperienced with mutillids, then either the test situation affected their behavior or they have an innate aversion to aposematically-colored arthropods.

The lizards were chosen because of their abundance and availability, and also because they represented some of the most likely vertebrate predators of *Phidippus* species. There is at least one record of a *Sceloporus* preying on a *Phidippus* (Gertsch and Woodbury, 1930). Another reason for using these particular lizard species is that *A. carolinensis* is primarily arboreal, whereas *S. undulatus* is more terrestrial. A close relative of the latter species, *S. woodi* (Stejneger), is almost exclusively terrestrial (Carr, 1940). Significantly perhaps, *S. woodi* occurs where *P. apacheanus* is most abundant, in sand pine scrub areas.

I have never seen a *Phidippus* individual of any age or size make a silken bridge-line from one plant to another, and only once observed an individual use a bridge-line made by another spider. This may be due in part to the relatively large size of these spiders as adults, not necessarily because of their weight (which the silk could probably support), but because of the exposure to predators such a maneuver would allow. More than likely, the foraging behavior of the spiders and the relative spacing of plants in the preferred habitats have also been factors in selection against bridge-making. Most arboreal species of *Phidippus* hunt primarily up and down the main stem of a plant, and in order for the spider to move from one plant to another, a second plant must be either touching or within jumping range, or the spider has to walk across the ground. Since most species live in semi-xeric to xeric habitats and the relative density of plants is low, traversing from plant to plant involves a considerable amount of travel on the ground. This has been observed for *P. audax* (Tessler, personal communication) in old fields (primary mesophytic situations) and probably occurs often in the xeric sand hill and sand pine habitats in Florida. It is in the primary successional stage of the latter habitat that *P. apacheanus* is most abundant in Florida. This habitat most resembles the conditions of its desert habitat in the southwestern U. S., where a number of congeneric apparent mutillid mimics occur.

The color pattern of adult *P. apacheanus* most resembles that of the western mutillid *Dasymutilla flammifera* Mickel; both model and mimic are solid red dorsally with black appendages. The large *D. occidentalis* (L.) of the eastern U. S. may be the model for eastern populations of *P. apacheanus*. Most of the western species of *Phidippus* alleged to mimic mutillids are red only on the dorsum of the abdomen and black elsewhere, as are the sympatric *Dasymutilla magnifica* Mickel and *D. nogalensis* Mickel. Both sexes of the western *Phidippus octopunctatus* (Peckham & Peckham) are gray dorsally, as are the sympatric *Dasymutilla magna* (Cresson) and *D. nocturna* Mickel.

The above-mentioned mutillids, medium to large in size (15 - 20 mm average), are about 5 - 10 mm longer than their alleged mimics. However, in life, mutillids run with their heads down, somewhat hidden by the thorax. The truncate anterior edge of the mutillid thorax becomes effectively the front of the animal, which is matched in shape by the front of the spider. The tucked head of the mutillid also makes the mutillid appear shorter, thus more similar to the mimic in size.

The fact that lizards (assuming they are among the most important vertebrate predators) have limited home ranges is important to the development of mimicry in *Phidippus*. It seems necessary that the predator, model, and mimic all occur together for the mimic to gain any advantage by being a mimic (although another possibility is examined later). In this case, the mutillids would presumably teach the lizards about the painful effects of trying to eat a velvet ant, the lizards would retain a visual image of the aposematic coloration of the mutillid, and would refrain from attempting to eat anything with a similar color pattern. This is particularly significant for *P. apacheanus*, since all except the first free-living instar have a red and black color pattern. Although the spiders are primarily arboreal, some of the smaller species of *Dasymutilla* are also partly arboreal; therefore a broader base of potential predators can learn about mutillids (hence the testing of both arboreal and terrestrial lizards).

I found that in the Florida State Collection of Arthropods, collections of mutillids revealed that the smaller species of *Dasymutilla* were present from May through August, the same time as immatures of *P. apacheanus*, whereas the large *D. occidentalis* was present from May through October, the latter month when *P. apacheanus* matures. This synchronization of different stages of the mimic with different models has been taken to an even higher specialization by some ant mimics (Reiskind, 1970).

Although *P. apacheanus* seems adapted to being a mutillid mimic throughout most of its life cycle, the same cannot be said of its sympatric congener, *P. cardinalis*. Only the adult male of *P. cardinalis* resembles a mutillid, and it matures the same time and in the same habitats as *P. apacheanus*. The immature stages of *P. cardinalis* are pale yellow and blend well with dead stems and grasses in the xeric habitat. In the subadult stages they turn orange and finally red as adults. Adult females are colored much like the males north of the range of *P. apacheanus*, but where the two spiders occur together in

Florida, at least, the females of *P. cardinalis* are more cryptic in coloration.

I suspect that the reason both *Phidippus* species do not mimic mutillids throughout their life cycle is that the combined populations of the juvenile stages would create a surplus of mimics, which would negate the advantage to being a mimic by too often presenting a palatable item to the predator population. The evolutionary result is that one species is a mimic, the other cryptic, in the immature stages.

While it is not difficult to hypothesize the evolution of this system, it is difficult to understand why each particular species evolved the way it did. The following evidence is available: *P. cardinalis* is an eastern species, *P. apacheanus* a southern and western species. However, where they occur together in Florida, *P. apacheanus* maintains somewhat higher population levels in the juvenile stages. In the western U. S., where *P. cardinalis* does not occur, *P. apacheanus* has a developmental color progression similar to that of *P. cardinalis*, with young immatures yellow, subadults orange, and adults red. The geographic origin of *P. apacheanus* is unclear, but it seems to be more numerous in the southwestern states. Also, occurrence of yellow females is frequent in the western populations, but extremely rare in eastern populations. This may reflect an increased selection for cryptic coloration, as reflected in juvenile color patterns of western populations, or mimicry of yellow mutillids. The eastern *Dasymutilla occidentalis* occurs rarely in a yellow form. In the northern part of the range of *P. cardinalis*, the reason for this species to have a changing color pattern is probably lack of sufficient numbers of models to support a larger mimic population.

Where *P. apacheanus* and *P. cardinalis* are sympatric in the southeastern U. S., mutillid populations are fairly high. The species which seems to be genetically the most variable, *P. apacheanus*, has taken best advantage of the increased model population by increasing its number of mimics, i.e., the juveniles which mimicked mutillids had a higher survival rate and genetically passed on this phenotypic advantage to succeeding generations. Lacking any other evidence, I would have chosen *P. apacheanus* as the most likely to increase its mimic population, as individuals of this species are bolder and more aggressive than individuals of *P. cardinalis*, a possible preadaptation to the types of behavior that enhance mimicry. With the more aggressive and genetically flexible species, *P. apacheanus*, filling the increased allowance for mimics, *P. cardinalis* is restricted from also changing its color pattern, because its survival depends on not flooding the area with mimics. Mimicry in *P. cardinalis* could still occur late in the life cycle because the combined populations of the two species would be lower in the adult stage due to juvenile mortality.

Males of *P. cardinalis* average smaller than those of *P. apacheanus*, which are only about half the size of the supposed model, *D. occidentalis*; the mutillid itself is uncommon in October. Perhaps size is unimportant relative to the similarity of the mimics' color patterns to mutillids, which may be sufficient to discourage predators. However, another possibility is that the predators have already learned about mutillids during the summer when *P. apacheanus* is a mimic as a juvenile, and this protection carries into the adult stage, where it is further amplified by the peculiar mutillid walk, which is mimicked by the adult males of both *Phidippus* species. But the question of what *P. cardinalis* is mimicking must be asked. Since P. cardinalis did not have a mimic stage during the hypothetical learning period of the predator when mutillids were relatively abundant, it could not have been synchronically mimicking the velvet ants (barring the possibility that males mimic the few remaining and much larger D. occidentalis). The primary advantage to P. cardinalis males would seem to be their resemblance to the memory of a velvet ant retained by a lizard. Since there is no evidence that either spider species is other than relatively innocuous, no Mullerian mimicry can be occurring.

In one further case of apparent mutillid mimicry, Phidippus whitmani, a relative of P. cardinalis, has a bright red dorsum and inhabits mesophytic leaf litter. At times, P. whitmani is extremely abundant, even as adults. Both sexes of P. whitmani are bright red south of the Appalachian Mountains, whereas only males are red in the northern part of the range and females are brown. Juveniles have a similar color pattern to females of their respective regions.

Assuming a greater number of mutillids on the warmer end of a longitudinal gradient would help explain the greater number of red P. whitmani in the southern states. What remains unexplained is the apparent lack of mutillids in the mesophytic habitat; possibly, the velvet ants are behaviorally cryptic (they hide in the litter) or the habitat is unsuitable, perhaps too moist for the life cycle of the mutillids or of their prey. Here seems to be a case where the mimic far outnumbers the model.

Another factor is the apparent dearth of diurnal, terrestrial, vertebrate predators. The possiblility must be considered that P. whitmani gains its greatest protection from transient predators (i.e., birds) which have gained experience with mutillids in other habitats. While it is difficult to postulate mimicry in the absence of a sufficient model, P. whitmani is sympatric-allotopic to its close relative P. cardinalis, and their common ancestor may have had a similar color pattern.

One complicating factor to this hypothesis is that P. whitmani is also allochronic to P. cardinalis, i.e., it matures in spring whereas P. cardinalis matures in the fall. Phidippus whitmani may not be mimicking Dasymutilla at all, but rather the similar genus Pseudomethoca, which also appears in the spring.

Obviously, a considerable amount of additional research is needed both on the biology of mutillids and on the relationships of various species of Phidippus to genera and species of mutillids. One final observation: I recently have noticed that color patterns of such neotropical salticid genera as Freya, Frigga, and Phiale are remarkably similar to such neotropical mutillid genera as Atillum, Cephalomutilla, Darditilla, Hoplocrates, Hoplognathoca, Hoplomutilla, and Traumatomutilla. Further research may show that mutillid mimicry may be at least as common as ant mimicry within the Salticidae.

CHAPTER 10
ECOLOGY OF *Phidippus* SPECIES

> "A sower went forth to sow, and when he sowed, some seeds fell by the wayside and the birds came and devoured them. Some fell upon stony places where they had not much earth and forthwith they sprang up; but they had no depth of earth, and when the sun was up they were scorched, and because they had no root they withered away. Some fell among thorns, and the thorns sprang up and choked them. Others fell into good ground and brought forth fruit, some a hundredfold, some sixtyfold, some thirtyfold."
>
> St. Matthew 13:3-8

Introduction

The above quote, first used in an ecological context by Dondale (1975) in reference to naturally dispersing arachnids, also reflects on the nature of survival of organisms. They must cope with predators and competitors in order to survive, and their ultimate success depends on the quantity and quality of resources they are able to locate and utilize.

Researchers in the last two decades, inspired by Hutchinson's (1959) famous question, 'Why are there so many kinds of animals?', have conducted numerous investigations of interspecific differences in use of resources. Most of these studies have assumed that competition is the major selective force limiting similarity among species. Various theoretical aspects have been discussed by MacArthur and Levins (1967), Schoener (1969, 1975), Colwell and Futuyma (1971), Vandermeer (1972), Pianka (1974), May (1975), Pielou (1975), and Hurlbert (1978). Connell (1975), Wiens (1977), and Caswell (1978) have discussed factors, such as predation and environmental variability, which can be more important than competition in regulating community composition. Many of these studies have been on various vertebrate groups, such as lizards (Schoener, 1968, 1970; Pianka, 1975), birds (MacArthur, 1958; Cody, 1968, 1974; Davis, 1973; Diamond, 1975), and rodents (DeLong, 1966; Brown, 1971, 1975). Marine invertebrates have been studied by Connell (1970), Kohn (1971), and Dayton (1971). Resource utilization of some terrestrial invertebrates has been analyzed by Rathcke (1976) and Malas and Wallace (1977) for insects, and Williams (1970) for scorpions.

Both Van Hook (1971) and Moulder and Reichle (1972) have attempted to quantify the role of spiders in trophic level regulation of communities. Investigations of resource partitioning in spiders have been limited to a few papers by Kuenzler (1958), Enders (1974), Gertsch and Riechert (1976), Uetz (1975, 1977), and Turner and Polis (1979). Enders (1974) noted vertical stratification between two species of orb-weavers in the immature stages. Gertsch and Riechert (1976) demonstrated spatial and temporal differences among closely related species of several spider families. Uetz (1977) concluded that spiders of the forest floor cursorial guild coexisted because of their distributions in space and time, and because of differences in sizes of prey utilized. Turner and Polis (1979) found similar time differences in a guild of herb zone ambushing spiders; they calculated niche overlap values and found little evidence of competition; due to the lack of limiting resources, they hypothesized that interference competition was a major factor in coexistence among guild members. Enders (1975) discussed theoretical comparisons of web-weavers versus salticids based on attack distance and prey size, and he (Enders, 1976) discussed the use of Dyar's Constant (equal to the minimum size differences between predators specializing on prey size proposed by Hutchinson, 1959) as a measure of difference in size between instars of a species and its relation to the prey-capture strategy of various species. He also came to the conclusion that interference competition could be a proximate cause for patterns of spider phenology and distribution. Supportive evidence was presented by Edgar (1969), who reported that *Lycosa* (*Pardosa*) *lugubris* was its own worst enemy. Other lycosids are known to prey extensively on conspecifics (e.g., Yeargan, 1975) and Turner (1979) found conspecifics of the oxyopid *Peucetia viridans* were the fourth major prey species. Jackson (1977b) noted conspecific predation by the salticid *Phidippus johnsoni*.

Luczak has analyzed communities of both web (1963) and wandering (1966) spiders in different strata; however, few studies of taxonomically closely related organisms have been conducted. MacArthur's (1958) warblers are a classic example. Among insects, comparisons of closely related leafhoppers (Ross, 1957), bumble bees (Brian, 1957), and butterflies (Clench, 1967) have been made. Of the spiders, three different species of lycosids (Kuenzler, 1958), two species of araneids (Enders, 1974), and an oxyopid with four species of thomisids (3 in the genus *Misumenops*; Turner and Polis, 1979) have been compared. No previous comparisons have been specifically aimed at salticid species, although basic comparisons of phenology and spatial distribution have been made by a number of authers (e.g., Gertsc- and Riechert, 1976). This type of information has been given by a number of authors (e.g., Kaston, 1948) for *Phidippus* species; data are summarized below for each species. Also included is a summary of other biotic factors affecting species of *Phidippus* reported in the literature.

The purposes of the ecological research presented here were twofold. First, I documented the major biotic factors affecting each species:

habitat, microhabitat, phenology, reproductive capacity, food, and enemies. Second, I compared the data among species for evidence of competition or resource subdivision, especially for species occurring in the same habitats.

Members of the genus _Phidippus_, especially in eastern North America, exhibit phenotypical characteristics which make them unusually suited to comparative autecological studies. Even though a graded series of species based on mean and range of body length of adults can be made (see Chapter 2), the means of all the species, with the exception of the largest species, _P_. _regius_, are not significantly different. Since body length is strongly correlated with body weight, which is the most widely accepted measure of size, and since the overall structures of the species are similar, all the species can be considered essentially the same size; _P_. _regius_ can be included also, with the exception of its last 2 instars, which are larger than the other species; _P_. _otiosus_ is also usually slightly larger than most of the species as adults. The conversions of body length to weight based on body shape developed by Zug and Zug (1979) give very good estimates when compared to actual weights of _Phidippus_ species given by Anderson (1978). Thus, with one or two exceptions, adults of different species occurring together at the same time are probably feeding on similar-sized prey. Analyses of prey size by different species under these circumstances may be superfluous, and habitat differences may be more important. But the opposite is the case when immatures of one species occur with adults of another. The same habitat resources could be shared if prey were different. These are examples of the types of ecologically significant comparisons analyzed later.

Methods

Field Observations

Three areas in Alachua County, Florida, were chosen for field observations based on differences in habitat and species composition. These were: 1) along the north edge of Burnt Pond at Camp McConnell (YMCA camp), 2) a pine-oak flatwoods north of Cross Creek in the Lochloosa Wildlife Refuge, and 3) a mixed xeric hammock-ecotonal area west of Gainesville. These habitats are described in Appendices C and D. The sites were chosen after extensive field work during research on the life history of Phidippus regius (Edwards, 1975), and, following the completion of this work, a number of field trips (many in collaboration with D. B. Richman) made in an attempt to determine the salticid fauna of Florida. Factors affecting choice of research sites were: 1) Burnt Pond - unlimited food supply and uniform habitat patches; 2) flatwoods - a population of P. pulcherrimus, about which literally nothing was known; and 3) mixed xeric hammock - apparent high species diversity and high species evenness. Research in these 3 primary areas was conducted from the spring of 1976 through the winter of 1977, on a weekly, biweekly, or monthly basis, depending on factors discussed below. A second habitat was studied near Burnt Pond during the fall and winter in the same time period.

Secondary areas, in particular along Newnan's Lake and in Ocala National Forest (see Appendices C and D), were studied during the spring and summer of 1977, on a biweekly or monthly basis. Observations were conducted in other areas at irregular time intervals prior, during, and subsequent to the time of concentrated field work. Much of the data on rare or habitat-restricted species was collected during these latter observations. More time was spent in habitats which produced more data per time expended; thus a bias toward Burnt Pond will be noted both because of frequency of predation observed, and because of the structured habitat which allowed for various analyses and observations of spider-plant associations.

Population sizes were made by actual counts of spiders observed (sometimes supplemented by sweep net samples). Turner and Polis (1979) also used this method; they examined all of the vegetation in their research area. This was feasible since the primary habitats studied were relatively small in area. I had originally intended to compare three sampling methods: d-vac, sweep net, and sight count (concurrent with hand collecting); however, this proved to be infeasible for the following reasons. The d-vac may be a suitable sampling device for row crop monocultures, such as soybeans (LeSar and Unzicker, 1978), but it is woefully inadequate as a sampling device in a heterogeneous environment. It is incapable of evenly sampling mixed shrubby habitats, and has the same problem in some habitats which it would seem well suited for. At Burnt Pond, the grass was so thick but fragile that in sampling even a small area (e.g., 20 m^2), the d-vac would accumulate so much vegetative material that the vacuum suction was reduced. Under these circumstances, I observed larger specimens of Phidippus to fall out of the d-vac after being initially picked up. The d-vac was therefore taking samples biased toward smaller individuals. Howell and Pienkowski (1971) observed that Salticidae and Thomisidae were more difficult to pick up with a d-vac than with a sweep net in alfalfa. I had intended also to estimate prey populations with d-vac samples, but with the failure of this method to give reliable results for spider populations, the d-vac was abandoned. Notes on apparent relative prey abundance are given where appropriate.

Turnbull (1973) states, "it is dismaying to find (the sweep net) still in use (as a sampler of populations)." He gives several examples of the inherent biases of this sampling method; however, he notes that Luczak and Wierzbowska (1959) have come to opposite conclusions: "Selectivity of the scoop (sweep net) method is always of a similar type and does not give differentiated deformations in the picture of the quantitative dynamics of ground flora spiders." I must agree with this latter view in terms of sampling for Phidippus, since, although the method is somewhat biased for age class (as pointed out later), the strata sampled are the same strata that I would have sampled by visual means. Field workers often develop a "search image" for the organisms they study, much like the objects of study (often predators), which supposedly form search images for their prey. The efficiency of this system can be high, as an understanding of the behavior patterns and knowledge of likely locations of object organisms contributes heavily to the success of the observation system. It can also lead to biases based on previous experience. But since the heterogeneity of a small sampling area is limited, so is the margin for potential error; therefore I consider sweep net sampling to be a short-cut method for determining the number of individuals in an area and to be roughly equivalent to the number of individuals I would have found if I had spent a longer amount of time searching the same stratum by visual means. At infrequent intervals, I spot-checked this assumption. On one occasion, a sweep sample captured 15 specimens of immature P. pulcherrimus. Subsequent inspection immediately following the sweep revealed only one additional specimen in the area sampled. I was confident that I would have been able to find these specimens by visual searching, given the same sampling area. Also, I note again the superiority of the sweep net to the d-vac in capturing Salticidae reported by Howell and Peinkowski (1971). Most supplemental sweeping was done in secondary research areas, as most of the time spent in primary areas was observation time. Where both types of samples were taken at a site, the samples are lumped together. This is justified by the preceding discussion.

Two strategies of observation were employed. In areas where population densities of target species were low (based on difficulty of visual location and subsequent confirmation by sweeping), continuous observation of single individuals was the method utilized. Observation times ranged from ½-3 hours, depending on the ultimate outcome of the activity pattern of the spider. In areas where population densities were high (e.g., Burnt Pond), the maximum number of significant encounters was optimized by moving slowly but steadily from individual to individual. The average amount of time spent per individual per day was about 10 minutes, and ranged from instantaneous (e.g., spider observed with prey at first sighting; spider with eggsac) to one hour. Activity patterns of individuals presumably hunting for prey were recorded. Individuals engaged in activities judged to be significant (e.g., prey capture; guarding eggsacs) were collected and brought back to the laboratory, where they were either preserved or maintained by procedures described in earlier chapters. Individuals and their prey were usually preserved, their lengths measured, and their lengths converted to approximate weights according to the conversion tables given by Zug and Zug (1979). Linear regression was used to correlate the significance of prey size to spider size. Number of eggs per eggsac were counted, and when possible, percent infertile eggs was also noted. Field-collected eggsacs were allowed to hatch in the laboratory in order to ascertain infertility rates and to obtain parasites. Eggsacs were categorized as first, second, third or fourth batches laid by a particular female based on number of eggs in the batch, known seasonal reproductive period, and in some cases, known previous reproductive history of the female in question. Comparisons of reproductive capability were made using Student's t test, and were based on the first eggsac, since the number of eggsacs varies between individuals and between species. This method will tend to underestimate the differences between species, since larger species have more eggsacs and more eggs per eggsac.

Comparisons of various other biotic categories among species were made in the following ways: 1) prey were lumped into orders, 2) characteristics of plant structure and specific plant associations were both analyzed, and 3) phenology of adults was compared using distributions of adults by month. Measures of nich overlap were made using the method of Pianka (1974), while niche breadth was calculated based on the formula used by Levins (1968). Both of these methods were used by Turner and Polis (1979) to analyze data for ambushing spiders. Uetz (1975) used the Shannon-Weaver index (Shannon, 1948) and Pielou's (1966) measure of equitability for a study of litter spiders. Hurlbert (1978) enumerates the reasons why overlap indices fail as measures of competition, but equalization (e.g., in interspecific size) of some of the parameters in this study may offset some of the inherent uncertainness of these measures.

Background

Phidippus apacheanus

Habitats. Muma and Muma (1949) found P. apacheanus (reported as P. nikites) in the herb stratum of grass prairie in Nebraska, dominated by big and little bluestem (Andropogon furcatus and A. scoparius), blue gramma (Bouteloua gracilis) and bluegrass (Poa pratensis). Fitch (1963) reported P. apacheanus from Kansas in low population numbers from hot and dry areas; it seemed to prefer rocky habitat with short grass prairie or pasture. Specific collections were made from bare ground, gravel road, fence post, barn, and a limestone slab in open woods. Gardner (1965) observed P. apacheanus in Utah in a sagebrush community, on sagebrush (Artemisia tridentata), rabbitbrush (Chrysothamnus nauseous), and four-winged saltbrush (Atriplex canescens). Carpenter (1972) found P. apacheanus in Texas to be abundant in arid areas on shrubs and bushes, especially the thorny kinds like mesquite and cactus, and on tall annuals like sunflowers. She reported that nests were made on the undersides of sunflower leaves and among the joints and thorns of cactus; the females were sedentary in nests, while the males wandered during the day on leaves and twigs. Jung and Roth (1974) reported P. apacheanus from upper canyons of the Chiricahua Mountains of Arizona, in areas of mixed pines, live oak, and manzanita. Museum records add 1 specimen from gum weed and 33 specimens from a heron rookery in Utah.

Prey. None reported.

Enemies. None reported.

Phenology and Reproduction. Carpenter (1972) reported cohabitation by P. apacheanus during September.

Phidippus audax

Habitats. The most frequently reported member of the genus from agricultural crops is P. audax. It has been found in alfalfa (Howell and Pienkowski, 1971; Wheeler, 1973), cotton (Kagan, 1943; Clark and Glick, 1961; Whitcomb et al., 1963), sorghum (Bailey, 1968; Bailey and Chada, 1968), and soybeans (LeSar and Unzicker, 1978). Whitcomb and Tadic (1963) and Warren et al. (1967) took P. audax in nests of the fall webworm (Hyphantria cunia), often on black walnut (Juglans nigra) or persimmon (Diospyros virginiana). Phidippus audax has been collected from peat meadows (Lowrie, 1942), mixed meadows (Cutler, 1965), old fields (Levi and Field, 1954; Cannon, 1965), overgrown pasture (Tolbert, 1975), and prairie (Muma and Muma, 1949). Other authors have reported it from forest border and mixed forest-prairie (Gibson, 1947; Peck, 1966), from young pines (Martin, 1966; Peck et al., 1971), apple trees (Specht and Dondale, 1960; McCaffrey and Horsburgh, 1980), on the holly Ilex opaca (Lamore, 1958), and under tree bark (Kaston, 1948; Fitch, 1963; Hollis and Branson, 1964). Several authors have noted the ubiquitous distribution of this species: it has been found in all successional stages of a beech-maple forest (Elliott, 1930); from pine dune, black oak dune, and beech-maple climax (Lowrie, 1948); abundant in field edges, prairie remnants, prairie groves, and waste areas (Snetsinger, 1955); common in a wide range of habitats but most often in dry open woods and grassland, nesting in ironweed (Vernonia interior) and milkweed (Asclepius kansana) (Fitch, 1963); extremely common under stones and boards, on trees, etc. (Kaston, 1948); and in all habitats studied, even the most desert-like, in Wichita County, Texas (Carpenter, 1972). Comstock (1940), Lowrie (1942), and Carpenter

(1972) all note that *P. audax* is more abundant in moist or humid areas. Most records were from the herb-shrub zone, but Kaston (1948), Muma and Muma (1949), and Fitch (1963) reported specimens on the ground as well. Several authors reported *P. audax* from barns, houses, and other buildings. Museum records added the following associations (one record unless indicated otherwise): ground, trash, under rocks (3), grass (2), garden, herbs, lawn (2), field, Kudzu (2), roadside, brick pile, sawdust pile, river bank, reservoir, bluff, nests in top of rushes (2), reed in rice field, barley field, bayshore (3), lake shore (2), live oak area (3), palmetto in cypress swamp (Texas), date palm (Texas), bromeliad (Mexico), avocado grove (2), under bark (12), under bark of black walnut, under bark of cottonwood (*Populus fremontii*), on a clothesline, and on buildings (30).

Prey. Representatives of the orders Odonata, Orthoptera, Hemiptera, Homoptera, Neuroptera, Coleoptera, Lepidoptera, Diptera, Hymenoptera, and Araneae have all been reported as prey of *P. audax* (Table 10-3). The most notable are various pests, including bugs (*Lygus* spp.), the boll weevil (*Anthonomus grandis*), the bollworm (*Heliothis zea*), the pink bollworm (*Pectinophora gossypiella*), the fall webworm (*Hyphantria cunea*) and the sorghum midge (*Contarinia sorghicola*) (Table 10-3).

Enemies. Several Hymenoptera of the families Pompilidae and Sphecidae, other spiders, and lizards have been reported as predators of *P. audax* (Table 10-4).

Phenology and Reproduction. Kaston (1948) noted that *P. audax* overwinters in the penultimate and younger instars in Connecticut, in hibernating aggregations of up to 30 individuals. He reported that adults matured in late April and early May, and eggs were laid in June and July; three eggsacs had 67, 88, and 150 eggs respectively, and two more together (laid by the same female?) had 252 eggs. Gibson (1947) reported maturity in late May, eggs laid in early July, and overwintering as immatures or adults in Tennessee. Snetsinger (1955) observed mature males as early as mid-March in Illinois (and noted that a few had matured in late fall of the previous year). He recorded cohabitation and mating from early May to mid-June, and eggs were laid from mid-June to late July; one female laid 3 consecutive eggsacs containing 85, 42, and 28 eggs, respectively. The Peckhams (1909) counted 90-166 eggs in sacs from the Britcher collection. Anderson (1978) reported a mean of 223 eggs for 4 eggsacs from Florida.

Phidippus borealis

Habitats. Levi and Levi (1951) report P. borealis (as P. altanus) to be abundant under the bark of standing dead trees in wet woods along the Snake River in Wyoming. The same authors (op. cit., 1955) report this species at Ptarmigan Falls, Glacier National Park, Montana. Museum records add the following associations: beach (2), grass and bark (2), near river (2), wet woods (2), in woods under bark (12), under bark (7; 1 with eggs), and under bark of dead aspen.

Prey. None reported.

Enemies. None reported.

Phenology and Reproduction. Gertsch (1934) collected adult specimens in June and July in Wyoming, Alberta, and Saskatchewan.

Phidippus cardinalis

Habitats. Muma (1944) reported P. cardinalis (as P. mccookii) from bushes and trees in open woodland and shaded field in Maryland. Kaston

(1948) reported *P. cardinalis* (as *P. mccookii*) as uncommon in Connecticut; it occurred on bushes, pine trees, and sandhill grass. Lowrie (1942, 1948) found a few specimens in black oak dune, but 34 in a peat meadow. Peck (1966) took *P. cardinalis* in a mixed forest-prairie situation, while Peck et al. (1971) found it rarely on young pines. Whitcomb et al. (1963) collected the species in cotton. Museum records added the following associations: sandhill (Florida), under stones, field, herbs (2), under log at edge of woods, in log in woods, woods, slash pine woods, on a sidewalk, and on buildings (2).

Prey. None reported.

Enemies. None reported.

Phenology and Reproduction. Kaston (1948) reports adults of *P. cardinalis* were taken in Connecticut from late May to October.

Phidippus clarus

Habitats. Barnes and Barnes (1955) reported that *P. clarus* was the most abundant spider species in the southeastern Piedmont abstract broomsedge community dominated by *Andropogon virginicus*. Berry (1970) also found *P. clarus* in the broomsedge community, but also in the transition and forest communities. Barnes (1953) found *P. clarus* rarely in non forest maritime communities in North Carolina, Muma and Muma (1949) collected *P. clarus* in grass prairie, Cutler (1965; as *P. rimator*) swept it from mixed meadow, Dondale (1971) considered it a resident rare species in grassland meadow in Ontario, and Judd (1965, 1977) found it on bushes in a bog and in nests in rolled leaves of the milkweed *Asclepias syriaca*. Kaston (1948) reported it as very common on tall grass and bushes, Tolbert (1975) found it in an overgrown pasture, and Elliott (1930) considered it typical of the transition stage between field and beech-maple forest. Lowrie (1942, 1948), in studies of dune succession, found *P. clarus* in 8 different successional stages, but most commonly in black oak dune and peat meadow. Drew (1967) found *P. clarus* in old fields and gardens, and in the herb-shrub zone of upland hardwood forest, while Snetsinger (1955; as *P. rimator*) found it to be abundant in field edges, prairie remnants, prairie groves, and waste areas. Fitch (1963) considered *P. clarus* abundant in tall-grass prairie, brome grass pasture, and old fields with broad-leaved herbs like sunflower and ironweed. Dowdy (1951) took a few *P. clarus* in the herb zone (dominated by *Andropogon virginicus*) of an oak-hickory community, Peck (1966) found it in a mixed forest-prairie, and Peck et al. (1971) found it in a pine plantation. Whitcomb and Tadic (1963) and Warren et al. (1967) found *P. clarus* in fall webworm nests. Research on crops has discovered *P. clarus* in alfalfa (Howell and Pienkowski, 1971), corn (Everly, 1938; as *P. multiformis*), and cotton (Whitcomb et al., 1963). Dondale (1956) and McCaffrey and Horsburgh (1980) found *P. clarus* on apple trees. Museum records add the following associations: golf course herbs, high grass (2), pasture (8), garden (6), tall grass and weeds (8), high prairie (5); along creek (2), pond, bog, cedar bog (2), and lake; bottomland pine and hardwood litter, pine barrens, lowland pine, and oak-hickory forest herbs; vines, raspberries (2), orchard (2), and on a building; gravid females on *Salix* sp. and *Saracenia* sp., and females with young on *Cornus* sp., *Rhus* sp. and *Solidago* sp.

Prey. Reportedly *P. clarus* has been found eating members of the orders Orthoptera, Hemiptera, Homoptera, Lepidoptera, Diptera, and Araneae. It preys on the bollworm, *Heliothis zea* (Table 10-3).

Enemies. Reported to be preyed upon by Hymenoptera of the families Pompilidae and Sphecidae as food for their young (Table 10-4).

Phenology and Reproduction. Kaston (1948) reports adults in Connecticut maturing in late June and early July and found through early October. He observed mating in June, and a single eggsac containing 75 eggs in July. Snetsinger (1955) in Illinois found males from early June through mid-August; females matured in late June and were present until early November. He found mating from late June through early August, with eggs laid from late August through mid-October; he thought the newly-hatched spiderlings might overwinter in the eggsac. Both Snetsinger (1955) and Fitch (1963) observed cohabitation; Fitch records pairs together in late July and early August.

Phidippus insignarius

Habitats. Barnes (1953) listed *P. insignarius* (as *P. fraudulentus*) from nonforest maritime communities in North Carolina, while Muma and Muma (1949) found it in prairie in Nebraska. Kaston (1948) reported it to be uncommon in Connecticut on brush and loose stones in wooded areas. Gibson (1947) collected 179 specimens from all strata (ground to tree) of a river-terrace forest in Tennessee. Lowrie (1942, 1948) reported it from 7 different habitats in studies of sand dune succession near Chicago; it was by far most numerous in the black oak dune stage, and also common in the peat meadow. Whitcomb and Tadic (1963) stated they found *P. insignarius* in fall webworm nests in Arkansas. Museum records add the following associations: cantrap (2), upland prairie (3), oak-savannah prairie, witchhazel stem, along creek, in bog with eggs, and on a building.

Prey. None reported.

Enemies. None reported.

Phenology and Reproduction. Gibson (1947) reported maturation in late May, eggs laid in early July, and the overwintering stages were immatures and adults. Kaston (1948) found adults from June to September; a female with an eggsac containing 47 eggs was found in late June, and another female with an eggsac (from which most of the spiderlings had already left) was found in July.

Phidippus mystaceus

Habitats. Kaston (1948) noted that P. mystaceus was rare in Connecticut. Cannon (1965) found it in an overgrown old field in Ohio, while Carpenter (1972) found it to be uncommon but widespread in drier areas, on mesquite bushes, salt cedar shrubs, patches of sunflowers, and in wild plum thickets in Texas. Berry (1970) considered P. mystaceus a member of the forest community in North Carolina, Peck et al. (1971) found it in a pine plantation, and it has been taken from fall webworm nests by Whitcomb and Tadic (1963) and Warren et al. (1967) (who erroneously reported it as P. carolinensis and P. incertus, respectively). Whitcomb et al. reported it from cotton (along with its synonym, P. hirsutus) in Arkansas, and Specht and Dondale (1960) beat it from apple trees. Museum records add the following associations: ground (2), gravid females under stones (2), meadow herbs, shrubs, mesquite (Prosopis juliflora), low tree branch in woods, woods, American elm, on a fence, and on a building (3).

Prey. Reported to feed on larvae of Lepidoptera; in particular, the bollworm (Heliothis zea) and the fall webworm (Hyphantria cunea) (Table 10-3).

Enemies. Collected as food for young by members of the family Sphecidae (Hymenoptera) (Table 10-4).

Phenology and Reproduction. Berry (1970) took P. mystaceus in May.

Phidippus otiosus

Habitats. Abbot (1792) states that a specimen was found on an oak tree (Richman, 1978). Muma (1975) reported the species from citrus groves. Museum records add the following associations: water hyacinth (2 immatures), pine bark, under hickory bark (female), live oak bark (2 females), on building (2).

Prey. None reported.

Enemies. None reported.

Phenology and Reproduction. None reported.

Phidippus pius

Habitats. Scheffer (1905) first recorded the species from rocky grassland in Kansas. Fitch (1963) also recorded the species from Kansas in xeric situations, "chiefly on barren soil of eroded upland fields." He also noted it from fence posts and a barn. Carpenter (1972) found the species in Texas to be rare; she found a male on a salt cedar bush. Both Barnes and Barnes (1955) and Berry (1970) reported *P. pius* (as *P. abboti*) as uncommon in southeastern piedmont broomsedge communities. No habitat data included with museum records.

Prey. None reported.

Enemies. Used as food for young by Sphecidae (Hymenoptera), and eaten by a cattle egret (Aves) (Table 10-4).

Phenology and Reproduction. Barnes and Barnes (1955) collected *P. pius* between June and early August, and Berry (1970) collected it in July. Cutler (1979) found 34 and 16 eggs in consecutive eggsacs of a single female.

Phidippus princeps

Habitats. Muma and Muma (1949) reported *P. princeps* from prairie in Nebraska. Barnes and Barnes (1955) found it in southeastern piedmont broomsedge communities, but Berry (1970), working in the same area, found it in the transitional zone between field and forest. Lowrie (1942, 1948) found it in pine woods, black oak dune, and beech-maple forest, but most often in a peat meadow. Cutler (1965) reported it from a park in the Bronx, while Peck (1966) reported it from mixed forest-prairie, and Dowdy (1951) reported it (as *P. insolens*) on litter and herbs in an oak-hickory community in Missouri. Dondale (1971) considered *P. princeps* as a rare resident species of a grassland meadow in Ontario, and Peck et al. (1971) found it on young pines in Arkansas. Kaston (1948) found *P. princeps* fairly common in Connecticut on bushes and tall grass, but Fitch (1963) considered it rare in Kansas; he found it in dry, fairly open woodland. Wheeler (1973) collected it in alfalfa, while Everly (1938; as *P. insolens*) collected it in corn. McCaffrey and Horsburgh (1980) beat it from apple trees. Warren et al. (1967) took it in fall webworm nests. Museum records add the following associations: gravel road, railroad track (2 males), under rock, pitfall in woods (8), ground in weeds, bluegrass, sedges, dried leaf on sedges with eggs, meadow (3 immatures), pasture (2 immatures), old field (4 immatures), field (12 immatures), along highway, by pond, by creek, on *Saracenia flava* (16), on oak, and on building.

Prey. None reported.

Enemies. Wasps of the families Pompilidae and Sphecidae (Hymenoptera) have been reported using individuals of *P. princeps* as food for their young (Table 10-4).

Phenology and Reproduction. Berry (1970) collected adults in April and June in North Carolina, Kaston (1948) reported maturity in late April and early May with adults found through July in Connecticut. Barnes and Barnes (1955) collected adults between June and early August, while Cutler (1965) reported a pair in September. Kaston (1948) reports courtship at the end of April and a female guarding an eggsac with 115 eggs in late May. Two other eggsacs had only 43 eggs and 27 young, respectively.

Phidippus pulcherrimus

Habitats. None reported.

Prey. None reported.

Enemies. None reported.

Phenology and Reproduction. A single female was taken in March by Banks (1904) at Biscayne Bay, Florida.

Phidippus purpuratus

Habitats. Kaston (1948) found *P. purpuratus* to be common in Connecticut on talus slopes and under stones and boards on the ground. Drew (1967) found it in Michigan under stump fragments, bark, stones, and boards in both field and forest. Whitcomb et al. (1963) reported it from cotton fields in Arkansas, while Dondale (1956) took a male from an apple tree. Museum records add a female with eggs taken from a hole in a cement post in Florida.

Prey. None reported.

Enemies. Individuals of *P. purpuratus* have been reported taken by Pompilidae and Sphecidae (Hymenoptera) as food for their young (Table 10-4).

Phenology and Reproduction. Kaston (1948) collected mature males from May to November, and females from May to September. He states (after Emerton) that they overwinter as adults. Mating occurred in June, and females guarding eggs were found in July and August; three eggsacs contained 100, 114, and 155 eggs, respectively. The Peckhams (1909) report 140 young in an eggsac in the Britcher collection. Kaston notes that there is evidence that females may make 2 eggsacs in a season.

Phidippus putnami

Habitats. Muma (1944) reports *P. putnami* as common on trees, bushes, and weeds in fields and orchards in Maryland. Fitch (1963) collected a male on a gravel driveway in reestablished prairie in Kansas. Warren et al. (1967) took it from fall webworm nests in Arkansas. Museum records add the following associations: pine, rosemary (penultimate male, Florida), and a Mahonia bush (Texas).

Prey. This species is known to prey on the fall webworm, *Hyphantria cunea* (Lepidoptera) (Table 10-3).

Enemies. Individuals of *P. putnami* have been taken by Pompilidae and Sphecidae (Hymenoptera) as food for their young (Table 10-4).

Phenology and Reproduction. Fitch (1963) collected an adult male in August.

Phidippus regius

Habitats. Muma (1975) reported *P. regius* from citrus groves. Edwards (1975) found it to be primarily an old field species, with adults showing a preference for palmettoes. Museum records add the following associations: ground (3), cane, lakeshore pasture, field by pond, swamp, waste land (2), highway poles (7), cement posts (12: 3 gravid females and 9 immatures), under bark (5), under bark of *Pinus palustris*, and on buildings (2).

Prey. Larvae of Lepidoptera and adult Diptera have been reported as prey (Table 10-3).

Enemies. Fungi have been found to attack the adults (Table 10-4).

Phenology and Reproduction. Edwards (1975) reported the primary season of maturation and breeding to be in the fall. One female made an eggsac containing 335 eggs. Five other females averaged 190, 131, 87, and 85 eggs, for the first, second, third, and fourth eggsacs, respectively. Anderson (1978) reported a single female laid an eggsac with 570 eggs.

Phidippus whitmani

Habitats. Berry (1970) considered P. whitmani a member of the forest community in North Carolina, Cutler (1965) found it in a park in New York, and Peck (1966) took it from a forest with some prairie influent in Missouri. Lowrie (1948) reported it from black oak dune near Chicago, and Gibson (1947) found it in Tennessee in river-terrace forest, but more common in the drier oak-hickory, in all strata. Kaston (1948) found it on bushes and weeds, and males were conspicuous on exposed rock surfaces. Barnes (1953) listed it from nonforest maritime communities, and Fitch (1963) reported it as uncommon in dry, open places, especially on broad-leaved herbs in old pastures, and also on fence posts and a barn. (Neither of the latter two reports seem likely; I have to question the determinations of the species involved.) Museum records add the following associations: short grass, sweet fern, near creek, in dead leaves, leaf litter, leaf mold, woods, beating oak, tent of Malacosoma americanum (eastern tent caterpillar; 1 male), and on a building (2).

Prey. None reported.

Enemies. Individuals of *P. whitmani* are reportedly used as food for young by Pompilidae and Sphecidae (Hymenoptera) (Table 10-4).

Phenology and Reproduction. Gibson (1947) reported *P. whitmani* to overwinter as immatures. Kaston (1948) states they overwinter in the penultimate instar and mature in early May. Males disappear by the end of June, but females can be found through October. One female was found guarding an eggsac containing 69 just hatched young in a rolled leaf on the ground during August. Berry (1970) found adults in June, July, and October, while Cutler (1965) reports an immature female in late September.

Phidippus xerus

Habitats. Edwards (1978) reported young immatures on small woody shrubs in timbered sandpine scrub, while older immatures and adults were collected on young scrub oaks.

Prey. None reported.

Enemies. None reported.

Phenology and Reproduction. Edwards (1978) reported adult males in late June and early July, with most females maturing in late July and August and found from mid-June through early September.

Results and Discussion

Habitats

No species was restricted to a single habitat, and in almost every habitat, at least three and often five or more species coexisted. However, no more than two species in any one habitat were significantly more numerous than the other species within the habitat; the more numerous species in a habitat are considered the dominant species for that particular habitat (Table 10-1).

Habitats are considered to be general indicators of the range of tolerance of abiotic factors for each species. To a great extent, soil type may be the single most influential factor, and the water table level is also important. These two factors determine the types of plants growing in a particular area, which will determine the amount of canopy and, therefore, the amount of exposure to the sun, which will affect the temperature and available moisture at ground surface level and above.

Three species, *P. mystaceus*, *P. pius*, and *P. purpuratus*, are too insufficiently known from Florida to be able to make any conclusions about their habitat associations. Combining literature reports with the little available data from Florida gives the following generalizations: *P. mystaceus* inhabitats a variety of sub-canopy and canopy communities, *P. pius* is primarily an old field inhabitant, and *P. purpuratus* lives in fields and open woods like many of the the other species.

Some of the species, i.e., *P. audax*, *P. clarus*, and *P. whitmani*, were not found in truly xerophytic environments, although they might occur in habitats that were periodically dry. Other species, i.e., *P. apacheanus*, *P. cardinalis*, and *P. xerus*, were never found in hydrophytic habitats. Most of the species showed fairly wide tolerances for habitat over two or all three major habitat subdivisions.

Microhabitats

I grouped the known specific plant (and other) associations (Table 10-2) into seven classifications based on general type of plant (e.g., shrub, tree) and plant structure (e.g., palm, tree) (Table 10-3). Chi-square analysis showed clear preferences for certain types of plant associations for most of the species of spiders. In the case of *P. regius*, clear differences in preferred plant associations were exhibited between younger immatures and the older categories.

All stages of *P. whitmani* preferred litter. All stages of *P. audax* and *P. clarus*, and the immature stages of *P. regius*, preferred grass and herbs; a large number of *P. pulcherrimus* immatures were in this association also. Adults of *P. clarus* were equally as likely to be found on woody perennials as on grass and herbs, and immatures of *P. apacheanus* were as likely to be found on woody herbs as on shrubs. Immatures of *P. pulcherrimus* and *P. putnami* were most likely to be found on shrubs, while adults of *P. pulcherrimus* tended to favor lower strata than adults of *P. putnami*. Trees were clearly favored by immatures and adults of *P. otiosus*. Subadults and adults of *P. regius* were associated with various palms, but adults were equally as likely to be on trees, buildings, or, to a lesser extent, shrubs. Almost all adult *P. regius* on grasses, herbs, and woody perennials were males, presumably wandering in search of females. The lower strata were preferred by *P. cardinalis* (all four records from the ground were males), while *P. xerus* favored the lower woody strata.

Phenology

Frequency of occurrence by month and sex is illustrated in Figure 10-1. Males typically mature 2-4 weeks before females; this is accomplished by the males maturing in an average of one less instar than females. Females are somewhat larger and probably need the extra growth period for development of their larger size and for ovarian development. The earlier development of males increases their chances of locating and cohabiting with a subadult female, improving the males chances of reproducing and reducing the chance of an aggressive encounter with a female (see Chapters 4 and 5). *Phidippus regius* females begin to lay eggs about a month after maturing and mating in the laboratory (Edwards, 1975); most of the other species are believed to have a similar reproductive cycle, although those species which overwinter as mated females (including *P. regius*) probably are able to delay egg-laying for several months.

The earliest peak maturation period is for *P. pulcherrimus*, in March and April. Maturation for *P. audax*, *P. princeps*, and *P. whitmani* is primarily May and June. *Phidippus borealis*, *P. insignarius*, and *P. pius* mature in June and July, while *P. clarus*, *P. purpuratus*, *P. putnami*, and *P. xerus* become adult in July and August. *Phidippus apacheanus* and *P. mystaceus* mature in September and October, while *P. cardinalis*, *P. otiosus*, and *P. regius* become adult from September through November.

The subtropical climate of peninsular Florida may have affected the reproductive periods of populations of three species. *Phidippus pulcherrimus* matures one to two months earlier than its northern sister species, *P. princeps*, perhaps due to earlier warm temperatures. Populations of *P. audax* exhibit summer and fall peaks of maturation as well as a spring peak; this is interpreted as increased survival of offspring from second and third eggsacs, which are maturing at different times than their older siblings. The longer growing period due to more warm days probably contributes to the success of the later offspring. Finally, P. regius has a second peak of maturation in the spring in south Florida, probably due to reasons similar to those stated above for P. audax. Unusual opportunities for interaction between species exist due to the atypical additional maturation dates of the above species, especially P. audax.

Recently, a few authors (e.g., Uetz, 1977) have noted that the larger of syntopic congeners matures and reproduces earlier in the year, so that the immature stages of the larger species are always larger than immatures of the smaller species, generally by a factor as large or larger than the ratio (1.28) proposed by Hutchinson (1959); presumably they utilize different sized prey. However, this generalization has been proposed for groups of genera (e.g., in lycosids, gnaphosids, and thomisids) which are restricted to a single microhabitat (leaf litter). The largest species of Phidippus (P. regius, P. otiosus) mature the latest in the year of any of the Florida species; the species of Phidippus are distributed unequally among several microhabitats. Apparently, competition for prey size is less critical than in the groups restricted to a single microhabitat.

Enemies

The most consistently observed predators of spiders are Pompilidae and Sphecidae (Table 10-4) which stock their burrows or mud nests with paralyzed spiders as food for the wasps' developing young. Phidippus species have been frequently reported as prey of both of the above groups, but in low numbers. Sphecids of the genus Trypargilum appear to specialize on vagrant spiders, especially salticids. In a collection

I made of nests of the mud-dauber *Trypargilum clavatum*, 78% of the 161 specimens collected were salticids (Appendix E). *Phidippus otiosus* was represented by 26 specimens, and *P. audax* by 2 specimens.

Mantispids are well known as spider egg predators, although they have been infrequently reported for salticids. In this study, *Mantispa viridis* was taken from eggsacs of several *Phidippus* species. The most severely affected was *P. clarus*, with *M. viridis* taken from 4 of the 26 field-collected eggsacs in this study. Three other *M. viridis* were taken in a sample of 20 eggsacs of *P. clarus* in an earlier study not included in the results presented here. Two *M. viridis* were taken from a single eggsac of *P. otiosus*. Figure 10-2 shows an *M. viridis* emergence.

Another group of egg predators were chloropids. Maggots of *Pseudogaurax signatus* (previously reported for web-weaving spiders; Eason et al., 1967) were found in 14 eggsacs of *P. clarus*, ranging from 3-18 per eggsac (average of 8). In one instance, 8 maggots and a specimen of *M. viridis* were found in the same eggsac. Another eggsac contained 2 maggots and a *M. viridis*. The maggots are considered predators because they destroyed several eggs apiece. Egg predators usually destroyed most of the eggs, leaving only 10-53 eggs (average of 20) to hatch into spiderlings.

Hymenopteran egg parasites of *Phidippus opifex* have been reported: *Tetrastichus phidippi* Burks (Eulophidae; Burks, 1963), *Arachnophaga picea* (Riley) (Eupelmidae: Howard, 1892), and *Idris saitidis* (Howard) (Scelionidae: Howard, 1890). Both Eupelmidae and Scelionidae of the same genera reported above were found in this study. An undetermined parasite that has not been collected is also reported, probably belonging to one of the above families. Eggsacs parasitized by this species have been found with the parasites already emerged; the eggs were hollowed out and a circular emergency hole was cut on one side. An eggsac of P. regius contained 101 parasitized eggs, and 1 infertile egg; an eggsac of P. otiosus had 73 parasitized eggs, 2 infertile eggs, and 24 young. No young survived in the P. clarus eggsac parasitized by Arachnophaga aldrichi.

A single dipteran parasitoid (Sarcophaga davidsonii Coquillett) has been reported on P. opifex by Coquillet (1892). Although Acroceridae are widely known as spider parasitoids (Schlinger, 1960; Eason et al., 1967) the report here of an as yet undetermined Ogcodes species emerging from a juvenile of P. princeps is only the second for the genus. Jackson (1976) reported an acrocerid emerging from a specimen of P. johnsoni.

I previously reported (Edwards, 1975) two species of fungi attacking P. otiosus and P. regius. A third fungus species, Gibellula leiopus, is now reported attacking P. audax.

Mermithid nematodes have been reported attacking other, usually terrestrial, spiders (e.g., lycosids; Eason, 1969). Two field-collected P. otiosus, an adult male and a subadult female, died in the laboratory when larval mermithids emerged from the spiders' abdomens. Since P. otiosus is arboreal and the life cycle of mermithids is closely tied to the soil, how these spiders became parasitized is open to speculation. Of all the species of Phidippus in this study, P. otiosus is the species I would have least likely suspected to be parasitized by mermithids, yet it is the only species from which this type of parasitoid was recovered.

Various vertebrate predators of Phidippus species have been reported in the literature. During the course of this study, the only evidence of vertebrate predation appeared to be on two eggsacs of

P. clarus, which were mostly missing due to the presence of a large circular hole in the middle, as though a bird's beak had pierced each eggsac. I report these as ?Aves in Table 10-4. Subsequent to my research, an immature *Phidippus* was taken from the stomach of an individual of the tree frog *Hyla cinerea* (A. Freed, personal communication).

Prey

Arthropods fed on by species of *Phidippus* belonged to the insect orders Odonata, Orthoptera, Hemiptera, Homoptera, Coleoptera, Lepidoptera, Diptera, and Hymenoptera; *Phidippus* species also fed on other spiders (Table 10-5). One of the 2 prey records for *P. apacheanus* was another spider, 17 of 94 records (18%) for *P. audax* were of other spiders, and 1 of 8 and 1 of 31 records were of spiders for *P. pulcherrimus* and *P. regius*, respectively. Spiders have also been reported as prey of *P. clarus* (Fitch, 1963; Tolbert, 1975). The percent predation on other spiders by *P. audax* compares favorably with that observed for *P. johnsoni* (11 of 33 records were of spiders; Jackson, 1977b). Jackson observed three instances of conspecific predation by *P. johnsoni* females on males. I also observed three instances of conspecific predation by *P. audax*, but they were by females on another female (1 record) and on subadult females (2 records). I did not observe conspecific predation by *P. audax* until the chironomid population was suddenly severely reduced in mid-August of 1976 at Burnt Pond; all three cases of conspecific predation were observed on the same day. Steve Tessler (personal communication) found eight cases of conspecific predation by *P. audax* females on other females on eaves of old buildings where females were making eggsacs. This suggests that competition for nesting sites was occurring.

Prey was distributed over several orders for those species of *Phidippus* for which more than a few records were available. Generally records were evenly distributed among prey orders, but a few instances of concentration on particular prey were noted. Chironomids constituted 55% of the recorded prey for *P. audax*, and 18% were other spiders which were also feeding primarily on chironomids. Nine records (10%) of prey captured by *P. audax* were of the cantharid *Chauliognathus marginatus*. Smaller immatures of *P. regius* tended to feed on nematoceran and acalypterate Diptera (26%), while subadults and adults tended to feed on adult and larval Lepidoptera, large Hemiptera, and large Orthoptera (55%). One interesting record was of an adult male *P. regius* feeding on an adult of *Diaprepes abbreviatus*, a weevil pest of citrus and sugar cane.

Predation of the chironomid *Glyptotendipes paripes* was recorded for *P. clarus*, *P. otiosus*, *P. pulcherrimus*, and *P. regius*, as well as by the salticids *Dendryphantes marginatus* and *Metaphidippus galathea* (Appendix F), in numbers approximately proportional to the relative abundances of these species in lake edge habitats. Webs of the various orb-weaving spiders, especially *Tetragnatha* species, captured many thousands of this same chironomid.

Prey size was significantly correlated with spider size in terms of both weight and length. Figures 10-3 and 10-4 illustrate and compare these correlations for *P. audax* and *P. regius*; prey of both species was represented by a substantial sample size. Prey of *P. regius* increased in size to a greater extent than did prey of *P. audax* as spider size increased; this reflects both a difference in types of prey taken by the two species, and the larger ultimate size of *P. regius*. For the species with smaller sample sizes, *P. clarus* (n=4) showed very high correlations with both weight (r=.996) and length (r=.997); *P. pulcherrimus* (n=7) showed significant correlation with length (r=.795) but not with weight. The other species did not show significant correlations with either length or weight.

Reproduction

Isolated observations of egg clutch size (see Background) have been observed for several species of *Phidippus*, but no systematic comparison has been made. In Table 10-6, I compare species of *Phidippus* for known clutch sizes and number of clutches using a combination of field-collected and laboratory data. Some unusually high infertility rates may be due to dessication under laboratory conditions. Data for *P. insignarius* and *P. purpuratus* are drawn from literature records, and included for comparative purposes.

Calculating reproductive potential is difficult since for most species, number of clutches and clutch size are poorly known. In this study, reasonable estimates of reproductive potential are available for *P. audax*, *P. clarus*, *P. otiosus*, and *P. regius*; the reproductive capacities of *P. pulcherrimus*, *P. whitmani*, and *P. xerus* are probably fairly accurately indicated as well. Assuming females produce the maximum number of eggsacs observed for a particular species, the mean (and maximum) reproductive capacities were 245 (292) for *P. audax*, 358 (555) for *P. clarus*, 350 (673) for *P. otiosus*, and 402 (715) for *P. regius*; for the smaller species, reproductive capacities were 59 (61) for *P. pulcherrimus*, 95 (121) for *P. whitmani*, and 47 (48) for *P. xerus*. The mean for *P. audax* compares well with means from different populations of *P. audax* bred in the laboratory by Taylor and Peck (1975); the results for *P. whitmani* match the single observation reported by Kaston (1948).

Since good estimates of the reproductive capacities of all species of Phidippus under study could not be made, I compared clutch size of the first eggsac among species. Significant differences (Table 10-6) in clutch size were found among species, indicating that larger species had larger clutches. A significant correlation between mean clutch size of the first eggsac and mean length of females provided corroboration (r=.815) (Figure 10-5; Florida records for P. clarus ommitted).

The only species which did not fit the correlation pattern between body size and clutch size was P. clarus. Inclusion of the data for P. clarus from Florida in the correlation analysis disrupted the correlation so that it was not significant (r=.547). However, when I substituted the clutch size (75 eggs) observed for a P. clarus female in Connecticut (Kaston, 1948), the correlation was hardly affected (r=.811). This anomaly suggests that the reproductive rates of P. clarus in Florida have been adjusted due to some evolutionarily significant pressure. This pressure is almost certainly from egg predators and parasites; 14 of 24 eggsacs of P. clarus in this study were attacked by arthropod egg predators and parasites. While egg parasites destroyed most or all of the eggs within an invaded eggsac, eggsacs attacked by egg predators almost always had at least 10% and up to 33% survival and emergence of spiderlings, whether the egg predators were mantispids, maggots, or both. This is significant theoretically, because the egg predators do not appear to be maximally exploiting a limited resource as they would be expected to do. For some unknown reason, the maximum number of eggs eaten is less than available. While one present theory would suggest that parasitism could be combated by producing more and smaller eggs, the smae strategy would be useless against egg predators, as the same amount of energy would be available. On the other hand, if the egg predators have an upper limit to eggs eaten, a female P. clarus could produce fewer eggsacs with more normal-sized eggs per eggsac, which would increase the number of young surviving egg predation; at the same time, the females would be expending more energy per eggsac, which would adversely affect the number of eggsacs they could produce. This hypothesis may explain the phenomena discussed in the following paragraphs.

Two females of P. clarus, which had their first eggsacs mostly destroyed by a combination of maggots and mantispids, made two and one subsequent eggsacs, respectively, in the laboratory, with surprising results. One female laid 247 eggs in the second eggsac and 168 eggs in the third eggsac (415 total) and the other female made a second eggsac which contained 247 young and 44 infertile eggs (291 total). The first total exceeds the mean reproductive capacity (for 3 eggsacs) for Florida females not affected by parasites, and the second total is nearly equal the maximum number of eggs reported for a first clutch of P. clarus. The number of eggs was over twice that for second or third eggsacs, respectively, made by females whose first eggsacs were not preyed upon.

Two conclusions are suggested from egg clutch size of P. clarus in Florida: 1) clutch sizes have been significantly increased due to pressure from egg predators and parasites, and 2) under the proper conditions (i.e., if sufficient food is acquired after destruction of the first eggsac), females can totally replace their normal reproductive output. This suggests that females rarely reproduce to their full potential, for which explanations must be sought. One obvious answer is that they starve to death first: in almost every case, a P. clarus female collected with her first eggsac had a severely shrunken abdomen; a few were found dead in the eggsac. I have only a few records of P. clarus making a second eggsac in the field in late fall. One observation which may be an alternate reproductive strategy was of a *P. clarus* female at Burnt Pond, with an eggsac on a dogfennel which I could see had fly pupae in it. When I returned a week later, this eggsac was abandoned, and what appeared to be the same female had constructed another eggsac in another dogfennel about a meter away. Upon examining the first eggsac, I found two fly pupae and about ten spiderlings.

I have observed the phenomenon of premature death for every one of the smaller species I have kept which produced eggsacs in the laboratory: *P. princeps*, *P. pulcherrimus*, *P. putnami*, *P. whitmani*, and *P. xerus*. The females will catch and eat prey if it approaches the opening to the nest, but they will rarely leave the nest to catch prey. Most wild females do not have the body reserves left to produce another eggsac, and few have the stregnth to hunt in order to replenish the reserves, so they starve to death. I have observed this to some extent in the larger species, also, such as *P. audax* and *P. regius*, but not on the first eggsac. In the field, I have found abandoned eggsacs of *P. audax*, *P. regius*, and *P. putnami* which still contained as yet undispersed first instar spiderlings.

Other questions about the reproduction of *P. clarus* remain unanswered. The first one concerns the exposed placement of the eggsac. Possibly competition with other species for nesting sites in the past history of *P. clarus* was responsible for the present choice of nesting sites. However, instead of competing (and losing) for better nesting sites, *P. clarus* may have followed the line of least resistance by making its eggsacs in a place and manner similar to its molting nests. Immatures of several species make silken shelters and molting nests in herbaceous plants; *P. clarus* may be best adapted to using these particular plants for nests during their reproductive season.

The second question, concerning P. clarus in particular and not only other Phidippus but other spiders in general which remain with the eggsac until the young hatch: Why is there such a high parasite and predation rate on the eggs? Most earlier researchers have presumed that the females primary function is to guard the eggs from predators and parasites; this function may work well against transient arthropod predators, e.g., coccinellids, but apparently females are somewhat ineffective at protecting the eggs from specialized predators and parasites. Evidence from two sources indicates another primary function for egg-guarding females. Eason (1964) reported that female wolf spiders take extremely good care of their eggsacs, mending holes cut or torn in the eggsac; the females even must open the eggsac so the young can emerge, a phenomenon known only for wolf spiders. I have noted previously (Edwards, 1975) that eggsacs of P. regius from which females were removed failed to hatch due to dessication. Both of these examples imply that one of the primary functions of parental care is to prevent the eggs from dessicating. This would explain in proximate terms why Phidippus females must stay with the eggs until they hatch, and explain why females often do not survive their first eggsac; after undergoing the energetically expensive construction of the eggsac and egg laying, the females must protect the eggs from dessication (by periodically adding more silk; apparently silk loses its water retention properties with time) for about two weeks until the eggs hatch. Females usually stay with the postembryos until they molt to first instars, another 10-14 days. By this time the female has gone without food for nearly a month, and her energy reserves are about spent. The ultimate causes of this reproductive strategy may be related to the life style of these spiders. Probably since webs are not used in prey capture, the spiders have not evolved the capacity for producing the elaborate eggsacs found in some of the araneids and theridiids; therefore the salticids would seem to have substituted time expenditure to compensate for their lack of specialized silk, even though they probably expend the maximal amount of silk available.

Generalities about expected reproduction by field populations can be made by considering each species' phenology, size, and known clutch production. Smaller species and species in more temperate areas would be expected to produce no more than two eggsacs due to either small reproductive capacities or seasonal limitations. Larger species, and species with high reproductive capacities that begin reproducing relatively early in the year in warmer climates, would be expected to produce as many as three eggsacs.

Populations

Prey populations. Prey were no where near as numerous in other habitats as they were in lake edge habitats. As expected, spider populations were also lower in non-lake edge habitats.

Spider populations. With the exception of the lake edge habitats, where populations were estimated in July, and the pine flatwoods habitat, where populations of *P. pulcherrimus* were readily followed (Figure 10-6), data on pupulations of species over time was inconclusive. I found only a few first instars for any species; *P. pulcherrimus* was best represented for this stage. I found a single *P. apacheanus* first instar on the ground, and the same stage for other species was usually found in very low herbaceous vegetation or near ground level on taller vegetation. The grasses *Echinochloa* and *Sacciolepis* along the edges of lakes have elongate decumbent stems; the dense growth of these grasses provides a distinct microhabitat with greater humidity than the higher parts of the plant. At Burnt Pond, I found Habrocestum bufoides Chamberlin and Ivie, a species characteristic of mesophytic forest litter, on the ground under the decumbent stems. Probably the youngest instars of P. audax were in this microhabitat; I did observe a few sitting on top of the decumbent part of the plant stems. However, it was impossible to observe directly in this microhabitat, and sampling would have been extremely difficult for a number of reasons. For several species, more adults were observed than were subadults; this is probably due to the relative ease of finding females in nesting sites for some species. Rather than trying to estimate population sizes where biases in sampling indicated more older stages than younger stages, I used comparisons of absolute numbers of individuals observed during the total research period to give comparative relative abundances for use in measures of, e.g., niche breadth. Table 10-7 gives the numbers of each species found in primary and secondary study habitats.

Discounting the anomalies presented by low numbers of first instars and high numbers of adults, general population trends can be presented. As expected, population sizes (with the exception of P. audax) decreased with increased age of spiderlings. A noticeable drop occurred in P. pulcherrimus after the fourth instar. This corresponds well with the instars (third through fifth) of P. otiosus taken by Trypargilum clavatum (Appendix E), and indicates that these stages may be severely affected by mud dauber predation. All stages of P. audax from the fourth instar and older were numerous in the lake edge habitats. Populations of all species seemed to remain fairly constant from year to year; the only changes were the addition or subtraction of species due to plant successional stages. Certain species were associated with plant successional stages, but this is discussed later (See Species Summaries). The only significant change in population numbers that I have observed over several years of collecting and observation was the Newnan's Lake population of *P. audax*, which was severely reduced following a rise in the water level of the lake, flooding most of the study area. The population of *P. otiosus*, a canopy species in the same area, was unaffected.

Field Behaviors

Ambush hunting. This sit-and-wait hunting strategy was observed in use by individuals of *P. apacheanus*, *P. audax*, *P. cardinalis*, *P. clarus*, *P. otiosus*, *P. pulcherrimus*, and *P. regius*. Typically, the spider would sit facing the ground on the main stem (or occasionally a large side stem) on tall grass, herbs or small shrubs, a few cm below the top of the plant (often under a flower or leaf petiole). Here the spider would sit motionless (for a few min. to three hours), unless a movement by another arthropod attracted its attention. Apparently the spider would scan the area below its position; arthropods moving below could be observed and analyzed as potential prey. Once I observed a female *P. audax* waiting near the top of an *Echinochloa* stem; it spotted a subadult conspecific moving through the vegetation below; it rapidly stalked down the stem to about two cm above the subadult, which was unaware of the female approaching from above; the female leaped on and killed the subadult.

Ambush hunting by *P. otiosus* is of a slightly different form, since it occurs in a horizontal rather than vertical plane. Individuals of *P. otiosus* were observed, especially at Newnan's Lake, to wait at the ends of branches at the periphery of a tree canopy, presumably waiting for insects to land on the outer edge of the canopy. Often an individual would be on the underside of an upper leaf in a clump of leaves at the end of a branch, where it could survey the leaves below it without being seen itself. In this respect, *P. otiosus* was like the other *Phidippus* species, which also observed strata below their own position.

Search hunting. The basic search behavior has been well described by Hill (1978) for *Dendryphantes marginatus* (a close relative of the genus *Phidippus*), and is applicable both to individuals hunting for prey, and to males searching for females. To summarize, a spider moves out side branches and explores both upper and lower surfaces of leaves, frequently stopping to visually scan the surrounding area, and orienting toward any nearby movement. The front legs are often waved around as if testing the air; laboratory observations by Forster (1977a) indicate that jumping spiders may be able to pick up nearby airborne vibrations caused by vibrating insect wings.

Agonistic encounters. I observed two equal-sized males of *P. audax* engage in a wrestling match on a *Sacciolepis* leaf at Newnan's Lake. The males locked chelicerae and pushed and pulled on each other with their legs for 10 min. Finally, they fell off the leaf and were separated by the force of the fall, after which fighting was not resumed and they separated. Why males should fight under such conditions is not clear, unless in localized populations, peck orders are set up among males, as was shown experimentally by Richman (1977) for the salticid *Corythalia canosa*. Smaller males usually flee from or only briefly challenge larger males when encounters occur while searching for females, but equal-sized males apparently reach more advanced stages of encounter before determining which is dominant. When a male locates a female, fighting with another male for possession of mating rights to the female is more readily understood. I observed a 40 min. fight between two equal-sized males of *Dendryphantes marginatus*; one of the males had been cohabiting with an immature female which appeared to be too young to be in the penultimate stage; this male eventually drove the other male away in a seesaw battle in which one and then the other appeared to be winning. Snetsinger (1955) observed a small male of *P. clarus* cohabiting with a female to successfully drive away a larger male which approached the nest.

Courtship and cohabitation. On several occasions at Newnan's Lake I observed *P. audax* males courting hunting females; however, only one of these males was observed to be successful. On the other hand, I observed two instances of cohabitation for *P. audax*, six instances for *P. regius* (one was with an obviously gravid female, not a penultimate female; on another occasion, two males were cohabiting with the same female, one in the usual adjacent cell made over the females nest, and another which had made a new nest 2 cm away), and two instances for *P. otiosus*. Hill (1978) reports four instances of cohabitation in *P. otiosus* observed by John A. Anderson, and Snetsinger (1955) reported cohabitation for both *P. clarus* and *P. audax*. Jackson (1977a) reported cohabitation for *P. johnsoni*.

As already noted in Chapter 4, John Anderson observed a mating between a *P. otiosus* male and a *P. regius* female. I observed a *P. clarus* male courting a *P. audax* female at Burnt Pond from a distance of 40-50 cm. Initially, each spider was on a separate herb, but the male, upon spotting the female, went down the stem of the plant it was on, across a grass blade, up the stem of the plant the female was on, and out on a side stem of that plant where the female was perched (total distance traversed was about 86 cm). The female watched the entire approach of the male. The male began courting when about 12 cm from the female, but the female backed away on the stem; the male moved forward to about 12 cm distance and again displayed, then advanced forward to where he could almost touch the female; the female backed away again; the male followed, but the female turned and jumped off the plant, ending the encounter. The male looked around in several directions, but not finding the female, turned and went back down the plant. Gardner (1965) reported males of other *Phidippus* species courting females of different species, but Snetsinger (1955) reported that individuals of *P. audax* and *P. clarus* gave each other scarcely more than passing notice when encounters occurred in the field. The above encounter occurred in mid-August, when females of *P. audax* would normally be nesting, but, as noted earlier (see Phenology), adults of *P. audax* occur throughout most of the year in peninsular Florida, creating additional opportunities for non-specific encounters.

Nesting. Almost all eggsacs of *P. otiosus* and *P. regius* were taken under either pine or oak bark. One *P. regius* female made a nest on the outside of the trunk of a young pine sapling, and another was found with an eggsac inside a hollow pole. Sometimes several *P. otiosus* females would make nests under the bark of a lightning-struck pine. A few *P. otiosus* were found nesting under frond petiole remnants on trunks of cabbage palms. One *P. otiosus* female made an eggsac on the top of a cabbage palm frond, as did a *P. audax* female. Other *P. audax* females were found nesting in rolled *Rubus* leaves, and one female had a nest in the top of a cattail seed head. This latter case was extraordinary, as the *P. audax* female's eggsac (which contained first instars nearly ready to emerge when observed) was right next to a *P. clarus* female's nest (which had eggs; probably this female's second eggsac). The two eggsacs were nearly touching, and I cannot believe that these females were not aware of each other's presence; neither can I explain why the close proximity of the other's eggsac was tolerated. Other females of *P. clarus* usually made their eggsacs in the tops of *Eupatorium*, *Solidago* and *Boehmeria*.

Few records of eggsacs of other species were noted in the field. A *P. apacheanus* female was found with an eggsac under oak bark. Two eggsacs of *P. putnami* containing postembryos and first instars were found on rosemary and in the curled tip of a saw palmetto frond, respectively, but the female had already left the eggsac in each case. A *P. xerus* female was found with an eggsac deep in the folds of a newly emerging saw palmetto frond. Two females of *P. cardinalis* were collected under hickory bark by D. B. Richman and J. Reiskind; one female later produced an eggsac in the laboratory. Jon Reiskind also collected a female *P. pulcherrimus* with an eggsac in a rolled sweet gum leaf. Kaston (1948) reported a *P. whitmani* female nesting in a rolled leaf on the ground.

Based on field records of eggsacs and first appearance of 1st instars, species of *Phidippus* appear to lay eggs in the following range of months: *P. apacheanus* (December to May), *P. audax* (primarily May to August; probably year round in peninsular Florida), *P. cardinalis* (February to May), *P. clarus* (August to November), *P. insignarius* (August to September), *P. mystaceus* (October to May), *P. otiosus* (January to June), *P. pius* (August), *P. princeps* (May to July), *P. pulcherrimus* (April to July), *P. putnami* (August to October), *P. regius* (mostly October to June in north Florida, probably March to September in south Florida), *P. whitmani* (May to August), and *P. xerus* (August to September).

Shelter. Individuals of *P. audax*, *P. clarus*, *P. otiosus*, *P. pulcherrimus*, *P. regius*, and *P. xerus* were observed to have built thin-walled silken retreats in which to spend the night. Spiders could be easily seen through the silk of these nests, which were built in rolled leaves or the tops of grasses and herbs, frequently in seed heads or flower umbels. I occasionally observed adults of *P. audax*, *P. otiosus*, and *P. regius* spend the night in shelters without spinning silken retreats, e.g., in hollow spaces under bark. I also observed the very thickly-woven molting nests of immatures of the above species, and observed individuals of *P. audax* and *P. pulcherrimus* on *Tradescantia* to make short hunting sorties of a few cm from their molting nests after molting,and then returning to the nest with prey. Tessler (personal communication) found *P. audax* to repeatedly use the same nests on wild carrot, and Jackson (1979) reported marked individuals of *P. johnsoni* in the field to make excursions as far as 1.2 m and return to the nest.

Territoriality. I marked 13 females of *P. regius* on 11 cabbage palms in a study of territoriality near Burnt Pond. Palms ranged from 1.6-3.1 m in height, and were either isolated (#3, 6, 7, 9, 10), associated with other palms (#2, 8), associated with shrubs (#4, 5), or associated with other types of trees (#1, 11). The palms approximately ringed the experimental area, beginning with palm #1 on the west side and moving counterclockwise to palm #10 on the northwest corner. Palm #11 was in the southeast corner. Female *P. regius* were usually found in nests on the youngest fully-developed fronds, in the center of the palm. On Oct. 13, 1976, I marked females (F) 1-5 and correspondingly marked the palms they were on. On Oct. 20, I rechecked these five palms: F-1 had been replaced by another female, which I marked and designated as F-1'; F-2 was missing; both F-3 and F-5 were on palm #3; and F-4 was

was missing. On this same date I marked females 6-10 and their corresponding palms, and I noted a cohabiting pair (male and penultimate female) in a palm near palm #1. On Oct. 27, F-1' was still on palm #1, F-5 was on palm #4, and F-10 was on palm #8; all other females were missing and all other palms were unoccupied. On Nov. 3, F-1' was on palm #1, and all other palms were unoccupied; I did find a new female on a palm which I had observed to have four unoccupied retreats on an earlier date. I marked both female and palm as #11. On Nov. 10, F-1' was still on palm #1, but all other palms were unoccupied; the same was observed on Jan. 14, 1977. On Jan. 28, F-1' was missing also.

The following conclusions can be made: 1) most females were transient, staying on a palm less than a week, 2) a few females stayed in the vicinity of one or a few palms for over a week; F-3 was on palm #3 for two consecutive weeks, F-10 was on palm #10 and the nearby palm #8 on consecutive weeks, and F-5 was on the closely spaced palms #3, 5, and 4 on three consecutive weeks, 3) a female may remain on a palm for a prolonged period of time; in this study, F-1' was on the same palm on all but the first and last observation days, and was on the palm a minimum of 56 days. Palm #1 was about 2.1 m in height and was clumped with a pine tree about 4.3 m high; the combination of the two plants may have provided a sufficient combination of shelter and foraging area for the spider to remain. A female with this combination of resources may actively exclude other individuals, and in effect establish a territory, using the palm as home base for excursions into the surrounding vegetation.

The cohabiting pair remained together through Nov. 10, a minimum of 21 days, but on Dec. 9, only the female was present (designated female and palm #12), presumably the same female which had finally matured and mated (I made this assumption because the penultimate female of the cohabiting pair was smaller than normal, and the adult female on the same palm on Dec. 9 was also small and of similar color. This female still was present on the same palm on Jan. 14; total time on the same palm, including the penultimate stage, was at least 92 days, and in the adult stage at least 36 days. A second smaller palm was clumped with palm #12.

Abiotic Factors

Temperature and humidity. I took measurements of temperature and relative humidity every two hours on days of observations in primary study habitats. Daily trends were a rise in temperature in the afternoon accompanied by a decrease in relative humidity. Only three observations seemed noteworthy in respect to these factors. First, of the two types of hunting strategies employed by species of *Phidippus*, the ambush strategy was used most often during the middle of the day by species in exposed habitats. This reduced activity pattern corresponds with peaks of daily temperature. Anderson (1970) reported peak oxygen consumption rates for *P. regius* in a laboratory experiment to be during mid-morning and late afternoon, which corresponds with field activity patterns of search hunting during warm (20-30° C) but not hot temperature periods. Second, at Burnt Pond I noted increased search hunting during early and mid-afternoon on overcast days; temperatures remained moderate and relative humidity was higher on these days. Third, I did not observe hunting for any species at temperatures less than 18° C, except for *P. pulcherrimus* in pine flatwoods (a habitat relatively protected from weather effects, e.g., wind chill), where I observed individuals hunting in temperatures as low as 15°C, and I obtained one prey record (an ichneumon wasp) for this species at this temperature. An interesting comparison can be made between individuals of *Dendryphantes* (*Eris*) *marginatus* at Burnt Pond, which had essentially the same type of activity patterns as *P. audax* in the same habitat, and *D. marginatus* in Oregon (Hill, 1978) which was most active during the mid-day heat (20°C) in that locality. The *D. marginatus* at Burnt Pond were most active during the moderate temperature range periods (mid-morning and late afternoon); the Oregon population was most active during the same temperature range, but this temperature occurred in mid-afternoon in Oregon. Mid-afternoon in Florida is too hot during the summer months, and activity is reduced.

Wind. Spiders were very difficult to observe or collect by sweeping on days when the wind was blowing consistently at approximately 15 mph or higher. Spiders mostly remain in shelters or cling tightly to the plant substrate under such conditions. Activity by both insects and spiders is probably reduced due to the precarious footing on plants moving back and forth; the constant plant movement probably also reduces the spider's ability to visually evaluate the surrounding area.

Light intensity. Individuals of *P. audax*, *P. clarus*, and *P. regius* were all observed to begin making resting nests about an hour before sunset. Although I did not measure light intensity, it seems likely that this is an important factor, since *Phidippus* cannot see in the dark (Jackson, 1977a).

Resource Analysis

The niche has been defined in a variety of ways, but most modern ecologists accept Hutchinson's (1957) definition of the niche as an n-dimensional hypervolume (Price, 1975). I analyzed six dimensions: habitats, microhabitats associated with hunting behavior, microhabitats associated with eggsac construction, prey (type and size), time of year in relation to size of individuals, and time of year in regard to mating season. Ten of the thirteen species of Phidippus known to occur in Florida (P. mystaceus, P. pius, and P. purpuratus were omitted due to insufficient data) were analyzed; a total of 45 pair-wise comparisons of species were possible. Where data for a particular niche dimension were lacking (i.e., prey or eggsac construction site), only remaining niche dimensions were compared for that species pair. All age groups are included in comparisons.

Species-specific diversity (β) of resource used was measured using Levins' (1968) niche breadth formula:

$$\log \beta = - \sum_{i}^{s} p_i \log p_i$$

where P_i is the proportion of a species which occupies or uses the discrete state i of a particular resource dimension.

Species overlap in resource utilization (α_{jk}) was calculated for each niche dimension using the method proposed by Pianka (1974):

$$\alpha_{jk} = \frac{\sum_{i}^{n} P_{ij} P_{ik}}{\sqrt{\sum_{i}^{n} P_{ij}^2 \sum_{i}^{n} P_{ik}}}$$

where P_{ij} and P_{ik} represent the proportions of resource i used by species j and k.

Estimating overall niche overlap is difficult since, although resources may be discrete, animals integrate resource use over space and time (Pianka, 1974; May, 1976). Cody (1974) measured overall multidimensional utilization in two ways, product alpha and summation alpha. Product alpha (product of overlap values of each niche dimension) is the best estimator when niche dimensions are completely independent; it is calculated

$$\alpha_{jk} = \prod^{n} (\alpha_{jk}R)$$

where $\alpha_{jk}R$ is the total niche overlap of species j on species k for n niche dimensions.

Where niche dimensions are entirely dependent the best estimator of overall overlap is summation alpha (arithmetic mean of the overlaps for all component dimensions), which is calculated

$$\alpha_{jk} = \frac{\sum^{n} (\alpha_{jk}R)}{n}$$

where $\alpha_{jk}R$ and n are as above. The true measure of overall niche overlap should fall somewhere between the values calculated by product alpha and summation alpha.

In most cases, summation alpha appears to be a better estimator of overall niche overlap for species of Phidippus, since the niche dimensions analyzed are dependent to some extent. Habitat will determine the number of available microhabitats for hunting and egg laying, and mating season and prey size are dependent on body size to some extent. Product alpha will be a good estimator when it is zero because of no overlap in habitat. Non-zero product alpha may be useful in comparing resource utilization for species which do not overlap in habitat.

Habitat

In the past, resource analysis comparisons have been made in single microhabitats (e.g., litter; Uetz, 1975), single communities (e.g., field; Turner and Polis, 1979), or between similar communities (e.g., deserts; Pianka, 1974); however, organisms with similar ecological requirements may or may not exploit similar types of resources in different habitats.

Based on an earlier discussion (see Results and Discussion), I consider the habitat(s) occupied by a species as a measure of its range of abiotic tolerance. Although one could argue that habitat limitations are really an expression of the realized niche based on competition for particular resources within a habitat, I have found no supporting evidence to substantiate this argument. On the contrary, where one might expect habitat overlap to occur in the absence of competitors in a particular microhabitat (e.g., *P. whitmani* on litter), overlap does not occur.

To analyze species diversity by habitat, I employed H', the Shannon-Weaver Index (Shannon, 1948). As a measure of species evenness within a habitat, I used J' (Lloyd et al., 1968). Only the primary and secondary study habitats were considered for analysis, except for the data for *P. whitmani* from San Felasco Hammock, which is included for comparative purposes.

Species diversity (H') and species evenness (J') were both greatest in xerophytic habitats (Table 10-7); each habitat supported six species, the species composition differing with the amount of canopy. No species was particularly numerous, but *P. apacheanus* and *P. xerus* were restricted to these habitats and appeared to be the dominant species in the timbered scrub field. Species diversity may be high due to the poor nutrient content of the soil in scrub habitats (Laessle, 1942). Low nutrient supply has been hypothesized as a factor in increased species packing due to greater niche segregation in plants (Woodwell, 1974); presumably this situation would be favorable to increased species packing at higher trophic levels.

Where a particular resource is excessively available, dominance by one or a few species best able to exploit that resource is expected (Patrick and Strawbridge, 1963). In the two habitats where food was unlimited (Burnt Pond and Newnan's Lake), *P. audax* was clearly dominant, and species evenness was low, although species diversity was moderately high in the non-canopy-affected habitat (Burnt Pond). In the absence of direct data, indirect data can be used: *P. regius* was clearly dominant in the transition habitat dominated by palms, whereas *P. clarus* was dominant in the old field community. Odum (1969) has shown that net community production is high in the early stages of a plant community; low species diversity would be expected in such a community (e.g., old field). On the other hand, Odum (1969) has shown that in mature plant communities, the net community production is low and available energy is primarily associated with detritus. Although only one species of *Phidippus* (*P. whitmani*) occurs in mature forests, it occurs on the litter as predicted. The lack of intrageneric diversity of *Phidippus* species in this habitat may be due to the fact that the genus as a whole seems to be more xeric-adapted, or it could be because *P. whitmani* is near the top of the food web in its trophic level, since it is one of the largest of a diverse assemblage of litter spiders (Drew, 1967; Berry, 1970), possibly precluding the presence of a similar competitor. The pine flatwoods habitat was clearly dominated by *P. pulcherrimus*; as with *P. regius*, the primary indicator was association with a particular microhabitat, in this case the shrub understory.

Microhabitat

Distribution of species of *Phidippus* by microhabitat has been discussed earlier (see Results and Discussion and Table 10-3). For purposes of analysis, I lumped all age groups (Table 10-8) within a microhabitat; the dominance of *P. whitmani* on litter, *P. audax* and *P. clarus* on grasses and herbs, *P. pulcherrimus* on shrubs, *P. regius* on palms, and *P. otiosus* on other trees was further emphasized.

Site of Eggsac Construction

Data on what microhabitats were utilized for eggsac construction were limited for most species (Table 10-9). Woody perennials were primarily used by *P. clarus*, which made a conspicuous white eggsac in the tops of the plants by tying together several of the top leaves. Both *P. otiosus* and *P. regius* utilized spaces under dead tree bark as their primary eggsac construction site.

Prey

In order to analyze types of prey captured, I lumped prey categories into orders (Table 10-10). As a rule, the greater the sample size of numbers of prey taken by a particular species of *Phidippus*, the greater the number of prey categories were represented. All nine orders of observed prey were taken by *P. audax*, which had the highest sample size for captured prey. As noted earlier, *P. audax* showed a decided preference for chironomids and other spiders, in that order; these were the two most numerous categories of available prey in the lake edge habitats frequented by *P. audax*, indicating that this species will feed proportionately on more numerous prey types. Also, it was clear from the size of the spider populations that high prey density attracted a large number of predators. This agrees with the observations of Turnbull (1964) on a web spider, in that spiders will move toward a higher prey density. Since *P. audax* is by far the most frequently observed species of *Phidippus* in agro-ecosystems (e.g., Whitcomb et al., 1963; LeSar and Unzicker, 1978), its ability to respond in a functional manner to high prey densities by both locating and feeding proportionally on them can make it a valuable controlling factor on pest populations. Other spiders are probably capable of similar responses.

Adult size

When only Florida records were considered, adult females of *P. regius* and *P. otiosus* were significantly larger than adult females of the other species studied (Table 10-11). Adult males were smaller than females. Males were more diverse in their size differences among species, but for the purposes of this study, these differences were not considered important. Since in most cases the species of *Phidippus* are similar in size (based on female size), this factor need not be analyzed with respect to resource utilization. In cases of high overall niche overlap between compared pairs of species, size differences can be used to explain coexistence of two species if one of the compared species is either *P. otiosus* or *P. regius*.

Female Phenology

The distribution in time of adult females is an indicator of when and for how long they reproduce (Table 10-12). The longer the active reproductive period, the greater the number of eggsacs produced, resulting in a greater distribution of age and size classes for a particular species at a particular time. This can be important if species normally subdivide resources on an allochronic basis, which would maintain a size differential between the species involved. If one species maintains a wide distribution of age and size classes throughout the year, other species utilizing the same resources will be directly competing with at least a portion of the population of the more widely age-distributed species. Both *P. regius* and especially *P. audax* maintain a wide diversity of age classes at any one time period. In the case of *P. audax*, this diversity may in part explain the dominance of this species in the lake edge habitats.

Male Phenology

The distribution in time of adult males is closely associated with the mating season for each species (Table 10-13). Since males will court non-conspecific females, and are sometimes successful in mating with them, the time when males are present in relation to females of other species could be an important factor in the development of allochronic isolation of syntopic species. Males of all species except *P. audax* and *P. regius* exhibited single distinct seasonal peaks of maturation and subsequent mating.

Niche Breadth

Niche breadth values for the six niche dimensions are listed in Table 10-14. Several species showed low values for habitat, indicating they were habitat restricted. Both P. apacheanus and P. whitmani were restricted to a single habitat in this study, and P. xerus, P. pulcherrimus, and P. audax also demonstrated low niche breadth values. Higher values were found for P. regius and P. putnami, indicating they were more generalists for habitat; the other species had intermediate values.

Low microhabitat values were found for most of the species, indicating that specialization for microhabitat may be one of the most important factors isolating syntopic species. Only P. regius appeared to be a generalist for microhabitat; the high flexibility of this species probably accounts for its frequency of occurrence on man-made structures. Extreme specialization was found for P. whitmani on litter and P. putnami on shrubs.

Prey niche breadth values were moderate to high; generally the higher the sample size, the higher the value. Prey type is not considered to be an important factor in resource utilization, since all the species appear to be generalists. However, prey size is significantly correlated with spider size in most cases (see Results and Discussion); therefore seasonal size of spider is important since spiders of the same size will capture similar-sized prey.

All species are fairly specific as to microhabitats in which they make their eggsacs.

Niche breadth values for distribution of females and hence size range of immatures was moderate for most, very high for P. audax and P. regius (indicating a wide range of age and size classes present at any one time), and low for _P. putnami_ and _P. pulcherrimus_ (which are frequently syntopic but allochronic, and in the same microhabitat).

All species except _P. audax_ and _P. regius_ had low to moderately low niche breadth values for mating season, with considerable allochrony between syntopic species. In accord with their high seasonal niche breadth of adult females and immature, values for mating season of _P. audax_ and _P. regius_ were also high.

Niche Overlap

Confidence in data comparison. I arbitrarily set a minimum of overlap of two categories between species for any single niche dimension as an indicator of the amount of confidence I had in the resultant comparison between any two species for that particular niche dimension. I based this minimum on two factors: 1) the amount of data available for a species for a particular niche dimension usually affected the number of categories represented in that niche dimension, and 2) a minimum of two category comparisons was necessary in order to obtain a statistically useful number. In those cases where one or both of a compared species pair was represented by only one category, overlap was represented by (1.0), and non-overlap was represented by 0. Where two or more categories could be compared between species, complete overlap is represented by 1.000, complete non-overlap by 0.000. The only major exception was habitat overlap of any other species with _P. whitmani_, which was indicated by a 0 since only one habitat containing _P. whitmani_ was included in the comparisons, but in this case is probably a true measure of non-overlap. Data sets giving values of 1.0 and 0 would probably be reduced or increased, respectively, with large sample sizes for that niche dimension, affecting overall niche overlap values to some extent (although probably not a significant amount in most instances).

Summation alpha. For the 45 pair-wise comparisons of 10 species of *Phidippus* (Table 10-15), summation alpha gave mostly moderate to high values of overall niche overlap. Mean summation alpha was 0.611 and only 5 comparisons had a value less than 0.4. Considering the close similarities and relationship of the species under study, and the interdependence of the niche dimensions examined, this result was not unexpected. The mean niche overlap for species of *Phidippus* using six niche dimensions was 33% higher than found by Turner and Polis (1979) for a guild of ambushing spiders, which included non-related species, using only four niche dimensions.

Non-zero product alpha. This measure of niche overlap is probably of limited usefulness in this study. It may serve as a measure of similarity of resource utilization for those niche dimensions which overlap between two species when there is no overlap of one or more niche dimensions. For example, two species could have identical requirements in all other niche dimensions as long as they had no habitat overlap.

Product alpha. Overall niche overlap of one species on another may in some cases be accurately assessed by product alpha. This is especially true when the confidence is high that niche overlap of at least one niche dimension is zero, and most important if a zero value is due to non-overlap of habitat. Where all six niche dimensions are represented by non-zero values, and the overall niche overlap of a more specialized species by a more generalized species is high, product alpha may be a reasonable measure of the reciprocal relationship between the two species, i.e., the amount of overlap of the more generalized species by the more specialized species. Where high overall niche overlap values existed between two species, they had low overlap values with high confidence for at least one niche dimension, either habitat, microhabitat, or mating season. Syntopic species often showed very high overlap of one dimension and no overlap of another dimension, thus demonstrating a subdivision of resources (Schoener, 1974).

Intraspecific Competition

One unusual statistic pointed out the probability that intraspecific competition among species of *Phidippus* has a greater limiting affect than interspecific competition on a particular species. This statistic consists of a comparison of all observations of intra-salticid predation reported by Jackson (1977b) and here (Table 10-5, Appendix F). Of 21 such observations, 4 were of intergeneric predation, and 17 were of intraspecific predation; there was not a single case of intrageneric predation. This implies that interference competition is highest within a species, which is exemplified by the predation on conspecifics by *P. audax* I observed during a period of low food availability, and the observations of conspecific predation by the same species made by Tessler (personal communication) during apparent competition for nesting sites. Interspecific interaction is probably low due to subdivision of one or more niche dimensions.

Species Summaries

P. apacheanus

This apparent mutillid mimic appears to be a specialist in all niche dimensions except microhabitat; it matures in the fall. It is limited to the lower strata since it occurs in xeric habitats lacking a canopy, where it appears to be one of the numerically dominant species. Overall niche overlap values with co-dominants *P. cardinalis* and *P. xerus* are high, but microhabitat utilization by immatures of *P. cardinalis* is different (and accentuated by their differences in color), and there is no overlap of mating season with *P. xerus* (temporal isolation).

P. audax

This species is a time generalist (with adults found all year) but a habitat and microhabitat specialist, found primarily on grass and herbs in habitats near bodies of water, whether the water is lake, stream, or ocean. It maintained by far the largest populations of any single species of *Phidippus*; this appeared to be in part due to unlimited food supply over a long growing season, and in part due to generalization in respect to age and size classes through time.

P. cardinalis

The adult males of this species are also apparent mutillid mimics, and adults mature in the fall. Categories of resource states utilized were very similar to *P. apacheanus*, from which it differed in microhabitat of immature stages, and to *P. xerus*, which it only slightly overlapped in mating season.

P. clarus

This species was moderately specialized for most niche dimensions, and found most often in the grass and herb zone of old fields, where it matured in late summer and was the dominant species. It was highly specialized in site of construction of eggsacs, mostly utilizing the tops of tall annuals and perennials within the fields.

P. otiosus

Another fall-maturing species, *P. otiosus* was neither especially specialized or generalized for any niche dimension except eggsac construction site, which was usually under bark, and microhabitat, which was primarily canopy. Adult females were present for several months of the year, giving the species a tendency toward being a time generalist. This species differed from *P. audax* and *P. regius* in low habitat overlap, from *P. putnami* and *P. cardinalis* by low microhabitat overlap, and from *P. pulcherrimus* in size.

P. pulcherrimus

This species is a specialist for most niche dimensions. It is found primarily in pine flatwoods (where it was dominant) on shrubs and it matures in the early spring. It has a high overall niche overlap with *P. putnami*, except there is no overlap in mating season between the two species.

P. putnami

This species has a resource utilization pattern very similar to that of *P. pulcherrimus*, except that *P. putnami* is less specialized for habitat, more specialized for microhabitat (shrubs), and matures in midsummer, so there is no mating season overlap with *P. pulcherrimus*. Highest populations of *P. putnami* were found in mature sand pine scrub, which was not included in this study. Microhabitat overlap with *P. xerus* is fairly low, but other niche dimensions are utilized in a similar manner.

P. regius

This species was both a time generalist and a space generalist, occurring in the widest variety of both habitats and microhabitats. It matures in the fall in north Florida. Adults and subadults show a preference for various palms, but smaller immatures live in the herb shrub zone. It only specializes in eggsac construction site, which is under bark. This is the largest species, and appears to be adaptable to a wide variety of environmental conditions.

P. whitmani

This species is an extreme specialist for habitat and microhabitat, occurring in mature forest on the litter unlike any other species studied. It matures in late spring.

P. xerus

This species is a specialist for xeric habitats and for mating season, maturing in mid-summer. It differs from the syntopic *P. apacheanus* and *P. cardinalis* in mating season, and from *P. putnami* in microhabitat in the younger immatures; *P. xerus* does not move onto shrubs until the subadult stage.

Table 10-1. Habitats in which species of *Phidippus* were collected. Double X (XX) indicates that the species was numerically dominant in that particular habitat. Underlined X's ($\underline{X}$) indicate that adults were collected in that habitat. X's in parentheses (X) indicate the species was reported from this habitat in another study, but was not taken from that habitat during the course of this study. Habitat designations are taken mostly from Laessle (1942).

Phidippus sp.	Agricultural Habitats		Xerophytic Habitats				
Occurring in Florida	Row Crops	Orchard	Timbered Scrub	Mature Scrub	Sand-hill	Xeric Hammock	Coastal Dune
P. apacheanus			XX		X	X	
P. audax	($\underline{X}$)	($\underline{X}$)					
P. cardinalis			$\underline{X}$			$\underline{X}$	$\underline{X}$
P. clarus	$\underline{X}$	$\underline{X}$					
P. mystaceus	(X)	($\underline{X}$)		X			
P. otiosus		$\underline{X}$		$\underline{X}$		$\underline{X}$	
P. pius							
P. pulcherrimus				X	$\underline{X}$	$\underline{X}$	
P. purpuratus	(X)				X		
P. putnami			X	$\underline{XX}$	$\underline{X}$	X	
P. regius	$\underline{X}$	$\underline{X}$	$\underline{X}$			$\underline{X}$	$\underline{X}$
P. whitmani							
P. xerus		X	$\underline{XX}$	X	$\underline{X}$	X	
Not in Florida							
P. borealis							
P. insignarius							($\underline{XX}$)
P. princeps							($\underline{X}$)

Table 10-1 continued.

Phidippus sp.	Mesophytic Habitats					
Occurring in Florida	*Abandoned Old Field*	*Roadside*	*Prairie*	*Pine Flatwoods*	*Mesic Hammock*	*Deciduous Forest*
P. apacheanus	*X*		(*X*)			
P. audax	(*X*)	X	(*X*)			(*X*)
P. cardinalis	*X*		(X)	X		
P. clarus	*XX*	X	(X)	X		
P. mystaceus						(*X*)
P. otiosus						
P. pius	X					
P. pulcherrimus	X	X		*XX*		
P. purpuratus	X					
P. putnami				X		(*X*)
P. regius	*XX*			*X*		
P. whitmani					*XX*	*XX*
P. xerus						
Not in Florida						
P. borealis						(*X*)
P. insignarius	(*X*)		(*X*)			(*X*)
P. princeps	(*XX*)		(*X*)			(*X*)

Table 10-1 continued.

Phidippus sp. Occurring in Florida	Hydrophytic Habitats: Grassy Pond Margin	Hydric Hammock	Lake Margin	River Swamp	"Prairie" Marsh	Salt Marsh
P. apacheanus						
P. audax			XX	(X)	X	X
P. cardinalis						
P. clarus	XX		X		X	X
P. mystaceus					X	
P. otiosus			XX	X	X	
P. pius						
P. pulcherrimus	X	X	X			
P. purpuratus					X	
P. putnami		X				
P. regius	X		X		X	X
P. whitmani		X		(X)		
P. xerus						
Not in Florida						
P. borealis						
P. insignarius				(XX)		
P. princeps						

Table 10-2. Plant associations of *Phidippus* species: A=adults, S=subadults, I=immatures, C=male and penultimate female cohabiting, E=female with eggsac (or unattended eggsac if under column A), S=spider in nest (shelter or for molting), H=spider hunting.

				Stage		
Phidippus sp.		Plant	Assoc.	I	S	A
P. apacheanus	Buxaceae:	*Ceratiola ericoides* Michx.	H	9		
	Compositae:	*Ambrosia artemisiifolia* L.	H		4	
		Eupatorium capillifolium (Lam.) Small	H,S	5	1	1(F)
		Heterotheca graminifolia (Michx.) Shinners	H	1		
	Fagaceae:	*Quercus chapmanii* Sarg.	H		1	1(M)
		Q. laevis Walt.	H		1	
		Q. myrtifolia Willd.	H	5		
		Q. virginiana var. *maritima* (Michx.) Sarg.	H	4		
		Quercus sp.	E			1(F)
	Palmae:	*Serenoa repens* (Bartr.) Small	H	1		
	Miscellaneous:	Mixed grass and herbs	H	1		
		Mixed grass and young trees	H	1		
		Mixed woody herbs in xeric field	H	17		
P. audax	Chenopodiaceae:	*Chenopodium ambrosioides* L.	H	4		
	Commelinaceae:	*Tradescantia ohiensis* Raf.	H,S	8		2
	Compositae:	*Bidens pilosa* L.	H	8	10	31
		Cirsium horridulum Michx.	H,S	4		
		Eupatorium capillifolium (Lam.) Small	H	3		3
		Heterotheca subaxillaris (Lam.) Britton & Rusby	H	10		
		Lactuca floridana (L.) Guert.	H,S	17	9	6
		Mikania scandens (L.) Willd.	H		2	1
		Solidago sp.	H	3		
		undetermined aster	H	1		
	Fagaceae:	*Quercus* sp. sapling	E			1
	Graminae:	*Andropogon virginicus* L.	H,S	2	1	10
		Echinochloa walteri (Pursh) Heller	H	35	32	32
		Paspalum notatum (Flugge)(bahia)	H	1		
		Sacciolepis striata (L.) Nash		14	9	42
		undetermined grasses	H	11	1	7

Table 10-2 continued.

Phidippus sp.		Plant	Assoc.	Stage		
				I	S	A
P. audax (cont.)	Leguminosae:	*Cassia fasciculata* Michx.	H			1
		Medicago sativa L.	H			1
	Malvaceae:	*Sida rhombifolia* L.	H			1
	Oleaceae:	*Fraxinus caroliniana* Mill.	H		3	3
	Onagraceae:	*Ludwigia peruviana* (L.) Hara	H			1
	Palmae:	*Sabal palmetto* (Walt.) Lodd.	E,S	5	10	8
	Pinaceae:	*Pinus* sp. seedling	H		2	1
	Rosaceae:	*Rubus* sp.	C,H,S	1	3	10
	Typhaceae:	*Typha latifolia* L.	E,H			6
	Vitaceae:	*Ampelopsis arborea* (L.) Koehne	H			1
	Miscellaneous:	Overgrown pasture	H	9		
		Wooden fence (under bark)	E			4
		Under board on ground	E,S	1		1
P. cardinalis	Juglandaceae:	*Carya tomentosa* Nutt.	E			2(F)
	Miscellaneous:	Ground, xeric field	H			2(M)
		Ground, sand dune	H			2(M)
		Mixed woody herbs and grasses, xeric field	H	15		
		Mixed herbs and grasses	H	6		
		Mixed grasses	H	6	1	
		Wood pile	S		1	
P. clarus	Anacardiaceae:	*Rhus copallinum* L.	E,H	4	2	1(F)
	Asclepidaceae:	*Asclepias* sp.	E			1(F)
	Compositae:	*Eupatorium capillifolium* (Lam.) Small	E,H	2		10(F)
		Heterotheca subaxillaris (Lam.) Britton & Rusby	H	1		1(F)
		Lactuca sp.	H			2
		Solidago microcephala (Greene) Bush	E,S	2		14(F)
		Solidago sp.	H	8		
		Undetermined aster	E,H	1		4(F)
	Ericaceae:	*Vaccinium myrsinites* Lam.	H	1	1	
	Euphorbiaceae:	*Acalypha graciliens* Gray	H	1		
		Aleurites Fordii Hemel	H			1(M)
	Fagaceae:	*Quercus* sp. sapling	H	2		

Table 10-2 continued.

Phidippus sp.		Plant	Assoc.	Stage		
				I	S	A
P. clarus (cont.)	Graminae:	*Andropogon virginicus* L.	H	6		
		Echinocloa Walteri (Pursh) Heller	H,S	1	7	1
		Mixed bahia and other grasses	H	24	6	8(7M)
	Leguminosae:	*Lespedeza* sp.	H,S	2		
	Magnoliaceae:	*Magnolia virginiana* L.	E			1(F)
	Malvaceae:	*Sida* sp.	H			1(M)
	Rosaceae:	*Rubus* sp.	H	2		
	Solanaceae:	*Physalis* sp.	H			1(F)
	Typhaceae:	*Typha latifolia* L.	E			1(F)
	Urticaceae:	*Boehmeria drummondiana* Wedd.	E,S		1	3(F)
	Miscellaneous:	Mixed grass and herbs; meadow	H	32	2	1(M)
		Mixed grass with shrubs or young trees	H	33	1	1(M)
		Undetermined herbs	H	3		
		Undetermined shrubs	H			2
P. mystaceus	Fagaceae:	*Quercus myrtifolia* Willd.	H		2	
		Quercus sp.	H		1	
P. otiosus	Buxaceae:	*Ceratiola ericoides* Michx.	H	1		
	Compositae:	*Ambrosia artemisiifolia* L.	H			1(M)
		Lactuca sp.	H		1	
	Ebenaceae:	*Diospyros virginiana* L.	H	1		
	Fagaceae:	*Quercus falcata* Michx.	E			2(F)
		Q. laevis Walt.	E			3(F)
		Q. virginiana Mill.	C,E,H,S	3	2	12(9F)
		Quercus sp.	E			5(F)
	Graminae:	*Sacciolepis striata* (L.) Nash	H	1	2	1
	Hamamelidaceae:	*Liquidambar styraciflua* L.	H	2	2	2(1M)
	Juglandaceae:	*Carya illinoinensis* Wangenh.	H	1		
		Carya sp.	H	1		
	Liliaceae:	*Asparagus setaceus* (Kunth) Jessup	H	1		
		Undetermined genus	H		1	

Table 10-2 continued.

Phidippus sp.		Plant	Assoc.	Stage		
				I	S	A
P. otiosus (cont.)	Oleaceae:	*Fraxinus caroliniana* Mill.	H		1	3
	Palmae:	*Sabal palmetto* (Walt.) Lodd.	E,S		1	7(F)
	Pinaceae:	*Pinus palustris* Mill.	E			19(F)
		Pinus sp.	E			1(F)
		Taxodium distichum (L.) Rich	H			6
	Rosaceae:	*Prunus* sp.	H	1		
	Rubiaceae:	*Cephalanthus occidentalis* L.	H		2	
	Urticaceae:	*Boehmeria cylindrica* (L.) Sw.	H		1	
	Miscellaneous:	Undetermined herb	H		1	
		Undetermined shrub	H			1(M)
P. pius	Miscellaneous:	Mixed roadside grass and herbs	H	6		
P. princeps	Graminae:	*Sorghum halepense* (L.) Persoon	H			1(M)
	Miscellaneous:	Mixed grass and herb meadow	H	18		
		Overgrown pasture	H	2		
		Hollow log	E			1(F)
P. pulcherrimus	Anacardiaceae:	*Rhus copallinum* L.	H	1	1	
	Annonaceae:	*Asimina* sp.	H	1		
	Aquifoliaceae:	*Ilex* sp.	H	1		
	Buxaceae:	*Ceratiola ericoides* Michx.	H	1		
	Commelinaceae:	*Tradescantia ohiensis* Raf.	S	1		
	Compositae:	*Lactuca* sp.	H	2		
		Heterotheca subaxillaris (Lam.) Britton & Rusby	H		1	
		Solidago microcephala (Greene) Bush	H	8		
		Undetermined genus	H	1	1	
	Ericaceae:	*Lyonia ferruginea* (Walt.) Nutt.	H,S	44	4	
		Vaccinium arboreum Marsh.		8		
		V. myrsinites Lam.	H	47		

Table 10-2 continued.

Phidippus sp.		Plant	Assoc.	Stage		
				I	S	A
P. pulcherrimus (cont.)	Fagaceae:	*Quercus laevis* Walt.	H	2		
		Q. nigra L.	H			1(M)
		Quercus spp. saplings	H	25		
	Graminae:	*Andropogon* sp.	H	7		
		Echinocloa Walteri (Pursh) Heller	H		1	
		Paspalum notatum Flugge	H	1		
		Mixed undetermined grasses	H	18		
	Lauraceae:	*Persea borbonia* (L.) Spreng.	H			4(2M)
	Leguminosae:	Undetermined genus	H	4		
	Liliaceae:	*Smilax* sp.	H	1	1	
	Nyctaginaceae:	*Pisonia rotundata* Griseb.	H	1		
	Pinaceae:	*Pinus* sp. sapling	H		1	
	Pontedericeae:	*Pontederia rotundifolia* L. f.	H		1	
	Rosaceae:	*Crataegus uniflora* Muench.	H			1(F)
		Rubus sp.	H		2	
	Solanaceae:	*Physalis* sp.	H	3		
	Urticaceae:	*Boehmeria drummondiana* Wedd.	S		1	
	Vitaceae:	*Vitis* sp.	H	1		
	Miscellaneous	Mixed grass and herbs	H	8		
		Mixed grass and young trees	H	17		1(M)
		Mixed slash pine understory	H	2	1	9(3M)
		Wooden fence post	H	1	1	
P. purpuratus	Miscellaneous:	Mixed grass and shrub xeric field	H	20		
		Mixed turkey oak understory	H	3		
P. putnami	Buxaceae:	*Ceratiola ericoides* Michx.	E,H	12		1(*)
	Fagaceae:	*Quercus incana* Bartr.	H		1	
		Q. laevis Walt.	H,S	5		
		Q. myrtifolia Willd.	H	3		
		Q. nigra L.	E,H	10		
		Q. virginiana var. *maritima* (Michx.) Sarg.	H	3		
		Quercus sp.	S	3		

Table 10-2 continued.

Phidippus sp.		Plant	Assoc.	Stage		
				I	S	A
P. putnami (cont.)	Lauraceae:	*Persea borbonia* (L.) Spreng.	H	1		
	Palmae:	*Serenoa repens* (Bartr.) Small	E,H			2(F,*)
	Pinaceae:	*Pinus palustris* Mill.	S			1(M)
	Miscellaneous:	Mixed slash pine understory	H	3		
		Mature deciduous woods understory	H		2	2(M)
		Mixed woody herbs, xeric field	H	1		
P. regius	Aceraceae:	*Acer saccharinum* L.				1(F)
	Anacardiaceae:	*Rhus copallinum* L.	H	1		
	Buxaceae:	*Ceratiola ericoides* Michx.	H	1		
	Commelinaceae:	*Tradescantia ohiensis* Raf.	H,S	2		
	Compositae:	*Eupatorium capillifolium* (Lam.) Small	H	14		3(M)
		Heterotheca subaxillaris (Lam.) Britton & Rusby	H	1		
		Lactuca sp.	H	3	3	2(M)
		Solidago microcephala (Greene) Bush	H,S	2	7	1(M)
		Undetermined aster	S		1	
	Cupressaceae:	*Cupressus arizonica* Greene	H	1		
		Juniperus sp.				1(M)
	Ericaceae:	*Lyonia* sp.	H	2		
	Euphorbiaceae:	*Manihot esculenta* Crantz	H	3		
	Fagaceae:	*Quercus falcata* Michx.	E			2(F)
		Q. laevis Walt.	E,S	3		3(2F)
		Q. virginiana Mill.	E,S			7(5F)
		Quercus sp.	E,S	1		3(F)
	Graminae:	*Andropogon virginicus* L.	H	2	2	1(F)
		Aristida stricta Michx.	H	1		
		Cenchrus echinatus L.	H	1		
		Echinochloa Walteri (Pursh) Heller	H	4	3	1(M)
		Zea mays L.	H	1		
		Mixed bahia and other grass	H	17		1

Table 10-2 continued.

				Stage		
Phidippus sp.		Plant	Assoc.	I	S	A
P. regius (cont.)	Leguminosae:	*Crotalaria spectabilis* Roth	H			1(M)
	Liliaceae:	*Yucca* sp.	H	2		1(M)
	Malvaceae:	*Hibiscus esculentus* L.	H	3		
		H. rosa-sinensis L.	H		1	
	Musaceae:	*Musa xparadisiaca* L.	H			1(M)
	Oleaceae:	*Ligustrum lucidum* Ait.	H			1(M)
	Palmae:	*Sabal palmetto* (Walt.) Lodd.	E,H,S	10	9	26(17)
		Serenoa repens (Bartr.) Small	H,S	1	20	11(5)
		Cocos nucifera L.	H		1	
	Pinaceae:	*Pinus elliottii* Engelm.	H			1(F)
		P. palustris Mill.	E,S		1	4(3F)
		Pinus sp. log	E			2(F)
		P. sp. seedling	H	2		
	Rosaceae:	*Rubus* sp.	H,S	1	2	
	Rubiaceae:	*Cephalanthus occidentalis* L.	H	2		
	Rutaceae:	x *Citrofortunella mitis* (Blanco) Ingram & Moore	H			5
		Citrus sinensis (L.) Osbeck	H			3
		C. paradisi Macf.	H			1
		Citrus sp.	H		1	4
		Fortunella sp.	H			1
	Simaroubaceae:	*Suriana maritima* L.	H			1(F)
	Urticaceae:	*Boehmeria drummondiana* Wedd.	H	1		1(M)
	Verbenaceae:	*Avicennia germinans* (L.) L.	H	1	1	
	Miscellaneous:	Undetermined herb	H			1(M)
		Mixed grass, herbs, and young palmettoes	H	12		
		Undetermined shrub	H	1		
		Mixed woody herbs and scrub oaks	H	2		
		Hollow metal pole	E			1(F)
		In and on buildings	H,S		2	17
		Cantrap	H		1	
		Insect flight trap	H			4

Table 10-2 continued.

Phidippus sp.		Plant	Assoc.	Stage I	 S	 A
P. whitmani	Miscellaneous:	Bayhead litter	H	1	1	
		Deciduous hardwood forest litter	H	8		28(15F)
		Mesic hammock litter	H	5	2	4(3F)
		Hydric hammock litter	H	2		
P. xerus	Buxaceae:	Ceratiola ericoides Michx.	H	1		
	Fagaceae:	Quercus chapmanii Sarg.	H			1(F)
		Q. myrtifolia Willd.	H	3	1	
		Q. virginiana var. maritima (Michx.) Sarg.	H	2	2	3(M)
	Malvaceae:	Hibiscus esculentus L.	H			1(M)
	Palmae:	Serenoa repens (Bartr.) Small	E,S			2(1F)
	Rutaceae:	Citrus sinensis (L.) Osbeck	H		1	
	Miscellaneous:	Mixed woody herbs, xeric field	H	9		
		Xeric woods understory	H		2	

Table 10-3. Associations of *Phidippus* species with type of substrate (Florida records only); numbers are actual number of specimens observed. Stages of spider are indicated by I=immatures, S=subadult, and A=adult. Underlined numbers indicate significantly more (X^2; $p<.05$) individuals occur on that association than the same stage within the same species of spider on different associations. Equally underlined numbers are not significantly different within a stage and species.

Phidippus sp.	Ground or Litter			Grasses and Herbs			Woody Perennials			Shrubs			Palms			Trees			Other		
	I	S	A	I	S	A	I	S	A	I	S	A	I	S	A	I	S	A	I	S	A
apacheanus	1			2	4		23	1	1	18	2	1	1					1			
audax				115	64	142	7	3	15		2		5	10	8			7	1		1
cardinalis			4	19			8	1										2		1	
clarus				90	17	26	14		24	18	3	4									
mystaceus											3										
otiosus				2	6	2				1	2	1		1	7	9	5	53			
pius				6																	
pulcherrimus				55	5	7	10	3		130	7	9							1	1	
purpuratus				20						3											
putnami							1			40	1	2			2			1			
regius		1		49	10	7	22	9	4	15	1	16	11	30	37		2	29		2	22
whitmani	15	3	30			1															
xerus						1	9	2		6	3	4			2		1				

Table 10-4. Predators and parasitoids of eastern U. S. *Phidippus* species. Synonyms used by various authors are placed in parentheses. Question marks in parentheses indicate uncertain identification by cited author. New records are indicated by an asterisk (*) followed by the number of new records and the number of instances per record if greater than one. Stages of *Phidippus* attacked: A=adult, N=nymph, E=egg.

Phidippus sp.	Stage		Taxon of Predator or Parasitoid	First Reference
P. audax		Hymenoptera		
	A	Pompilidae:	*Dipogon pulchripennis* (Cresson)	Cresson, 1867
			Auplopus architectus (Say)	Krombein, 1961
			A. caerulescens subcorticalis (Walsh.)	Evans & Yoshimoto, 1955
			A. mellipes (Say)	Rau, 1926
			Ageniella fulgifrons (Cresson)	Evans, 1959
			Sericopompilus apicalis (Say)	Peckham & Peckham, 1898
			Anoplius marginatus (Say)	Peckham & Peckham, 1898
			A. splendens (Dreisbach)	Evans, 1951
	A	Sphecidae:	*Trypargilum clavatum* (Say)	Rau, 1928; *2
			T. johannis (Richards)	Krombein, 1967
			T. texense (Saussure)	Hartman, 1905
			Trypoxylon or *Sceliphron* spp.	Dorris, 1969
	E	Scelionidae:	*Idris* sp.	*3: > 50
		Neuroptera		
	E	Mantispidae:	*Mantispa viridis* Walker	*1
		Araneae		
	A	Araneidae:	*Argiope aurantia* (Lucas)	Bilsing, 1920
	?		*A. trifasciata* (Forskal)	Bilsing, 1920
	N	Salticidae:	*Dendryphantes marginatus* (Walckenaer)	*1
	A,N		*Phidippus audax* (Hentz)	*3; *8, Tessler (pers. comm.)
	A	Theridiidae:	*Achaearanea tepidariorum* (Koch)	Edwards, 1977
		Fungi		
	A	Hyphomycetes:	*Gibellula leiopus*	*2
		Reptilia		
(*variegatus*)	?	Iguanidae:	*Crotaphytus collaris* Say	Fitch, 1963 (38)
(*variegatus*)	?	Scincidae:	*Eumeces fasciatus*	Fitch, 1963 (many)

Table 10-4 continued.

Phidippus sp.	Stage		Taxon of Predator or Parasitoid	First Reference
P. clarus		Hymenoptera		
(rimator)	A	Pompilidae:	Auplopus adjunctus (Banks)	Kurczewski & Kurczewski, 1968
			Anoplius marginatus (Say)	Peckham & Peckham, 1898
			A. splendens (Dreisbach)	Evans, 1951
			Aporinellus completus Banks	Evans, 1951
	A	Sphecidae:	Sceliphron caementarium (Drury)	Peckham & Peckham, 1898
			Trypargilum clavatum (Say)	Rau, 1928
			T. johannis (Richards)	Krombein, 1967
(rimator)			T. texense (Saussure)	Hartman, 1905
(rimator)			Trypoxylon or Sceliphron spp.	Dorris, 1969
	E	Eupelmidae:	Arachnophaga aldrichi Gahan	*1: > 50
		Diptera		
	E	Chloropidae:	Pseudogaurax signatus (Loew)	*14:2-18
		Neuroptera		
	E	Mantispidae:	Mantispa viridis Walker	*7
		Fungi		
	A	Hyphomycetes:	Nomuraea atypicola (Yasuda) Samson	*1
		Aves?		
	?E,?A	undetermined		*2
P. mystaceus		Hymenoptera		
		Sphecidae:	Sceliphron caementarium (Drury)	Rau, 1935
			"wasp nest" (S. caementarium?)	Muma, 1944
			Trypoxylon or Sceliphron spp.	Dorris, 1969
			1 of 4 species not differentiated	Muma & Jeffers, 1945

Table 10-4 continued.

Phidippus sp.	Stage		Taxon of Predator or Parasitoid	First Reference
P. otiosus		Hymenoptera		
	N	Sphecidae:	*Sceliphron caementarium* (Drury)	*2, (B. Saffer, coll.)
			Trypargilum clavatum (Say)	*26
			undetermined genus	*1
	E	undetermined family		*1: 73 of 99 eggs
		Neuroptera		2: 1,2
	E	Mantispidae:	*Mantispa viridis* Walker	*1
		Nematoda		
	A,N	Mermithidae:	undetermined species	*2
		Fungi		
	A	Hyphomycetes:	*Acrodontium crateriforme* (van Beyma) de Hoog	*1
P. pius		Hymenoptera		
	A	Sphecidae:	*Sceliphron caementarium* (Drury)	Horner & Klein, 1979
		Aves:Ciconiiformes		
	A	Ardeidae:	*Bubulcus ibis*	*1, (H. K. Wallace, coll.) (reported as *Phidippus* sp., Fogerty & Wallace, 1973)
P. princeps		Hymenoptera		
	A	Pompilidae:	*Auplopus architectus* (Say)	Krombein, 1961
(*insolens*)	A	Sphecidae:	1 of 4 species not differentiated	Muma & Jeffers, 1945

Table 10-4 continued.

Phidippus sp.	Stage		Taxon of Predator or Parasitoid	First Reference
P. princeps (cont.)		Diptera		
	N	Acroceridae:		*1
P. pulcherrimus		Odonata		
	N	Libellulidae:	*Erythemis simplicicollis* (Say)	*1
P. purpuratus (?)		Hymenoptera		
	A	Pompilidae:	*Dipogon brevis* (Cresson)	Cresson, 1867
			Anoplius marginatus (Say)	Krombein, 1959
	A	Sphecidae:	*Trypoxylon* or *Sceliphron* spp.	Dorris, 1969
P. putnami		Hymenoptera		
	A	Pompilidae:	*Sericopompilus apicalis* (Say)	Peckham & Peckham, 1898
	A	Sphecidae:	1 of 4 species not differentiated	Muma & Jeffers, 1945
		Araneae		
	A	Theridiidae:	undetermined genus	*1
P. regius		Hymenoptera		
	E	Scelionidae:	*Idris* sp.	*2
	E	undetermined family		*1: 101 (100%)
		Neuroptera		
	E	Mantispidae:	*Mantispa viridis* Walker	*1
		Araneae		
	N	Salticidae:	*Thiodina sylvana* (Hentz)	*1

Table 10-4 continued.

Phidippus sp.	Stage		Taxon of Predator or Parasitoid	First Reference
P. regius (cont.)		Fungi		
	A	Hyphomycetes:	*Acrodontium crateriforme* (van Beyma) de Hoog	*1
			Nomuraea atypicola (Yasuda) Samson	*5
		Aves:Ciconiiformes		
	A	Ardeidae:	*Bubulcus ibis*	*1, (H. K. Wallace, coll.)
P. whitmani		Hymenoptera		
	A	Pompilidae:	*Dipogon sayi* Banks	Banks, 1941
(?)			*Auplopus architectus* (Say)	Krombein, 1961
			Sericopompilus apicalis (Say)	Peckham & Peckham, 1898
			Anoplius rectangularis (Dreisbach)	Kurczewski & Kurczewski, 1968
(?)			*Aporinellus medianus* Banks	Peckham & Peckham, 1898
	A	Sphecidae:	*Trypoxylon* or *Sceliphron* spp.	Dorris, 1969
P. sp.		Hymenoptera		
	N	Pompilidae:	*Dipogon papago anomelus* Dreisbach	Dreisbach, 1953
			D. brevis ochraceus Townes	Townes, 1957
			Auplopus mellipes (Say)	Rau, 1926
			A. nigrellus (Banks)	Krombein, 1955
			Ageniella fulgifrons (Cresson)	Evans, 1959
			Sericopompilus apicalis (Say)	Peckham & Peckham, 1898
			Pompilus scelestus Cresson	Peckham & Peckham, 1898
			Aporinellus medianus Banks	Peckham & Peckham, 1898
	N	Sphecidae:	*Sceliphron caementarium* (Drury)	Peckham & Peckham, 1898
			S. assimile (Dahlbom)	Dow, 1932
			Trypargilus californicum Saussure	Mathews & Mathews, 1968
			T. clavatum (Say)	Rau, 1928
			T. johannis (Richards)	Krombein, 1967

Table 10-4 continued.

Phidippus sp.	Stage	Taxon of Predator or Parasitoid		First Reference
P. sp. (cont.)				
(*audax* or *otiosus*)	E	undetermined family		*1: > 50 (100%)
		Amphibia		
	N	Hylidae:	*Hyla cinerea*	*1, (A. Freed, coll.)
		Reptilia		
	N	Iguanidae:	*Crotaphytus collaris* Say	Fitch, 1963 (17)
	N		*Sceloporus graciosus* (B. & G.)	Gertsch & Woodring, 1930

Table 10-5. Prey captured by eastern U.S. *Phidippus* species. New records are followed by an asterisk (*) followed by number of new records. Stages of predator and prey: A=adult, N=nymph, L=larva, W=worker ant, ?=stage unknown.

Phidippus sp.	Stage		Taxon of Prey	Stage	Reference(s)
P. apacheanus		Lepidoptera			
	N	Stenomidae:	*Antaeotricha vestalis* (Zeller)	L	*1 (J. Carroll, coll.)
		Araneae			
	N	Gnaphosidae:	undetermined genus	N	*1
P. audax		Odonata			
	N	Libellulidae:	*Perithemis tenera* (Say)	A	*1
	?	undetermined family		A	Fitch, 1963
		Orthoptera			
	?	Acrididae:	*Melanoplus differentialis* (Thos.)	A	Bilsing, 1920
	A		*Paroxya* sp.	N	*1
	?	Acrididae, Blattidae, Gryllidae		?	Bilsing, 1920
	?	Blattellidae:	*Ischnoptera pennsylvanica*	A	Bilsing, 1920
	?	undetermined family		?	Snetsinger, 1955; Fitch, 1963
		Hemiptera			
	?	Capsidae:	undetermined genus	?	Bilsing, 1920
	A	Coreidae:	*Althos obscurator* (Fabr.)	A	*1
	?	Miridae:	*Adelphocoris rapidus* (Say)	A	Kagan, 1943
			Lygus lineolaris (P. deBeauvois)	A	Whitcomb and Bell, 1964
			L. pratensis (L.)	A	Bilsing, 1920
	A	Pentatomidae:	*Thyanta custator* (Fabr.)	N	*1
	?	undetermined family		?	Snetsinger, 1955

Table 10-5 continued.

Phidippus sp.	Stage	Taxon of Prey		Stage	Reference(s)
P. audax (cont.)		Homoptera			
	N	Cicadellidae:	*Homalodisca insolita* (Walker)	A	*1
	N	Delphacidae:	*Pissonotus* sp.	A	*1 (R. Crocker, coll.)
	?	undetermined family		?	Snetsinger, 1955
		Neuroptera			
	?	Chrysopidae:	*Chrysopa* sp.	A,L	Bailey and Chada, 1968
		Coleoptera			
	A,N	Cantharidae:	*Chauliognathus marginatus* (Fabr.)	A	*9
	?	Coccinellidae:	undetermined genus	A,L	Bailey and Chada, 1968
	?	Curculionidae:	*Anthonomis grandis* Boheman	A	Whitcomb et al., 1963(3)
		Lepidoptera			
	?	Noctuidae:	*Alabama argillacea* (Hubner)	L	Kagan, 1943
	A,N		*Heliothis zea* Boddie	A,L	Kagan, 1943; Whitcomb et al., 1963; Lincoln et al., 1967; Bailey and Chada, 1968
	?		*Pectinophora gossypiella* (Saunder)	A	Clark and Glick, 1961(5)
	?	Arctiidae:	*Hyphantria cunea* (Drury)	L	Riley, 1887; Whitcomb and Tadic, 1963; Oliver, 1964; Warren et al., 1967
	?	undetermined family		A,L	Fitch, 1963
	N	undetermined family		A,L	*2
		Diptera			
	?	Asilidae:	undetermined genus	A	Whitcomb et al., 1963
	N	Bibionidae:	*Dilophus sayi* (Hardy)	A	*2
	A		undetermined genus	A	*2
	N	Cecidomyiidae:	*Contarinia sorghicola* (Coq.)	A	Bailey and Chada, 1968
	A,N	Chironomidae:	*Glyptotendipes paripes* (Edwards)	A	*51
	?	undetermined family		A	Snetsinger, 1955; Fitch, 1963
	N	undetermined family		A	*1

Table 10-5 continued.

Phidippus sp.	Stage	Taxon of Prey		Stage	Reference(s)
P. audax (cont.)		Hymenoptera			
	A,N	Apidae:	*Apis mellifera* L.	A	*2
	N	Braconidae:	*Apanteles* sp.	A	*1
	N	Formicidae:	*Monomorium* sp.	A	*1
	?	Vespidae:	*Vespula germanica* (Fabr.)	A	Bilsing, 1920
	?		undetermined genus	A	Bilsing, 1920
		Araneae			
	A	Atypidae:	*Atypus* sp.	A	Fitch, 1963
	N	Araneidae:	*Acanthepeira* sp.	N	*1
	?		*Argiope aurantia* Lucas	N	Tolbert, 1975
	?		*Argiope trifasciata* (Forskal)	N	Tolbert, 1975
	?		*Mecynogea lemniscata* (Walckenaer)	A	Lamore, 1958
	A		*Nuctenea cornuta* (Clerck)	A,N	*2
	?	Lycosidae:	*Lycosa rabida* Walckenaer	A	Fitch, 1963
	A		*Sosippus* sp.	N	*1
	?	Philodromidae:	*Philodromus vulgaris* Emerton	A	Bilsing, 1920
	?	Thomisidae:	*Xysticus gulosus* Keyserling	A	Bilsing, 1920
	?	Theridiidae:	*Achaearanea tepidariorum* (C. L. Koch)	A	Fitch, 1963
	A,N	Tetragnathidae:	*Tetragnatha* spp.	A,N	*10
	A	Salticidae:	*Phidippus audax* (Hentz)	A,N	*3; *8 (Tessler, per. comm.)
	?	undetermined family		?	Fitch, 1963
P. clarus		Orthoptera			
	A	Gryllidae:	*Gryllus pennsylvanicus* ?	N	*1 (MCZ)
	?	undetermined family		?	Snetsinger, 1955
		Hemiptera			
	?	undetermined family		?	Snetsinger, 1955

Table 10-5 continued.

Phidippus sp.	Stage	Taxon of Prey		Stage	Reference(s)
P. clarus (cont.)		Homoptera			
	N	Dictyopharidae:	*Phylloscelis atra* (Germar)	A	*1
	?	undetermined family		?	Snetsinger, 1955
		Lepidoptera			
	?	Noctuidae:	*Heliothis zea* (Boddie)	L	Lincoln et al., 1967
	?	undetermined family		A,L	Fitch, 1963
		Diptera			
	N	Chironomidae:	*Glyptodentipes paripes* (Edwards)	A	*2
	?	undetermined family		A	Snetsinger, 1955; Lincoln et al., 1967
		Araneae			
	?	Araneidae:	*Argiope aurantia* Lucas	N	Tolbert, 1975
	?		*Argiope trifasciata* (Forskal)	N	Tolbert, 1975
	?	undetermined family		?	Fitch, 1963
P. mystaceus		Lepidoptera			
	?	Arctiidae:	*Hyphantria cunea* (Drury)	L	Whitcomb and Tadic, 1963 Warren et al., 1967
	?	Noctuidae:	*Heliothis zea* (Boddie)	L	Lincoln et al., 1967
P. otiosus		Odonata			
	A	Libellulidae:	*Erythemis simplicicollis* (Say)	A	*1 (E. Tryon, coll.)
		Hemiptera			
	N	Reduviidae:	*Emesaya brevipennis* (Say)	A	*1

Table 10-5 continued.

Phidippus sp.	Stage		Taxon of Prey	Stage	Reference(s)
P. otiosus (cont.)		Lepidoptera			
	N	Arctiidae:	*Hyphantria cunea*?	L	*1
	N	Notodontidae:	*Datana integerrima* Grote & Robinson	L	*1 (D. Richman, coll.)
		Diptera			
	N	Chironomidae:	*Glyptotendipes paripes* (Edwards)	A	*1
		Hymenoptera			
	A	Formicidae:	*Formica pallidefulva* ?	W	*1
P. pulcherrimus		Homoptera			
	N	Aphididae:	undetermined genus	N	*1
	N	Derbidae:	*Cedusa* sp.	A	*1
		Coleoptera			
	N	Chrysomelidae:	*Oedionychus saturalis* (Fabr.)	A	*1
		Lepidoptera			
	N	Noctuidae:	undetermined genus	L	*1
		Diptera			
	N	Chironomidae:	*Glyptotendipes paripes* (Edwards)	A	*1
		Hymenoptera			
	N	Formicidae:	*Leptothorax pergandei* Emery	W	*1
	N	Ichneumonidae:	*Lymeon orbum* (Say)	A	*1
		Araneae			
	N	Tetragnathidae:	*Tetragnatha* sp.	N	*1 (G. Buckingham, coll.)

Table 10-5 continued.

Phidippus sp.	Stage		Taxon of Prey	Stage	Reference(s)
P. putnami		Lepidoptera			
	?	Arctiidae:	*Hyphantria cunea* (Drury)	L	Warren et al., 1967
		Diptera			
	A	Tabanidae:	*Tabanus*? sp.	A	*1 (SIU)
P. regius		Orthoptera			
	A	Acrididae:	*Schistocerca* sp.	A	*1 (R. Woodruff, coll.)
	N		undetermined genus	N	*1
	A	Tettigoniidae:	*Belocephalus subapterus* Scudder	A	*1
	N		*Orchelimum* sp.	N	*1
		Hemiptera			
	N	Lygaeidae:	*Blissus insularis* Barber	A	*1
	N	Pentatomidae:	*Acrosternum hilare* (Say)	A	*1 (Sue Edwards, coll.)
	A,N		*Alcaeorrhyncus grandis* (Dallas)	N	*2
	N	Reduviidae:	*Zelus cervicalis* Stal	A	*1
		Coleoptera			
	N	Cantharidae:	*Chauliognathus marginatus* (Fabr.)	A	*1
	A	Curculionidae:	*Diaprepes abbreviatus* (L.)	A	*1 (D. Gowan, coll.)
	N	Malachiidae:	*Collops* sp.	A	*1
		Lepidoptera			
	N	Arctiidae:	*Hypoprepia* sp.	A	*1
	A		*Estigmene acrea* (Drury)	L	*1
	A	Lymantriidae:	*Hemerocampa leucostigma* (Abbot & Smith)	L	Edwards, 1975
	N	Notodontidae:	*Schizura ipomoeae* Doubleday	L	Edwards, 1975
	N	Nymphalidae:	undetermined genus	L	*1
	N	Pyralidae:	*Crambus leachellus* (Zincken)	L	*1
	N		*Geshna cannalis* (Quaintance)	L	*1
	A	? :	*Artipus floridana*	A	*1
	N	undetermined family		L	*1

Table 10-5 continued.

Phidippus sp.	Stage		Taxon of Prey	Stage	Reference(s)
P. regius (cont.)		Diptera			
	N	Bibionidae:	*Dilophus sayi* (Hardy)	A	*1
	N	Chironomidae:	*Glyptotendipes paripes* (Edwards)	A	*3
	N	Chloropidae:	*Hippelates* sp.	A	*1
	N	Ephydridae:	*Scatella* sp.	A	*2
	A	Tabanidae:	*Tabanus* sp.	A	Edwards, 1975
	N	undetermined family		A	*1
		Araneae			
	N	Araneidae:	undetermined genus	N	*1
P. whitmani		Hemiptera			
	A	Pentatomidae:	*Menecles insertus* (Say)	N	*2
		Coleoptera			
	N	Chrysomelidae:	*Chlamisus* sp.	L	*1 (J. Reiskind, coll.)
P. spp.		Lepidoptera			
	N	Noctuidae:	*Heliothis zea* (Boddie)	L	Whitcomb et al., 1963; Whitcomb, 1967
		Araneae			
	N	Tetragnathidae:	*Tetragnatha laboriosa* Hentz	A	Everly, 1938

Table 10-6. Reproduction by eastern *Phidippus* species. Number (n) of eggsacs, mean ($\bar{X}$) number of eggs per eggsac ± standard error of the mean, *range* (r), and infertility rate (in parentheses) are given. Data for *P. insignarius* and *P. purpuratus* are taken from literature records. Letters following statistics of the first eggsac indicate no significant difference between species with the same letter for that eggsac.

Phidippus sp.	1st eggsac	2nd eggsac	3rd eggsac	4th eggsac
P. audax	n=5 $\bar{X}$=121.2 ± 15.8, bc r=80-161 (6%)	n=4 $\bar{X}$=57.2 ± 3.3 r=49-63(10%)	n=2 $\bar{X}$= 27.0 ± 1.0 r=26-28 (33%)	n=1 $\bar{X}$= 40.0 ± 0 r=40 (2.5%)
P. clarus	n=10 $\bar{X}$=191.7 ± 16.7, a r=98-292 (0.3%)	n=9 $\bar{X}$=106.1 ± 15.9 r=67-147 (9%)	n=4 $\bar{X}$=59.8 ± 21.6 r=25-116 (4%)	
P. insignarius	n=1 $\bar{X}$=47.0 ± 0 r=47 (?%)			
P. mystaceus		n=1 $\bar{X}$=12.0 ± 0 r=12 (0%)		
P. otiosus	n=40 $\bar{X}$=149.6 ± 8.6, b r=89-314 (3%)	n=37 $\bar{X}$=82.7 ± 5.5 r=43-203 (4%)	n=19 $\bar{X}$=59.6 ± 4.5 r=29-98 (8%)	n=1 $\bar{X}$=58.0 ± 0 r=58 (0%)
P. princeps	n=6 $\bar{X}$=68.3 ± 4.7, d r=56-84 (14%)			

Table 10-6 continued.

Phidippus sp.	1st eggsac	2nd eggsac	3rd eggsac	4th eggsac
P. pulcherrimus	n=3 $\bar{X}=42.0 \pm 3.2$, e r=37-44 (5%)	n=1 $\bar{X}=13.0 \pm 0$ r=13 (0%)		
P. purpuratus	n=4 $\bar{X}=127.2 \pm 12.4$, b r=100-155 (?%)			
P. putnami	n=2 $\bar{X}=71.0 \pm 3.0$, cd r=68-74 (0%)			
P. regius	n=31 $\bar{X}=183.4 \pm 9.5$, a r=102-375 (6%)	n=22 $\bar{X}=96.1 \pm 6.2$ r=44-149 (7%)	n=14 $\bar{X}=73.5 \pm 7.6$ r-36-123 (15%)	n=2 $\bar{X}=48.5 \pm 19.5$ r=29-68 (55%)
P. whitmani	n=4 $\bar{X}=72.8 \pm 3.2$, d r=66-80 (0%)	n=3 $\bar{X}=22.3 \pm 9.3$ r=13-41 (1.5%)		
P. xerus	n=2 $\bar{X}=31.5 \pm 0.5$, e r=31-32 (0%)	n=1 $\bar{X}=16.0 \pm 0$ r=16 (0%)		

Table 10-7. Total number of individuals of each species of *Phidippus* observed throughout the research periods for primary and secondary study habitats. Totals for *P. whitmani* were taken on two days at San Felasco Hammock. The Shannon-Weaver Index (H') is used as a measure of species diversity within a habitat. Values in parentheses to the right are row proportions, values in parentheses below are column proportions, in this and following tables.

Phidippus sp.	Timbered Scrub	Xeric Woods	Old Field	Burnt Pond
P. apacheanus	33 (1.0) (.375)			
P. audax				191 (.554) (.764)
P. cardinalis	15 (.556) (.170)	11 (.407) (.177)		
P. clarus			50 (.658) (.909)	13 (.171) (.052)
P. mystaceus	3 (1.0) (.034)			
P. otiosus		23 (.434) (.371)		1 (.019) (.004)
P. pulcherrimus		13 (.068) (.210)		10 (.052) (.040)
P. putnami	7 (.500) (.080)	4 (.286) (.065)		
P. regius	6 (.070) (.068)	9 (.106) (.145)	5 (.059) (.091)	35 (.412) (.140)
P. whitmani				
P. xerus	24 (.923) (.273)	2 (.077) (.032)		
Totals	88	62	55	250
H' (diversity)	1.523	1.570	0.305	0.785
J' (evenness)	0.850	0.876	0.440	0.488

Table 10-7 extended.

Newnan's Lake	Transition Field	Pine Flatwoods	Deciduous Woods	Totals
				33
154 (.446) (.851)				345
		1 (.037) (.006)		27
		13 (.171) (.071)		76
27 (.509) (.149)	2 (.038) (.050)			53
	2 (.011) (.050)	166 (.869) (.907)		191
		3 (.214) (.016)		14
	36 (.423) (.900)			91
			36 (1.0) (1.0)	36
				26
181	40	183	36	895
0.421	0.394	0.369	0	
0.607	0.359	0.266	0	

Table 10-8. Total number of individuals of each species of *Phidippus* for each microhabitat (see Table 10-3); *P. mystaceus*, *P. pius*, and *P. purpuratus* deleted from this and following tables due to insufficient data.

Phidippus sp.	Ground or Litter	Grasses and Herbs	Woody Perennials	Shrubs	Palms	Trees	Other	Totals
P. apacheanus	1 (.018) (.019)	6 (.105) (.010)	25 (.438) (.154)	23 (.403) (.080)	1 (.018) (.009)	1 (.018) (.009)		57
P. audax		321 (.845) (.514)	25 (.066) (.154)	2 (.005) (.007)	23 (.061) (.201)	7 (.018) (.064)	2 (.005) (.069)	380
P. cardinalis	4 (.114) (.074)	19 (.543) (.030)	9 (.257) (.057)			2 (.057) (.018)	1 (.029) (.034)	35
P. clarus		133 (.678) (.213)	38 (.194) (.242)	25 (.128) (.087)				196
P. otiosus		10 (.112) (.016)		4 (.045) (.014)	8 (.090) (.070)	67 (.753) (.609)		89
P. pulcherrimus		67 (.294) (.107)	13 (.057) (.083)	146 (.640) (.507)			2 (.009) (.069)	228
P. putnami			1 (.021) (.007)	43 (.915) (.149)	2 (.043) (.018)	1 (.021) (.009)		47
P. regius	1 (.004) (.019)	66 (.247) (.106)	35 (.131) (.223)	32 (.120) (.111)	78 (.292) (.684)	31 (.116) (.282)	24 (.090) (.828)	267
P. whitmani	48 (.980) (.888)	1 (.020) (.002)						49
P. xerus		1 (.036) (.002)	11 (.393) (.070)	13 (.464) (.045)	2 (.071) (.018)	1 (.036) (.009)		28

Table 10-9. Total number and distribution by microhabitat of eggsacs of each species of *Phidippus*.

Phidippus sp.	Grass and Herbs	Woody Perennials	Shrubs	Palms	Trees	Other	Totals
P. apacheanus					1 (1.0) (.019)		1
P. audax	2 (.400) (.333)	2 (.400) (.083)		1 (.200) (.091)			5
P. cardinalis							2
P. clarus	4 (.154) (.667)	20 (.769) (.917)	2 (.077) (.500)				26
P. otiosus				7 (.175) (.636)	33 (.825) (.611)		40
P. pulcherrimus			1 (1.0) (.250)				1
P. putnami			1 (.500) (.250)	1 (.500) (.091)			2
P. regius				1 (.050) (.091)	18 (.900) (.333)	1 (.050) (1.0)	20
P. xerus				1 (1.0) (.091)			1
Totals	6	24	2	11	54	1	98

Table 10-10. Total number of prey of each species of *Phidippus*, lumped by order (see Table 10-5).

Phidippus sp.	Odonata	Orthoptera	Hemiptera	Homoptera	Coleoptera
P. apacheanus					
P. audax	1 (.011) (.500)	1 (.011) (.167)	2 (.021) (.200)	2 (.021) (.400)	9 (.096) (.643)
P. clarus		1 (.250) (.167)		1 (.250) (.200)	
P. otiosus	1 (.167) (.500)		1 (.167) (.100)		
P. pulcherrimus				2 (.250) (.400)	1 (.125) (.071)
P. putnami					
P. regius		4 (.129) (.666)	5 (.161) (.500)		3 (.097) (.215)
P. whitmani			2 (.667) (.200)		1 (.333) (.071)
Totals	2	6	10	5	14

Table 10-10 extended.

Lepidoptera	Diptera	Hymenoptera	Araneae	Totals
1 (.500) (.067)			1 (.500) (.050)	2
2 (.133)	56 (.596) (.800)	4 (.042) (.571)	17 (.181) (.850)	94
	2 (.500) (.029)			4
2 (.333) (.133)	1 (.167) (.014)	1 (.167) (.143)		6
1 (.125) (.067)	1 (.125) (.014)	2 (.250) (.286)	1 (.125) (.050)	8
	1 (1.0) (.014)			1
9 (.290) (.600)	9 (.290) (.129)		1 (.033) (.050)	31
15	70	7	20	149

Table 10-11. Sizes of *Phidippus* species based on length (Florida records only). Species are listed in descending order by mean length of females. Species followed by the same letter are not significantly different within that sex (Duncan's Multiple Range Test). Number of specimens measured are given (n).

	Females			Males		
Phidippus sp.	n	$\bar{x}$		n	$\bar{x}$	
P. regius	66	14.93	a	53	11.96	a
P. otiosus	52	14.53	a	16	10.49	b
P. audax	54	11.16	b	41	8.92	c
P. apacheanus	11	10.82	b	8	8.54	c d
P. cardinalis	14	10.70	b	8	6.55	e
P. clarus	26	10.36	b	27	7.55	c d e
P. putnami	8	10.30	b	7	7.31	c d e
P. xerus	13	10.20	b	13	7.70	c d e
P. pulcherrimus	19	9.88	b	20	7.30	c d e
P. whitmani	6	9.70	b	5	6.74	d e

Table 10-12. Distribution by month of numbers of females of species of *Phidippus* (Florida records only); used to compare seasonal differences in size and age distribution.

Phidippus sp.	Jan.	Feb.	Mar.	Apr.	May	Jun.
P. apacheanus				1 (.100) (.024)	1 (.100) (.024)	
P. audax	1 (.008) (.077)	8 (.061) (.667)	16 (.122) (.327)	11 (.084) (.262)	20 (.057) (.488)	14 (.107) (.560)
P. cardinalis						
P. clarus						
P. otiosus	8 (.163) (.615)	1 (.021) (.083)	12 (.245) (.245)	5 (.102) (.119)		
P. pulcherrimus			8 (.533) (.163)	5 (.333) (.119)		1 (.067) (.040)
P. putnami						
P. regius	4 (0.47) (.308)	2 (.024) (.067)	11 (.129) (.224)	12 (.141) (.286)	11 (.129) (.268)	5 (.059) (.200)
P. whitmani			2 (.080) (.041)	8 (.320) (.190)	9 (.360) (.220)	4 (.160) (.160)
P. xerus		1 (.063) (.083)				1 (.063) (.040)
Totals	13	12	49	42	41	25

Table 10-12 extended.

Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Totals
		4 (.400) (.103)	3 (.300) (.115)	1 (.100) (.025)		10
13 (.099) (.325)	17 (.130) (.321)	4 (.030) (.103)	3 (.023) (.115)	15 (.115) (.375)	9 (.069) (.429)	131
					2 (1.0) (.095)	2
5 (.094) (.125)	22 (.415) (.415)	16 (.302) (.410)	6 (.113) (.231)	4 (.076) (.100)		53
	1 (.021) (.019)		3 (.061) (.115)	13 (.265) (.325)	6 (.122) (.256)	49
1 (.067) (.025)						15
3 (.200) (.075)	3 (.200) (.056)	9 (.600) (.230)				15
13 (.153) (.325)	2 (.024) (.037)	3 (.035) (.077)	11 (.129) (.423)	7 (.083) (.175)	4 (.047) (.190)	85
1 (.040) (.025)	1 (.40) (.019)					25
4 (.250) (.100)	7 (.437) (.132)	3 (.187) (.077)				16
40	53	39	26	40	21	401

Table 10-13. Distribution by month of numbers of males of species of *Phidippus* (Florida records only); used to compare mating seasons.

Phidippus sp.	Jan.	Feb.	Mar.	Apr.	May	Jun.
P. apacheanus	---	---	---	---	---	---
P. audax	1 (.007) (.500)	5 (.037) (.714)	9 (.066) (.429)	10 (.074) (.500)	26 (.191) (.765)	17 (.12 (.607)
P. cardinalis	---	---	---	---	---	---
P. clarus	---	---	---	---	---	1 (.02 (.036)
P. otiosus	---	---	---	---	---	---
P. pulcherrimus	---	1 (.091) (.143)	7 (.636) (.333)	2 (.182) (.100)	---	---
P. putnami	---	---	---	---	1 (.050) (.029)	2 (.10 (.071)
P. regius	1 (.019) (.500)	1 (.019) (.143)	5 (.096) (.238)	---	1 (.019) (.029)	1 (.01 (.036)
P. whitmani	---	---	---	8 (.471) (.400)	6 (.353) (.177)	3 (.11 (.107)
P. xerus	---	---	---	---	---	4 (.36 (.143)
Totals	2	7	21	20	34	28

Table 10-13 extended.

Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Totals
---	---	4 (.800) (.085)	---	1 (.200) (.030)	---	5
15 (.110) (.246)	11 (.081) (.239)	10 (.074) (.213)	8 (.059) (.276)	19 (.139) (.576)	5 (.037) (.714)	136
---	1 (.067) (.022)	8 (.533) (.170)	6 (.400) (.207)	---	---	15
21 (.412) (.344)	24 (.470) (.521)	5 (.098) (.106)	---	---	---	51
---	1 (.059) (.022)	7 (.412) (.149)	5 (.294) (.172)	3 (.176) (.091)	1 (.059) (.143)	17
---	---	---	---	1 (.091) (.030)	---	11
11 (.550) (.180)	4 (.200) (.087)	2 (.100) (.043)	---	---	---	20
8 (.154) (.131)	4 (.077) (.087)	11 (.212) (.234)	10 (.193) (.345)	9 (.173) (.273)	1 (.019) (.143)	52
---	---	---	---	---	---	17
6 (.545) (.099)	1 (.091) (.022)	---	---	---	---	11
61	46	47	29	33	7	335

Table 10-14. Niche breadth values for six niche dimensions of species of *Phidippus* (see Tables 10-7 through 10-13).

Phidippus sp.	Habitat	Microhabitat	Prey	Egg Site	Seasonal Size	Mating Season
P. apacheanus	1.000	3.259	2.000	1.000	4.131	1.649
P. audax	1.988	1.854	3.738	2.872	10.208	10.046
P. cardinalis	2.257	3.301	---	1.000	1.000	2.418
P. clarus	2.409	2.327	2.828	1.989	4.019	2.790
P. otiosus	2.473	2.259	4.767	1.590	6.138	3.916
P. pulcherrimus	1.662	2.342	5.657	1.000	2.897	2.813
P. putnami	2.814	1.461	1.000	2.000	2.586	3.529
P. regius	3.109	5.552	5.028	1.483	10.108	7.667
P. whitmani	1.000	1.103	1.889	---	4.416	2.795
P. xerus	1.312	3.160	---	1.000	3.936	2.501

Table 10-15. Niche overlap values between species pairs of _Phidippus_ based on four to six niche dimensions (see Table 10-14). Overall niche overlap is in the range between summation α and product α. Overlap of only one of several categories within a niche dimension is indicated by 1.0; non-overlap of only one category for one or both species compared within a niche dimension by 0. Complete overlap or non-overlap of two or more categories of a niche dimension for both compared species is indicated by 1.000 and 0.000, respectively.

Phidippus pairs	Habitat	Micro-habitat	Eggsac Site	Type of Prey	Seasonal Size	Mating Season	$\Sigma\ \alpha$	non-zero $\Pi\ \alpha$	$\Pi\ \alpha$
apacheanus x _audax_	0	0.324	0	0.715	0.466	0.639	0.357	0.069	0
apacheanus x _cardinalis_	1.0	0.682	1.000	---	0	1.0	0.736	0.682	0
apacheanus x _clarus_	0	0.799	0	0	0.948	1.0	0.458	0.757	0
apacheanus x _otiosus_	0	0.148	1.0	1.0	0.553	0.978	0.613	0.080	0
apacheanus x _pulcherrimus_	0	0.586	0	1.00	1.0	1.0	0.598	0.586	0
apacheanus x _putnami_	1.0	0.494	0	0	1.0	1.0	0.582	0.494	0
apacheanus x _regius_	1.0	0.384	1.0	0.848	0.764	0.866	0.810	0.215	0.215
apacheanus x _whitmani_	0	0.886	---	0	0.997	0.000	0.377	0.863	0.000
apacheanus x _xerus_	1.0	0.980	0	---	1.0	0.000	0.596	0.980	0.000
audax x _cardinalis_	0	0.683	0	---	1.0	0.868	0.510	0.593	0
audax x _clarus_	1.0	0.827	0.766	0.594	0.708	0.548	0.741	0.146	0.146
audax x _otiosus_	0.762	0.180	1.0	0.617	0.561	0.831	0.659	0.039	0.039
audax x _pulcherrimus_	1.0	0.266	0	0.567	0.719	0.733	0.548	0.079	0
audax x _putnami_	0.000	0.160	1.0	1.0	0.568	0.604	0.555	0.055	0.000

Table 10-15 continued.

Phidippus pairs	Habitat	Micro-habitat	Eggsac Site	Type of Prey	Seasonal Size	Mating Season	$\Sigma \alpha$	non-zero $\Pi \alpha$	$\Pi \alpha$
audax x regius	1.0	0.456	1.0	0.398	0.755	0.702	0.719	0.069	0.069
audax x whitmani	0	1.0	---	0.519	0.804	0.810	0.627	0.338	0
audax x xerus	0.000	0.337	1.0	---	0.794	0.952	0.617	0.255	0.000
cardinalis x clarus	1.0	0.972	0	---	0	0.323	0.459	0.314	0
cardinalis x otiosus	1.0	0.537	1.0	---	1.0	1.000	0.907	0.537	0.537
cardinalis x pulcherrimus	0.258	0.929	0	---	0	0.000	0.237	0.240	0.000
cardinalis x putnami	0.984	0.823	0	---	0	0.554	0.472	0.449	0
cardinalis x regius	0.947	0.527	1.0	---	1.0	0.988	0.892	0.493	0.493
cardinalis x whitmani	0	0.928	---	---	0	0.000	0.232	0.928	0.000
cardinalis x xerus	0.772	0.892	0	---	0	1.0	0.533	0.689	0
clarus x otiosus	1.0	0.946	0.000	1.0	0.194	0.340	0.580	0.062	0
clarus x pulcherrimus	0.832	0.496	1.0	0.994	1.0	0.000	0.720	0.410	0.000
clarus x putnami	1.0	0.382	1.0	1.0	0.857	0.833	0.845	0.273	0.273
clarus x regius	0.592	0.954	0.000	1.0	0.551	0.646	0.624	0.201	0.000
clarus x whitmani	0	1.0	---	0	0.809	1.0	0.562	0.809	0

Table 10-15 continued.

Phidippus pairs	Habitat	Micro-habitat	Eggsac Site	Type of Prey	Seasonal Size	Mating Season	$\Sigma \alpha$	non-zero $\Pi \alpha$	$\Pi \alpha$
clarus x *xerus*	0.000	0.766	0	---	0.907	0.462	0.427	0.321	0.000
otiosus x *pulcherrimus*	0.980	0.800	0	0.893	0.984	1.0	0.776	0.689	0
otiosus x *putnami*	1.0	0.096	1.0	1.0	1.000	0.569	0.778	0.055	0.055
otiosus x *regius*	0.288	0.481	0.858	0.996	0.786	0.945	0.726	0.064	0.064
otiosus x *whitmani*	0	1.0	---	1.0	0.619	0.000	0.524	0.619	0.000
otiosus x *xerus*	1.000	0.245	1.0	---	0.708	1.0	0.791	0.173	0.173
pulcherrimus x *putnami*	0.452	0.993	1.0	1.0	1.0	0.000	0.741	0.449	0.000
pulcherrimus x *regius*	0.400	0.311	0	0.893	0.794	0.991	0.565	0.087	0
pulcherrimus x *whitmani*	0	1.0	---	1.0	0.693	1.0	0.739	0.693	0
pulcherrimus x *xerus*	1.0	0.660	0	---	0.807	0.000	0.493	0.533	0.000
putnami x *regius*	0.900	0.280	1.0	1.0	0.529	0.715	0.737	0.095	0.095
putnami x *whitmani*	0	0.000	---	0	1.000	0.802	0.360	0.802	0.000
putnami x *xerus*	0.844	0.590	1.0	---	0.719	0.804	0.791	0.288	0.288
regius x *whitmani*	0	0.179	---	0.998	0.821	0.940	0.588	0.138	0
regius x *xerus*	0.527	0.527	1.0	---	0.749	0.708	0.702	0.147	0.147

Table 10-15 continued.

Phidippus pairs	Habitat	Micro-habitat	Eggsac Site	Type of Prey	Seasonal Size	Mating Season	$\Sigma \propto$	non-zero $\Pi \propto$	$\Pi \propto$
whitmani x *xerus*	0	1.0	---	---	0.411	1.0	0.603	0.411	0
Average and standard error	0.523 ±0.068	0.611 ±0.046	0.517 ±0.083	0.715 ±0.072	0.679 ±0.049	0.671 ±0.054	0.611 ±0.024	0.384 ±0.042	0.058 ±0.019

Figure 10-1. Adult phenology of eastern U. S. species of *Phidippus*. Numbers given are actual numbers of specimens examined. Florida records should be subtracted from total to find number of non-Florida records. Note different scales for each histogram. Key to symbols is as follows:

	Males	Females
Non-Florida	☐	⬚
Florida	■	⁘

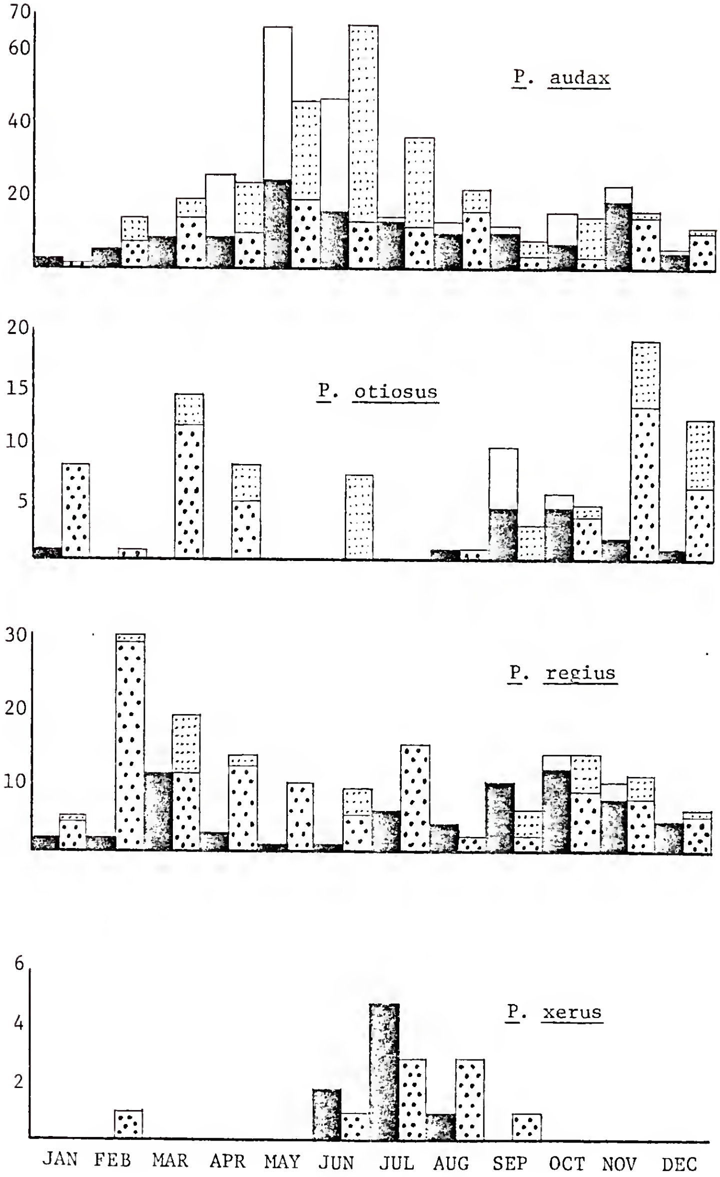

70
60
40
20
P. audax
20
15
10
5
P. otiosus
30
20
10
P. regius
6
4
2
P. xerus
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

Figure 10-1 (continued).

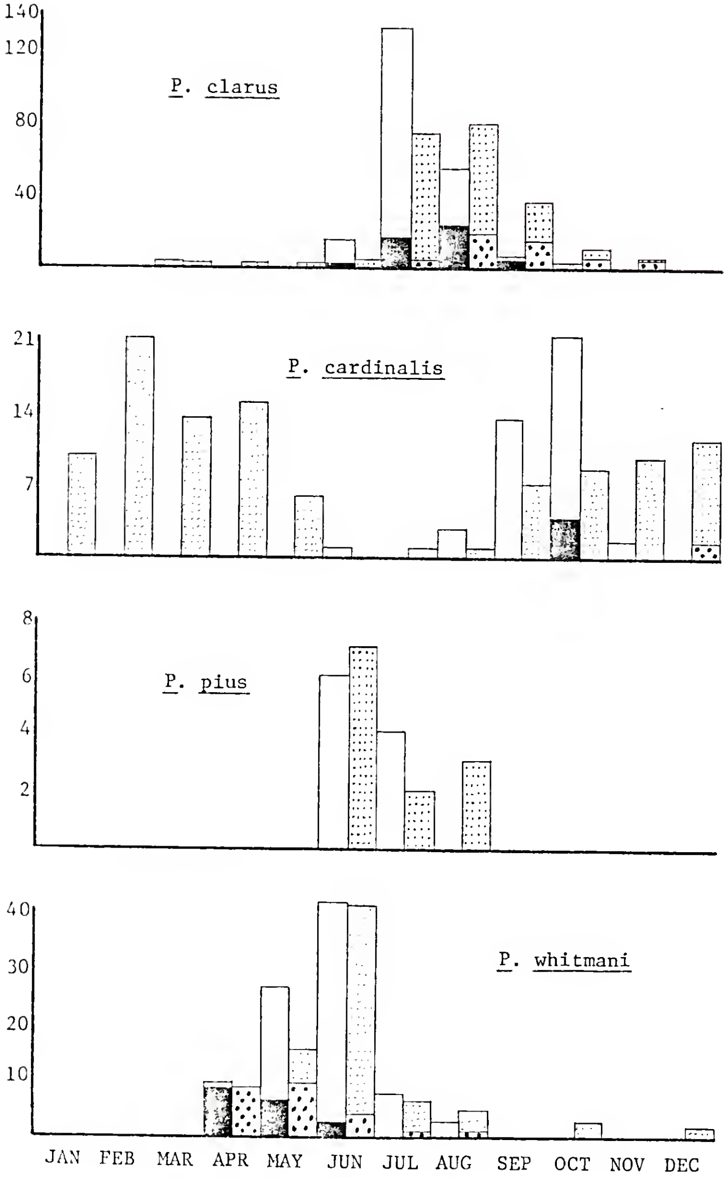

140
120
80
40
P. clarus
21
14
7
P. cardinalis
8
6
4
2
P. pius
40
30
20
10
P. whitmani
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

Figure 10-1 (continued).

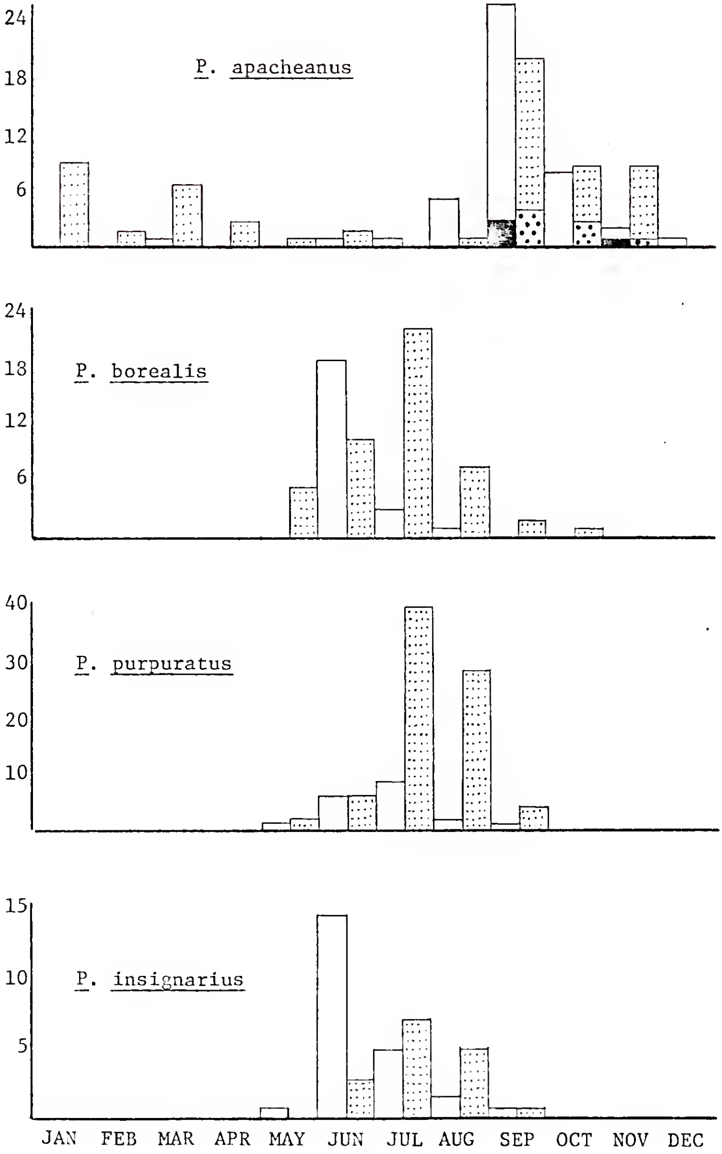

24
18
12
6
P. apacheanus
24
18
12
6
P. borealis
40
30
20
10
P. purpuratus
15
10
5
P. insignarius
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

Figure 10-1 (continued).

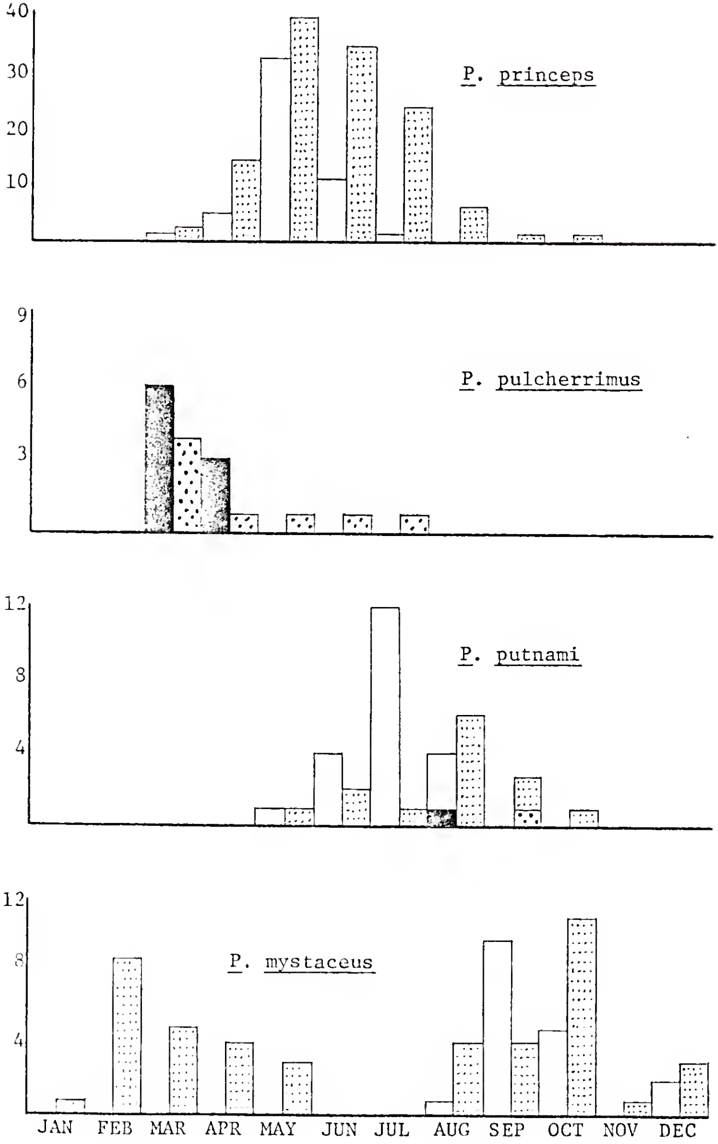

40
30
20
10
P. princeps
9
6
3
P. pulcherrimus
12
8
4
P. putnami
12
8
4
P. mystaceus
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

Figure 10-2. Pharate adult of *Mantispa viridis* emerging from eggsac of *Phidippus clarus*; November, 1976. Photograph taken in old field section of xeric ecotone study area.

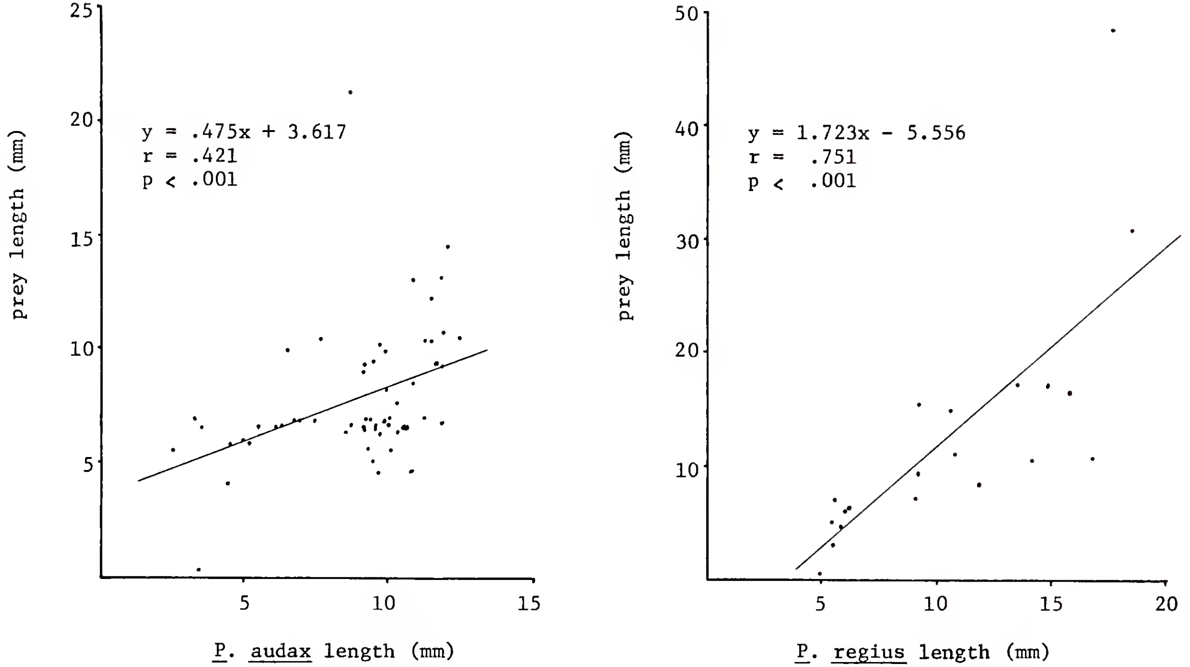


Figure 10-3. Comparison of prey length to spider length for P. audax and P. regius.

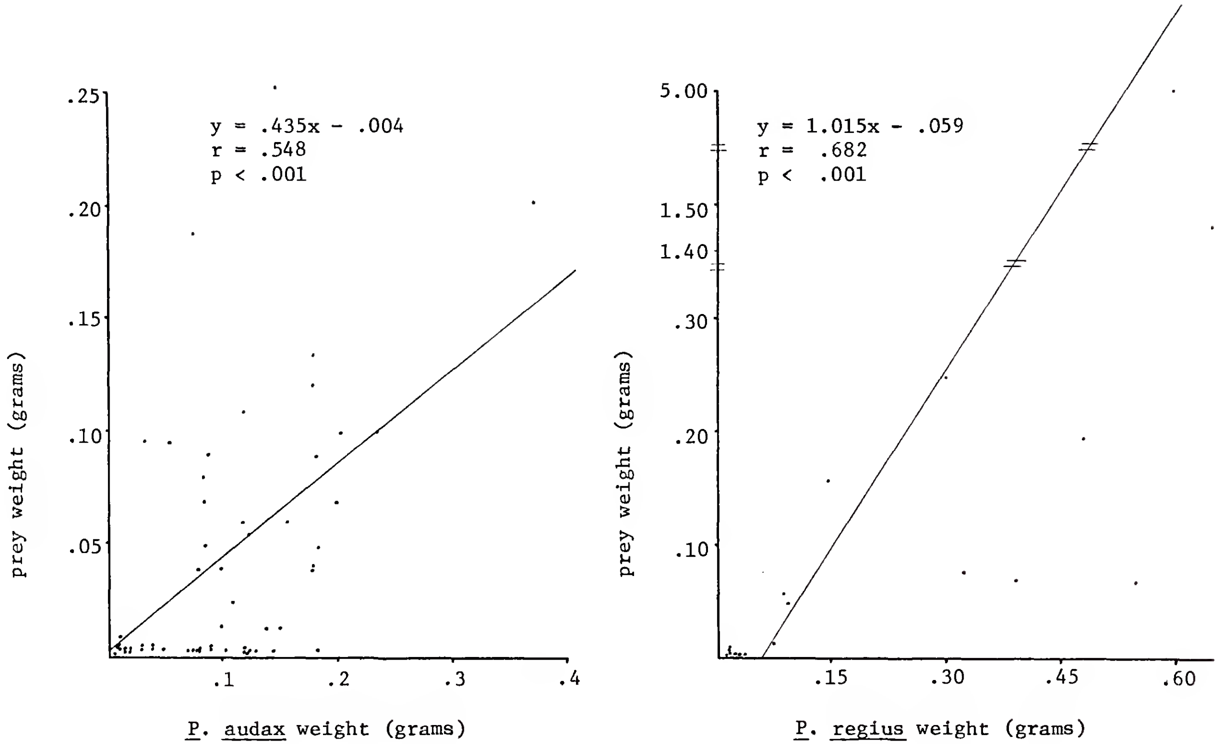


Figure 10-4. Comparison of prey weight to spider weight for _P. audax_ and _P. regius_.

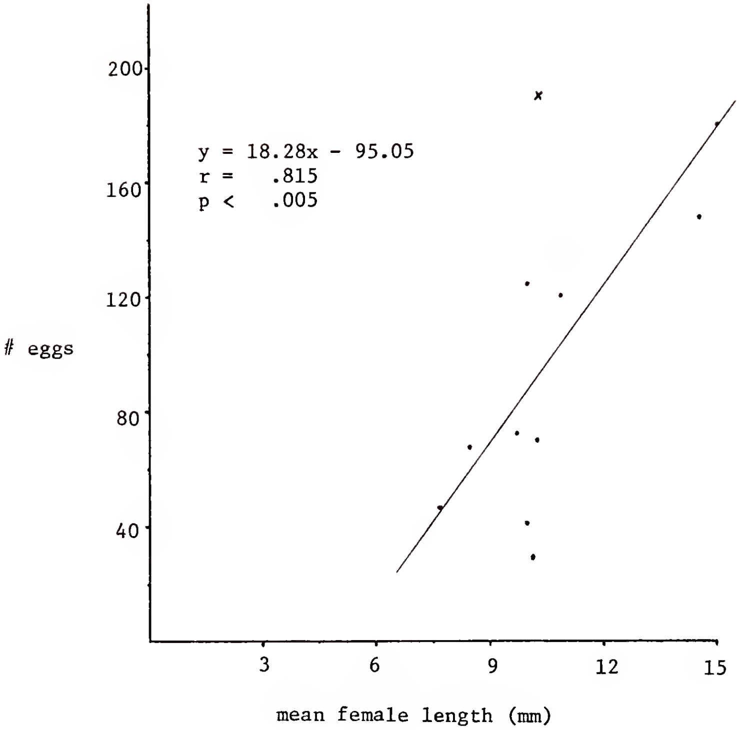


Figure 10-5. Correlation of mean female length to clutch size for first eggsac of eastern species of Phidippus (Florida P. clarus not included). Florida P. clarus indicated by an x.

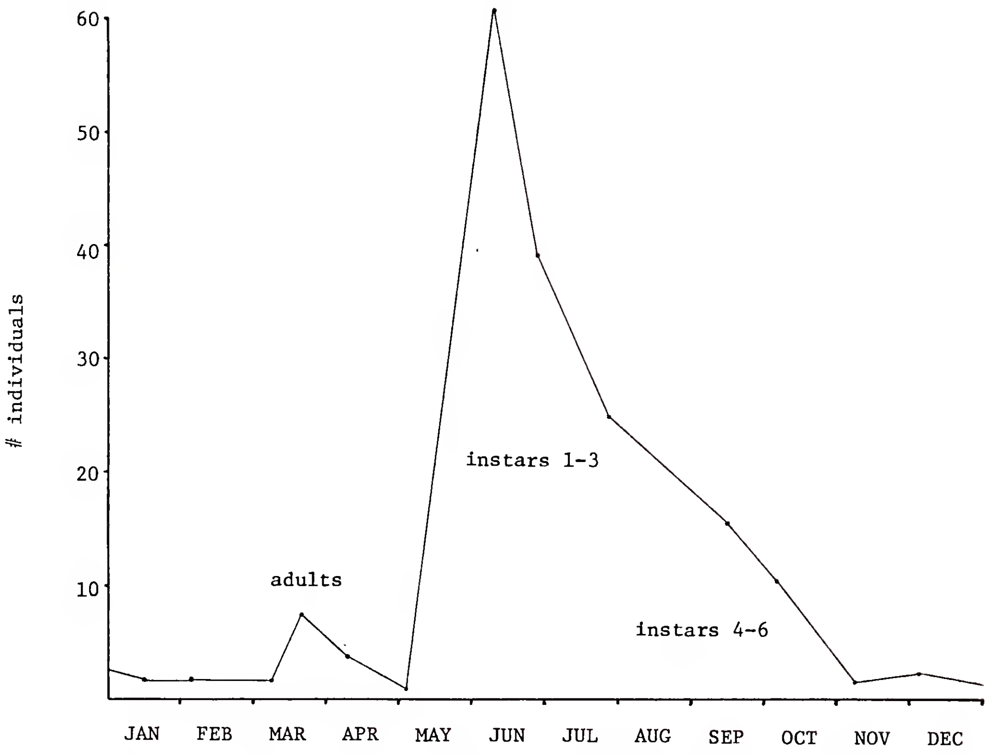


Figure 10-6. Number of individuals of P. pulcherrimus observed and/or collected by sweep net during 1976 on a 0.1 hectare plot in a pine flatwoods 4 miles north of Cross Creek, Alachua Co., Florida.

CHAPTER 11
SYNTHESIS

Two subgenera, *Phidippus* (the nominate form) and *Anipalpus* (new subgenus) are represented in eastern North America. Courtship behavior of members of the subgenus *Phidippus* is similar among species, but the two species placed in *Anipalpus* (*P. putnami* and *P. mystaceus*) have distinctly different courtships, both from the other species and from each other. The peculiar rotary courtship of *P. putnami* and the stridulatory courtship of *P. mystaceus* are so different that this subgenus as presently defined may actually consist of two phylogenetic lines. The stridulatory courtship of *P. mystaceus* is the first known for the family. *Phidippus whitmani* is the first known salticid to use vibration during its visual (Type I) courtship; other species of *Phidippus* use vibration during tactile (Type II) courtship (Edwards, 1975; Jackson, 1977).

In a little over a decade, understanding of the visual system and associated visually-oriented behaviors of salticids has improved from a position of relative obscurity to a point where research on the complex visual system of these spiders is revealing some amazing capabilities. Papers by Land (1969a, b, 1971, 1972), Forster (1977a, 1979), and Hill (1979) have demonstrated that salticids can see in color to infinity, can scan and focus with their main eyes, and can accurately turn the body so as to orient the main eyes to evaluate stimuli detected by the secondary eyes; then they can accurately guage the distance of the stimulus object with their binocular vision. The possibility that prey may be detected through reception of aerial vibrations (Forster, 1979) deserves further study.

Hill (1979) has shown that *Phidippus* can orient on distant targets, whether those targets are plant configurations or other animals, and the spiders can attain a target location by a circuitous route without having to constantly view the target, indicating a short-term memory for locations. Jackson (1979) found that *Phidippus* could forage a considerable distance and then return to the nest, indicating a memory capability for locations of a somewhat longer-lasting type than demonstrated by Hill; evidence presented for *P. regius* herein indicates that under certain conditions, females may become territorial and forage repeatedly from a single nest for several weeks. Individual *Phidippus* frequently assume perches near the tops of tall plants, where they can survey the surrounding area for prey.

Not only can *Phidippus* approach prospective prey in a circuitous manner, but I have shown (Chapter 7) that once within striking range, the spider will use an attack strategy that minimizes the prey's escape and defense capabilities, depending on the size and motility of the prey. The spider probably evaluates both morphological and behavioral attributes of the prey when choosing an attack strategy. More motile prey are approached in a more stealthy manner and attacked from farther away than slow-moving prey; this behavior appears to be instinctive, as the same attack behaviors were demonstrated by naive spiderlings. On the other hand, naive spiderlings will attack any prey, but quickly learn to avoid ants, further demonstrating their memory capabilities. *Phidippus* species fed on a wide variety of prey under natural conditions, and *P. audax* demonstrated a capability of exploiting a high density monospecific prey source.

The hypothesis that *Phidippus* (and other vagrant females) guard their eggsacs from egg predators and parasites is untenable (or at least the females are unsuccessful), considering the high infestation rate of exposed eggsacs (e.g., of *P. clarus*). A more likely explanation is that due to physiological constraints, perhaps due to energetically expensive specializations (e.g., vision in salticids), females lack sufficient resources to construct adequately-protective eggsacs, so must care for the eggs to ensure that they hatch.

The most important enemies of free-living instars of *Phidippus* both in the literature and in this study were found to be Hymenoptera, especially Sphecidae. However, a strong vertebrate predation pressure is indicated by some species (in open, especially xerophytic, habitats) which have apparently evolved mutillid mimicry in both color pattern and behavior. Species of *Phidippus* living in the herb-shrub zone frequently traverse from plant to plant via the ground and virtually never use bridge lines (Hill, 1978; Tessler, personal communication; personal observation); mutillids are mostly terrestrial. Fitch (1963) reported numerous instances of lizards preying on *P. audax* in a prairie habitat. Similar habitats are frequented by *P. apacheanus* and *P. cardinalis*, males of which are strikingly marked with red and black like many mutillids; other stages of *P. apacheanus* are also red or yellow and black. Since males of most species lacking a red dorsal pattern are black with white markings, one could speculate that these species might mimic pompilids. Females and immatures of most species are cryptic in coloration.

Of the three species of eastern *Phidippus* not occurring in Florida, only *P. borealis* does not have a southern counterpart and is poorly known. The allopatric species pairs *P. insignarius* - *P. xerus* and *P. princeps* - *P. pulcherrimus*, especially the latter pair which are allopatric sister species, appear to be ecological replacements based on a comparison of literature records of habitat, museum records of adult phenology, and this study. I have collected *P. princeps* on several occasions from Maryland to Missouri, always from fields and transitional areas (see also Hill, 1977c). Lowrie's studies (1942, 1948) indicate *P. insignarius* to be an inhabitant of fields and open xeric woodland understory. The habitats of both of these species correspond well with those of *P. pulcherrimus* and *P. xerus*, respectively, which replace them in Florida. The maturation seasons of *P. insignarius* and *P. xerus* are identical, while *P. pulcherrimus* matures a little earlier than *P. princeps*, but their reproductive periods are similar.

Sympatric species of *Phidippus* showed clear patterns of competition avoidance, subdividing available resources by habitat, microhabitat, or season; in only 1 of 45 species pair comparisons with 10 species was it necessary to invoke size differences as a partial explanation of resource subdivision; only two closely related species (*P. otiosus* and *P regius*), which were shown to hybridize in the wild as well as under laboratory conditions, were significantly larger than the other species studied. Most species occured in the herb-shrub zones throughout part or all of their life cycle. However, *P. whitmani* was specialized for mesophytic leaf litter, and *P. otiosus* was primarily a canopy species. Where palms were available in old field or transitional habitats, they were occupied by subadults and adults of *P. regius*.

Intraspecific interference competition (especially cannibalism) appeared to be more important than interspecific interactions in population regulation.

APPENDIX A
GLOSSARY

ALE - Anterior lateral eyes, the outer pair of eyes in the first eye row; these eyes detect motion and are important in depth perception.

AME - Anterior median eyes, the inner pair of eyes in the first eye row; these eyes are used to focus on target objects; they have the following capabilities: focus to infinity, scanning, and color vision.

Apophysis - An integumental projection; in spiders, usually referring to a projection of the palpus, most often on the retrolateral (or ectal) surface of the palpal tibia; it engages in a median notch of the epigynum to properly orient the embolus for mating.

BL - Body length, measured from the front of the anterior median eyes (AME) to the end of the opisthosoma (abdomen), not including the spinnerets; measurement taken from life-like position of spider, with slight overlap of prosoma and opisthosoma.

Brush - A multiple fringe, covering three or all four sides of a leg segment (see fringe).

CL - Carapace length, including anterior median eyes.

CW - Carapace width, across widest point just behind posterior lateral eyes (PLE).

Clypeus - That part of the carapace between the anterior eye row and the chelicerae.

Cymbium - The palpal tarsus of the male, when formed into a bowl shape to contain the reproductive organ.

Embolus - The intromittent organ; usually spine-like or spatulate in shape.

Endite - A modified palpal coxa; the pair of endites are used as accessory mouthparts and assist in manipulating food items.

Epigynum - A sclerite associated with the female gonopore, containing openings through which sperm is passed to the spermathecae during copulation.

Fan - A row of setae oriented perpendicular to the long axis of the leg segment; also perpendicular to the integument, and since the segment is rounded, the setae are arranged in the shape of a fan; a transverse fringe.

File - A series of integumental ridges which is moved against an inner branch (plectrum) of the palpal tibial apophysis in P. mystaceus, producing a trill during courtship.

Fringe - A row or rows of usually very long setae oriented along one surface of the long axis of a leg or palpal segment; often in alternating color patterns on alternate leg segments (see brush). Also used to refer to rows of setae on other body parts, e.g., on clypeus, above eyes.

Guide - An expanded part of the anterior lateral rim of the epigynum, forming an inner groove which alines the embolus with the spermathecal duct opening.

LOQ - Length of ocular quadrangle, measured from anterior edge of anterior median eyes (AME) to posterior edge of posterior lateral eyes (PLE).

Macroseta - An enlarged seta, with a basal diameter at least twice that of a vestitural seta, and usually much less attenuate and proportionally shorter than a vestitural seta.

Ocular Quadrangle - A rectangular area on top of the cephalic area of the carapace which is bounded by the anterior and posterior lateral eyes (ALE and PLE).

PLE - Posterior lateral eyes, the pair of eyes forming the third eye row; these eyes detect motion over a wide field of view to each side of the spider.

PME - Posterior median eyes, a pair of very small eyes which form the second eye row; their function is unknown.

Plectrum - An integumental projection moved against a file during stridulation; in this case, an inner branch of the palpal tibial apophysis of male P. mystaceus which contacts a file on the cymbium, producing an audible trill.

Protegulum - The distal-most part of the tegulum, separated from the tegulum by a suture; generally present in dendryphantine salticids, and often highly rugose, especially in Phidippus species. The embolus arises from the protegulum.

Septum - An anterior longitudinal keel or ridge midway between the two copulatory openings of the epigynum.

Tegulum - A sclerotized bulbous structure, fitting into the "bowl" of the cymbium, which contains the sperm storage duct of the male.

Tuft - A minimum of three elongate vestitural setae, noticeably longer than surrounding setae, which are more closely spaced (concentrated into a small area of the integument) than surrounding setae; especially prominent in and near the ocular quadrangle; sometimes present on femur I of males.

APPENDIX B
PLACE NAMES

Explanations are provided below for abbreviations of institutions used in the text.

AMNH - American Museum of Natural History
New York, New York
Curator of Arachnida and Myriapoda: Dr. N. I. Platnick

BMNH - British Museum (Natural History)
London, Great Britain
Curator of Arachnida: Mr. F. R. Wanless

MCZ - Museum of Comparative Zoology
Cambridge, Massachusetts
Curator of Arachnida and Myriapoda: Dr. H. W. Levi

SIU - Southern Illinois University
Carbondale, Illinois
Curator of Arachnidae: Dr. J. A. Beatty

USNM - United States National Museum
Washington, D. C.
Curator of Arachnida and Myriapoda: Dr. R. A. Crabill

OSU - Ohio State University
Columbus, Ohio
Curator: Dr. C. A. Triplehorn

APPENDIX C
LAKE EDGE HABITATS

I compared spider populations along the shores of Burnt Pond (YMCA Camp McConnell) and Newnan's Lake (1976 and 1977, respectively). Both populations of spiders were greatly influenced by populations of chironomids, especially _Glyptodentipes paripes_ (Edwards), which occur literally by the millions during the warmer months of the year and provide food for many different predators. Species are listed by descending order of abundance, and population estimates are given for the more abundant species per 0.004 hectare. Population estimates were made from a combination of visual sighting, hand collecting, and sweeping. Only arboreal species are represented. All but the last species in each list are either orb weavers or jumping spiders, the latter marked with asterisks (*).

Burnt Pond

*_Dendryphantes marginatus_ (Walckenaer)	> 200
*_Phidippus audax_ (Hentz)	> 100
Tetragnatha spp.	> 50
Acanthepeira sp.	> 20
*_Thiodina peurpera_ (Hentz)	> 20
*_Phidippus regius_ C. L. Koch	> 20
*_P. pulcherrimus_ Keyserling	
*_P. clarus_ Keyserling	
*_P. otiosus_ (Hentz)	
Argiope aurantia (Lucas)	
*_Dendryphantes galathea_ (Walckenaer)	
*_Zygoballus rufipes_ Peckhams	
Sosippus floridanus Simon	

Newnan's Lake

Tetragnatha guatemalensis O.P.-C.	> 1000
T. elongata Walckenaer	> 1000
T. nitens (Audouin)	> 100
*_Phidippus audax_ (Hentz)	> 100
Nuctenea cornuta (Clerck)	> 20
*_Phidippus otiosus_	> 20

Newnan's Lake (cont.)

Argiope aurantia (Lucas)
Nephila clavipes (L.)
*Marpissa bina (Hentz)
Neoscona domiciliorum (Bryant)
N. hentzi (Keyserling)
*Zygoballus nervosus (Peckhams)
Araneus bicentenarius (McCook)
Tidarren sisyphoides (Walckenaer)

Lake Edge Habitat without Canopy

This habitat was located on the north edge of Burnt Pond, east of the pier; approximately 0.01 hectare. Vegetation stratified away from lake edge, in order of further distance from lake: Typha acalypha (cattail); Echinochloa Walteri (a broad-leaved grass); Lactuca sp. (composite); mixed grasses and herbs; Rubus sp. (blackberry), Andropogon virginicus (broomsedge), and perennials such as Eupatorium and Boehmeria. The north edge was bounded by Paspalum notatum (bahia grass) and Liquidambar styraciflua L. (sweet gum), while the northeast corner was bordered by several Sabal palmetto (cabbage palm)(Figures C-1, C-2).

Lake Edge Habitat with Canopy

This area was on the west edge of Newnan's Lake, just south of unmarked public boat landing; approximately 0.004 hectare. Primarily it consisted of a mixture of Sacciolepis striata (a broad-leaved grass) and Bidens pilosa (shepherd's needle), with some Lactuca floridana along the west edge. It was bordered on north and south edges by Taxodium distichum (bald cypress), Fraxinum caroliniana (pop ash), and Liquidambar styraciflua; on west edge by bahia grass and road.

Figure C-1. Part of study site at Burnt Pond, consisting of dense growth of *Echinochloa Walteri*.

Figure C-2. Northeast corner of study site at Burnt Pond, showing *Sabal palmetto* and *Eupatorium capillifolium*. Undergrowth consists of *Rubus* sp. as well as numerous small grasses and herbs.

APPENDIX D
OTHER STUDY HABITATS

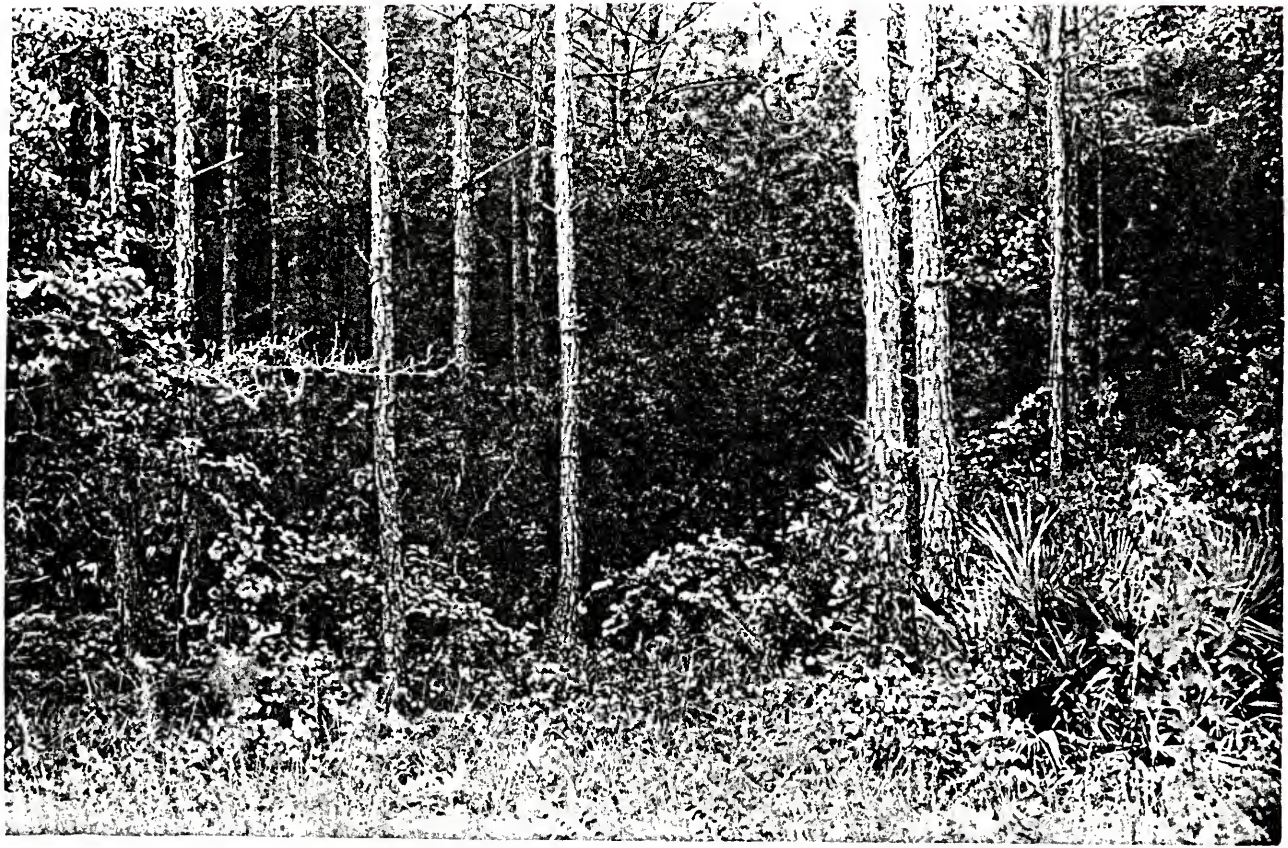
Primary Habitats

Mixed xeric ecotone. This habitat was located four miles east of Interstate 75 on hwy 24, Alachua Co., FL. A xeric hammock with mixed ecotonal areas, consisting of open woodland or xeric old field with scattered trees. Dominant ground cover plants were *Andropogon virginicus* (broomsedge), *Rubus* sp. (blackberry), *Eupatorium capillifolium* (dogfennel), *Boehmeria* sp., *Vaccinium arboreum*, and numerous mixed grasses and small herbs. Trees were a mixture of *Quercus* spp., including *Q. virginiana* (live oak), *Q. laevis* (turkey oak), and *Q. falcata* (southern red oak), and *Carya tomentosa* (pignut hickory). *Aristida stricta* (wire grass) is the predominant ground cover in areas of extensive turkey oak. The primary study area was approximately 0.5 hectare which was divided into old field and open woods habitats (Figure D-1).

Pine flatwoods. This habitat was located four miles north of Cross Creek on hwy 325, Alachua Co., FL. A mixed pine-oak flatwoods, with varying amount of understory. *Serenoa repens* (saw palmetto) and *Lyonia ferruginea* each formed dense thickets in some areas, whereas more open areas were dominated by *Vaccinium myrsinites* and *Quercus* spp. saplings, as well as numerous small herbs and grasses. Primary canopy species were *Pinus elliottii* (slash pine) and *Quercus nigra* (water oak). Boundaries were the south edge of a *Lyonia* thicket, a path on the east, and the north and west sides of a small clearing extended. Primary study area was approximately 0.1 hectare (Figure D-2).

Figure D-1. Interface of field and woods, mixed xeric ecotone, 4 miles west of Gainesville.

Figure D-2. Pine flatwoods with hardwood understory, near Cross Creek.

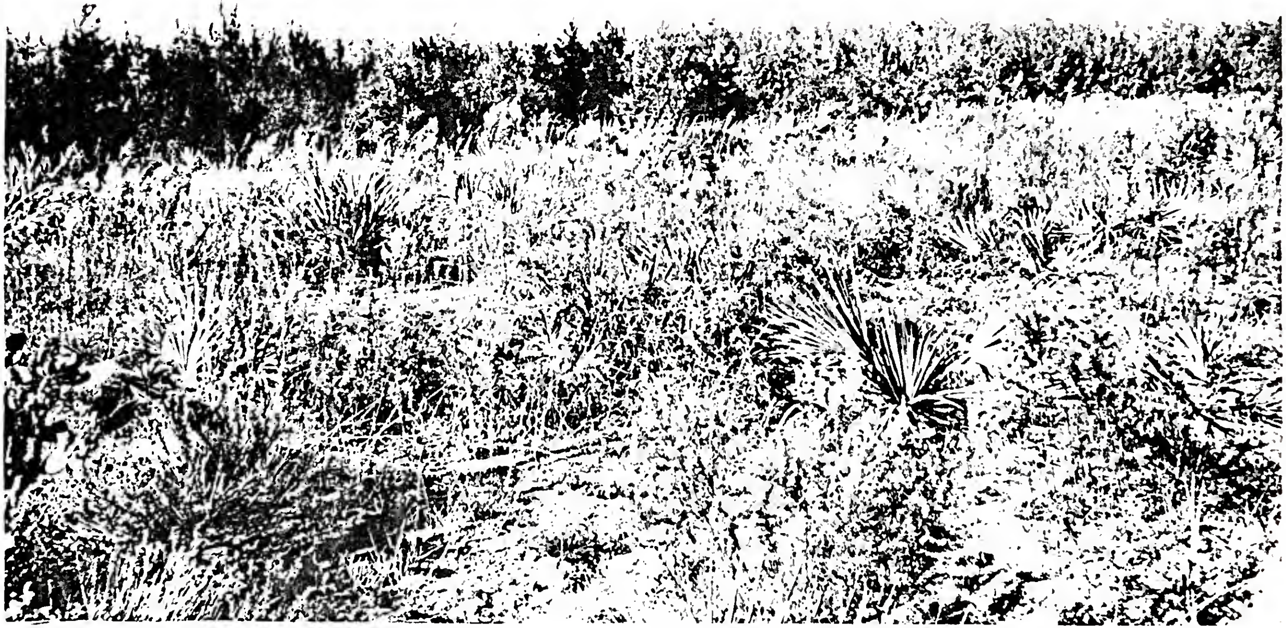


Secondary Habitats

Xerophytic field. This area was half a mile west of the Central Tower on the north side of hwy 40, Ocala National Forest, Marion Co., FL. In an area cleared for a powerline, this very xeric field featured a sparse ground cover of some of the hardier old field plants (e.g., Eupatorium), scattered small herbs and grasses (including Cenchrus sp. sandspurs), Opuntia sp. (prickly pear cactus), Serenoa repens, Ceratiola ericoides (rosemary), and 4 species I classified and lumped together as woody herbs: Vaccinium myrsinites, Garberia heterophylla, Baptisia lecontei, and Calamintha ashei. The east and west boundaries were typical sand pine scrub, a mixture of Pinus clausa (sand pine), Quercus virginiana var. maritima (scrub live oak), Quercus myrtifolia (myrtle oak), Quercus chapmanii (Chapman's oak), Quercus laevis, Ceratiola ericoides, Sabal etonia (blue palmetto), Serenoa repens, and Lyonia spp. The north boundary was an almost bare gound area, and the road was the south boundary. Primary study area was approximately 0.2 hectare (Figure D-3) including the edges of the woods on both sides; especially important were edge areas where scrub oaks had grown back but no pines were present.

Mesophytic field-forest transition. This area was at the top of a hill about 100 m north of Burnt Pond; approximate area was 0.2 hectare. The study area was essentially a rectangle of Sabal palmetto (cabbage palm) surrounding low herbaceous growth, with a clump of Liquidambar styraciflua (sweet gum) occupying much of the middle along the longitudinal axis of the rectangle (east-west). Eleven palms were numbered and female P. regius occupying each of these numbered palms were correspondingly marked on the legs (in a unique manner for each specimen) with yellow acrylic paint.

Figure D-3. Timbered scrub (xerophytic field) in Ocala National Forest.



APPENDIX E
PREY OF MUD DAUBERS

Below is a list of the spiders (Araneae) taken from nests of the mud dauber, *Trypargilum clavatum* (Say). The collection was made July 18, 1974, near Tall Timbers Research Station, Leon County, Florida. Approximately 20 cells belonging to 12 mud nests are represented.

Taxon	♂	♀	im.	Total	%
Araneidae				(4)	2.5
Araneus prunus Levi		1		1	
Araneus spp.			2	2	
Eustala anastera (Walckenaer)		1		1	
Mimetidae				(1)	0.6
Mimetus notius Chamberlin		1		1	
Philodromidae				(5)	3.1
Philodromus placidus Banks		1	4	5	
Pisauridae				(1)	0.6
Dolomedes sp.			1	1	
Salticidae				(126)	78.3
Dendryphantes marginatus (Walckenaer)	13	12	23	48	
D. pineus (Kaston)	2	1		3	
Hentzia mitrata (Hentz)	5	4	4	13	
H. palmarum (Hentz)	6	6	3	15	
Lyssomanes viridis (Walckenaer)		1		1	
Metacyrba undata (De Geer)		2		2	
Phidippus otiosus (Hentz)			26	26	
P. audax (Hentz)			2	2	
Thiodina sylvana (Hentz)		2	11	13	
Tutelina n. sp.		1		1	
Zygoballus nervosus (Peckhams)		2		2	
Thomisidae				(23)	14.3
Coriarachne versicolor (Keyserling)		1		1	
Misumenops oblongus (Keyserling)	2				
Tmarus floridensis Keyserling	4	6	4	14	
Tmarus rubromaculatus Keyserling	2	3	1	6	
				161	

APPENDIX F
NEW RECORDS OF PREY CAPTURED BY SALTICIDS OTHER THAN *Phidippus*

The format follows that used in Table 10-5. These records were mostly taken incidental to research with species of *Phidippus*.

Salticid Species	Stage	Taxon of Prey		Stage	# Records
Corythalia canosa (Walckenaer)					
		Isoptera			
	A	Rhinotermitidae:	*Reticulitermes lageni* Banks	A	1
		Dermaptera			
	A,N	Labiduridae:	*Euborellia annulipes* (Lucas)	A,N	2
		Psocoptera			
	A	Caeciliidae:	*Caecilius flavidus* (Stephens)	A	1
		Hemiptera			
	A	Miridae:	undetermined genus	A	1
		Diptera			
	N	Mycetophilidae:	*Mycetophila* sp.	A	1
		Hymenoptera			
	N	Formicidae:	*Camponotus nearcticus* Emery	W	1
	A		*Conomyrma* n. sp.	W	1
	A		*Solenopsis geminata* (Fabr.)	W	1
		Araneae			
	A	Salticidae:	*Corythalia canosa* (Walckenaer)	A	1
	A	Undetermined family		N	1

Salticid Species	*Stage*	Taxon of Prey		*Stage*	*# Records*
Dendryphantes marginatus (Walckenaer)		Diptera			
	A,N	Chironomidae:	*Glyptotendipes paripes* (Edwards)	A	23
		Araneae			
	N	Salticidae:	*Phidippus audax* (Hentz)	N	1
Habrocestum bufoides		Homoptera			
Chamberlin & Ivie	A	Aphidoidea:	undetermined family	N	1
Hentzia grenada (Peckham & Peckham)		Diptera			
	N	Chironomidae:	*Chironomus brunneipennis* Johannsen	A	1
Hentzia palmarum (Hentz)		Diptera			
	N	Dolichopodidae:	*Sciapus variegatus* (Loew)	A	1
	N	Tipulidae:	*Gonomyia puer* Alexander	A	1
	A	Undetermined family		A	1
		Hymenoptera			
	A	Formicidae:	*Monomorium*? sp.	A	1
	A		*Pseudomyrmex pallidus* F. Smith	W	1
Lyssomanes viridis (Walckenaer)		Diptera			
	A	Dolichopodidae:	*Condostylus crinitus* (Ald.)	A	1
	N		*Condostylus graenicheri* Van D.	A	1
Maevia inclemens (Walckenaer)		Araneae			
	A	Salticidae:	*Maevia inclemens* (Walckenaer)	A	2
Metacyrba undata (De Geer)		Psocoptera			
	N	Lepidopsocidae:	*Echmepteryx youngi* Mockford	A	1

Salticid Species	Stage		Taxon of Prey	Stage	# Records
Metaphidippus galathea (Walckenaer)	Hemiptera				
	A	Pentatomidae:	*Acrosterum* sp.	N	1
		Diptera			
	A	Bibionidae:	*Plecia nearctica*	A	1
	N	Chironomidae:	*Glytotendipes paripes* (Edwards)	A	1
		Araneae			
	A	Thomisidae:	*Misumenops celer* (Hentz)	A	1
Pellenes brunneus Peckham & Peckham		Collembola			
	A	Entomobryidae:	undetermined genus	A	1
Pellenes carolinensis Peckham & Peckham		Araneae			
	A	Salticidae:	*Phlegra hentzi* (Marx)	N	1
Pellenes trimaculatus (Bryant)		Orthoptera			
	A	Tetrigidae:	*Nomotettix cristatus* Scudder	N	1
		Hymenoptera			
	A	Formicidae:	*Pheidole* sp.	A	1
Thiodina peurpera (Hentz)		Araneae			
	A	Oxyopidae:	*Peucetia viridans* (Hentz)	N	1
Thiodina sylvana (Hentz)		Orthoptera			
	A	Acrididae:	undetermined genus	N	1
	N	Gryllidae:	*Cycloptilum* sp.	N	1

Salticid Species	Stage	Taxon of Prey		Stage	# Records
Thiodina sylvana (Hentz) (continued)					
		Lepidoptera			
	A	Satyridae:	*Euptychia hermes sosybia* (Fabr.)	A	1
	A	Undetermined microlepidopteran		A	1
		Diptera			
	N	Undetermined family		A	1
		Hymenoptera			
	A	Formicidae:	*Camponotus* sp.	A	1
		Araneae			
	A	Araneidae:	*Leucage venusta* (Walckenaer)	N	1
	N	Salticidae:	*Phidippus regius* C. L. Koch	N	1
	A	Theridiidae:	*Achaearanea tepidariorum* (C. L. Koch)	N	1
	A	Thomisidae:	*Misumenoides formocipes* (Walckenaer)	N	1
Zygoballus rufipes Peckham & Peckham		Hemiptera			
	A	Miridae:	*Reuteroscopus ornatus* (Reuter)	A	1

APPENDIX G
Attus otiosus HENTZ, 1846, (ARANEAE: SALTICIDAE): PROPOSED PRESERVATION UNDER THE PLENARY POWERS

The jumping spider known as Phidippus otiosus (Hentz) is common to the southeastern portion of the United States of America and a well-known spider of the region. The species was described as Attus otiosus Hentz, 1846; the name has become well-established and has only once been challenged until recently.

Walckenaer (1837) described many species of American spiders; in most cases these descriptions were based on the drawings of John Abbot (1792). American araneologists considered Walckenaer's descriptions invalid, as there were no specimens on which the descriptions were based, and the drawings of Abbot were presumed lost. However, McCook (1888) discovered Abbot's manuscript in the British Museum (Natural History), but it was not until Chamberlin & Ivie (1944) studied Abbot's drawings that any en masse changing of names in favor of Walckenaer occurred. By this time, the names of Hentz had been in continual usage for nearly 100 years.

Walckenaer described 3 of Abbot's drawings as Attus pulcher, Attus pulcher pallida, and Attus peregrinus. Chamberlin & Ivie decided, correctly, that all 3 illustrations represented the same species; they therefore synonymized A. pulcher pallida and A. peregrinus with A. pulcher, which had page and figure number priority. They also synonymized Attus otiosus Hentz with A. pulcher. In so doing, they synonymized an established name in favor of a name which had not even been properly placed to genus before 1944 (Bonnet, 1955, in a review of all araneological works through 1939, lists the species as Attus pulcher). Even though Chamberlin and Ivie resurrected the name as Phidippus pulcher (Walckenaer), P. otiosus (Hentz) continued to be the name used by American authors, even by Kaston (1978) and Muma (1975) who otherwise have followed Chamberlin and Ivie's resurrections of older names. Recently, the name P. otiosus has been used in the fields of physiology (Anderson, 1966), morphology (Hill, 1979), and ethology (Edwards et al., 1974; Edwards, 1977; Richman, 1977).

The first revisors of Phidippus, the Peckhams' (1901, 1909) on both occasions used the name P. otiosus (Hentz) for the species in question. The name otiosus has been used more than 20 times in the literature, mostly as Phidippus otiosus, rarely as Dendryphantes otiosus or Attus otiosus; since 1930, it has been used at least 13 times by 11 different authors; it is Phidippus otiosus in the popular books by Kaston (1972, 1978, How to Know the Spiders, 2nd and 3rd editions), Gertsch (1979, American Spiders, 2nd edition), and in all printings of Levi and Levi (1968-1978, Spiders and Their Kin). The name Phidippus pulcher, first used in 1944, has been used since then only 3 times. Richman (1978), while attempting to determine the status of Walckenaer's names as they applied to various salticid species, agreed with Chamberlin & Ivie that P. otiosus was a synonym of P. pulcher, and used the name in a salticid checklist (Richman and Cutler, 1978). However, Richman (personal communication, 1978) has agreed that P. otiosus is the name that is used most often and, based on this reason, has no objection to its continued usage.

To preserve usage as it has been for 132 out of 134 years of existence of the name otiosus, the Commission is requested:

(1) to use its plenary powers:

  (a) to suppress the specific name *pulcher* Walckenaer, 1837, as published in the binomen *Attus pulcher*, for the purposes of the Law of Priority but not for those of the Law of Homonymy;

  (b) to suppress the specific names *pulcher pallida* Walckenaer, 1837, and *peregrinus* Walckenaer, 1837, as published in the trinomen *Attus pulcher pallida* and the binomen *Attus peregrinus*, both junior subjective synonyms of *Attus pulcher* Walckenaer, for the purposes of the Law of Priority but not for those of the Law of Homonymy;

(2) to place the specific name *otiosus* Hentz, 1846, as published in the binomen *Attus otiosus*, on the Official List of Specific Names in Zoology;

(3) to place the specific and subspecific names *pulcher* Walckenaer, 1837, *pulcher pallida* Walckenaer, 1837, and *peregrinus* Walckenaer, 1847, as published in the combinations *Attus pulcher*, *Attus pulcher pallida*, and *Attus peregrinus* (as suppressed under the plenary powers in (1)(a) and (1)(b) above) on the Official Index of Rejected and Invalid Specific Names in Zoology.

REFERENCES CITED

Abbot, J. 1792. A manuscript of 592 annotated illustrations of the spiders of Georgia. Kept at the British Museum (Natural History).

Anderson, J. F. 1966. The excreta of spiders. Comp. Biochem. Physiol. 17: 973-982.

_____. 1970. Metabolic rates of spiders. Comp. Biochem. Physiol. 33: 51-72.

_____. 1978. Energy content of spider eggs. Oecologia 37: 41-57.

Bailey, C. L. 1968. Life history of the spider Phidippus audax Hentz in relation to biological control of grain sorghum insects. Ph.D. Thesis, Oklahoma State University, 59 p.

Bailey, C. L. and H. L. Chada. 1968. Spider populations in grain sorghums. Ann. Ent. Soc. America 61: 567-572.

Banks, N. 1892. A classification of North American spiders. Canadian Ent. 24: 88-97.

_____. 1893. Notes on spiders. J. New York Ent. Soc. 1: 123-134.

_____. 1895. Some new Attidae. Canadian Ent. 27: 96-102.

_____. 1896. New North American spiders and mites. Trans. American Ent. Soc. 23: 57-77.

_____. 1901. Notes on some spiders of Walckenaer, Koch, and others. J. New York Ent. Soc. 9: 182-189.

_____. 1904. The arachnida of Florida. Proc. Acad. Natur. Sci. Philadelphia 56: 120-147.

_____. 1910. Catalogue of nearctic spiders. Bull. U. S. Nat. Mus. 72: 1-80.

_____. 1913. Notes on the types of some American spiders in European collections. Proc. Acad. Natur. Sci. Philadelphia 65: 177-188.

_____. 1941. Apartition of our Cryptochilus, with some new Psammocharidae (Hymenoptera). Canadian Ent. 73: 119-122.

Barnes, R. D. 1953. The ecological distribution of spiders in non-forest maritime communities at Beaufort, North Carolina. Ecol. Monogr. 23: 315-337.

Barnes, R. D. and B. M. Barnes. 1955. The spider population of the abstract broomsedge community of the southeastern Piedmont. Ecology 36: 658-666.

Barrows, W. M. 1919. New spiders from Ohio. Ohio J. Sci. 19: 355-360.

Berry, J. W. 1970. Spiders of the North Carolina piedmont old-field communities. J. Elisha Mitchell Sci. Soc. 86: 97-105.

Bilsing, S. W. 1920. Quantitative studies in the food of spiders. Ohio J. Sci. 20: 215-260.

Bonnet, P. 1933. Cycle vital de _Philaeus chrysops_ Poda (Araneide, Salticide). Arch. zool. exper. 75: 129-144.

_____. 1958. Bibliographia Araneorum, Tome II (4). Toulouse. pp. 3027-4230.

Brady, A. R. 1972. The spider genus _Sosippus_ in North America, Mexico, and Central America. Psyche 69: 129-164.

Brian, A. D. 1957. Differences in the flowers visited by four species of bumble-bees and their causes. J. Anim. Ecol. 26: 71-98.

Bristowe, W. S. 1958. _The World of Spiders_. Collins, London, 305 p.

Bristowe, W. S. and G. H. Locket. 1926. The courtship of British lycosid spiders, and its probable significance. Proc. Zool. Soc. London 1926: 317-345.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. American Natur. 105: 467-478.

_____. 1975. Geographical ecology of desert rodents, in, M. L. Cody and J. M. Diamond (eds.). _Ecology and Evolution of Communities_. Belknap Press, Cambridge, Massachusetts, pp. 315-341.

Bryant, E. B. 1942. Descriptions of certain North American _Phidippus_ (Araneae). American Midl. Natur. 28: 693-707.

_____. 1943. The salticid spiders of Hispaniola. Bull. Mus. Comp. Zool. Harvard 92: 445-522.

Burch, T. L. 1979. The importance of communal experience to survival for spiderlings of _Araneus diadematus_ (Araneae: Araneidae). J. Arachnol. 7: 1-18.

Burks, B. D. 1963. Ten new reared species of Tetrastichus (Hymenoptera: Eulophidae). Proc. Biol. Soc. Washington 76: 48

Cannon, S. S. 1965. A comparison of the spider fauna of four different plant communities found in Neotoma, a small valley in south central Ohio. Ohio J. Sci. 65: 97-110.

Carpenter, R. M. 1972. The jumping spiders (Salticidae) of Wichita County, Texas. Southwest. Natur. 17: 161-168.

Carr, A. F., Jr. 1940. A contribution to the Herpetology of Florida. Univ. Florida Publ., Biol. Sci. Ser. 3: 1-118.

Caswell, H. 1978. Predator mediated coexistence: a nonequilibrium model. American Natur. 102: 107-147.

Chamberlin, R. V. and W. J. Gertsch. 1929. New spiders from Utah and California. J. Ent. Soc. Claremont 21: 101-112.

Chamberlin, R. V. and W. Ivie. 1935. Miscellaneous new American spiders. Bull. Univ. Utah 26: 1-79.

_____. 1944. Spiders of the Georgia region of North America. Bull. Univ. Utah 35: 1-267.

Chickering, A. M. 1944. The Salticidae (jumping spiders) of Michigan. Pap. Michigan Acad. Sci. 1943: 139-222.

Clark, E. W. and P. A. Glick. 1961. Some predators and scavengers feeding upon pink bollworm moths. J. Econ. Ent. 54: 815-816.

Clarke, C. A. and P. M. Sheppard. 1953. Further observations on hybrid swallowtails. Ent. Rec., J. Variation 65 (Supple.): 1-12.

Clench, H. K. 1967. Temporal dissociation and population regulation in certain hesperiine butterflies. Ecology 48: 1000-1006.

Cody, M. L. 1968. On the methods of resource division in grassland bird communities. American Natur. 100: 371-376.

_____. 1974. Competition and Structure of Bird Communities. Princeton University Press, Princeton, New Jersey.

Colwell, R. K. and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

Comstock, J. H. 1912. The Spider Book. Garden-City, New York, 721 p.

_____. 1940. The Spider Book. Revised and edited by W. J. Gertsch. Doubleday, Doran and Co., New York, 729 p.

Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. Balanus glandula and several predatory species of Thais. Ecol. Monogr. 40: 49-78.

_____. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments, in, M. L. Cody and J. M. Diamond (eds.). Ecology and Evolution of Communities. Belknap Press, Cambridge, Massachusetts, pp. 460-490.

Coquillet, D. W. 1892. Insect Life. 5: 24.

Crane, J. 1949. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. Zoologica 34: 159-214.

Cresson, E. T. 1867. Notes on the Pompilidae of North America. Trans. American Ent. Soc. 1: 85-150.

Crosby, C. R. and S. C. Bishop. 1936. Aeronautic spiders with a description of a new species. J. New York Ent. Soc. 44: 43-49.

Cutler, B. 1965. The jumping spiders of New York City. J. New York Ent. Soc. 73: 138-143.

_____. 1977. A preliminary list of the Salticidae of Minnesota. Peckhamia 1: 40.

_____. 1979. Musings of a jack pine savage II. Peckhamia 1: 126.

Davis, J. 1973. Habitat preferences and competition of wintering juncos and golden-crowned sparrows. Ecology 54: 174-180.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351-389.

DeLong, K. T. 1966. Population ecology of feral house mice: interference by Microtus. Ecology 47: 481-484.

Diamond, J. M. 1975. Assembly of species communities, in, M. L. Cody and J. M. Diamond (eds.). Ecology and Evolution of Communities. Belknap Press, Cambridge, Massachusetts, pp. 342-444.

Dondale, C. D. 1956. Annotated list of spiders (Araneae) from apple trees in Nova Scotia. Canadian Ent. 88: 697-700.

_____. 1964. Sexual behavior and its application to a species problem in the spider genus *Philodromus* (Araneae: Thomisidae). Canadian J. Zool. 42: 817-827.

_____. 1967. Sexual behavior and classification of the *Philodromus rufus* complex in North America (Araneida: Thomisidae). Canadian J. Zool. 45:453-459.

_____. 1971. Spiders of Heasman's Field, a mown meadow near Belleville, Ontario. Proc. Ent. Soc. Ontario 101: 62-69.

_____. 1975. Ecology of Arachnida. Proc. 6th Int. Arachnol. Congr. 1974: 67-70.

Dorris, P. R. 1969. Spiders collected from mud-dauber nests in Clark County, Arkansas. Proc. Arkansas Acad. Sci. 23: 88-90.

Dow, R. 1932. Biological notes on Cuban wasps and their parasites. Psyche 39: 8-19.

Dowdy, W. W. 1951. Further ecological studies on stratification of the Arthropoda. Ecology 32: 37-52.

Drees, O. 1952. Untersuchungen uber die angeborenen Verhaltensweisen bei Springspinnen (Salticidae). Z. Tierpsychol. 9: 167-173.

Dreisbach, R. R. 1953. Additional new species in the genera *Anopompilinus*, *Anoplius*, and *Pycnopompilus* (Hymenoptera: Psammocharidae) and corrections to previous papers. American Midl. Natur. 48: 145-160.

Drew, L. C. 1967. Spiders of Beaver Island, Michigan. Publ. Mus. Michigan State Univ., Biol. Ser. 3: 153-208.

Eason, R. R. 1964. Maternal care as exhibited by wolf spiders (Lycosids). Proc. Arkansas Acad. Sci. 18: 13-19.

_____. 1969. Life history and behavior of *Pardosa lapidicina* Emerton (Araneae: Lycosidae). J. Kansas Ent. Soc. 42: 339-360.

Eason, R. R., W. B. Peck, and W. H. Whitcomb. 1967. Notes on spider parasites, including a reference list. J. Kansas Ent. Soc. 40: 422-434.

Eberhard, W. G. 1975. The 'inverted ladder' orb web of *Scoloderus* sp. and the intermediate orb of *Eustala* (?) sp. (Araneae: Araneidae). J. Natur. Hist. 9: 93-106.

Edgar, W. D. 1969. Prey and predators of the wolf spider, *Lycosa lugubris*. J. Zool. 159: 405-411.

Edwards, G. B. 1975. Biological studies on the jumping spider, Phidippus regius C. L. Koch. M. S. Thesis, University of Florida, 64 p.

_____. 1977. Comments on some genus and species problems in the Salticidae, including Walckenaerian names. Peckhamia 1: 21-23.

_____. 1978. Two new southern Phidippus. Florida Ent. 61: 77-82.

_____. 1979. Rebuttal of objections to designation of Attus audax Hentz, 1845, as type species of Phidippus Koch, 1846 (Araneae). Z. N. (S.) 1904. Bull. Zool. Nomencl. 36: 4.

_____. 1980. Experimental demonstration of the importance of wings to prey evaluation by a salticid spider. Peckhamia 1(7), in press.

Edwards, G. B., J. F. Carroll, and W. H. Whitcomb. 1974. Stoidis aurata (Araneae: Salticidae), a spider predator of ants. Florida Ent. 57: 337-346.

Edwards, G. B. and D. E. Hill. 1978. Representatives of the North American salticid fauna. Peckhamia 1: 110-117.

Elliott, F. R. 1930. An ecological study of the spiders of the beech-maple forest. Ohio J. Sci. 30: 1-22.

Emerton, J. H. 1875. Notes and descriptions, in, The Spiders of the United States, a collection of the arachnological writings of Nicholas Marcellus Hentz. Occ. Pap. Boston Soc. Natur. Hist. 2: 1-171.

_____. 1877. A comparison of the spiders of Europe and North America. Proc. Boston Soc. Natur. Hist. 19: 68-72.

_____. 1891. New England spiders of the family Attidae. Trans. Connecticut Acad. Arts Sci. 8: 220-252.

Enders, F. 1974. Vertical stratification in orb-web spiders (Araneidae, Araneae) and a consideration of other methods of coexistence. Ecology 55: 317-328.

_____. 1975. The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae, and Salticidae). American Natur. 109: 737-763.

_____. 1976. Size, food-finding, and Dyar's constant. Environ. Ent. 5: 1-10.

Evans, H. E. 1951. A taxonomic study of the Nearctic spider wasps belonging to the tribe Pompilini (Hymenoptera: Pompilidae). Part II: Genus Anoplius Dufour. Trans. American Ent. Soc. 76: 207-361.

_____. 1959. Prey records for some midwestern and southwestern spider wasps (Hymenoptera: Pompilidae). J. Kansas Ent. Soc. 32: 75-76.

Evans, H. E. and C. M. Yoshimoto. 1955. An annotated list of pompilid wasps taken at Blackjack Creek, Pottawatomie Co., Kansas (Hymenoptera). J. Kansas Ent. Soc. 28: 16-19.

Everly, R. T. 1938. Spiders and insects found associated with sweet corn with notes on the food and habits of some species. I. Arachnida and Coleoptera. Ohio J. Sci. 38: 136-148.

Fitch, H. S. 1963. Spiders of the University of Kansas Natural History Reservation and Rockefeller Experimental Tract. Misc. Publ. Univ. Kansas Mus. Natur. Hist. 33: 1-202.

Fogarty, M. J. and H. K. Wallace. 1973. Spiders in the summer diet of cattle egrets. Florida Scientist 36: 189-192.

Forster, L. M. 1977a. A qualitative analysis of hunting behaviour in jumping spiders (Araneae: Salticidae). New Zealand J. Zool. 4: 51-62.

_____. 1977b. Some factors affecting feeding behaviour in young Trite auricoma spiderlings (Araneae: Salticidae). New Zealand J. Zool. 4: 435-443.

_____. 1979. Visual mechanisms of hunting behaviour in Trite planiceps, a jumping spider (Araneae: Salticidae). New Zealand J. Zool. 6: 79-93.

Franganillo Balboa, P. 1930. Arcnidos de Cuba. Mas aracnidos nuevos de la isle de Cuba. Inst. nac. invest. cien. 1: 47-99.

Galiano, M. E. 1967. Ciclo biologico y desarrollo de Loxosceles laeta (Nicolet, 1849)(Araneae, Scytodidae). Acta Zool. Lilloana 23: 431-464.

Gardner, B. T. 1964. Hunger and sequential responses in the hunting behavior of salticid spiders. J. Comp. Physiol. Psychol. 58: 167-173.

_____. 1965. Observations on three species of Phidippus jumping spiders (Araneae, Salticidae). Psyche 72: 133-147.

Gerhardt, U. 1928. Biologische Studien en griechischen, corsischen und deutschen Spinnen. Zeits. Morph. Okol. Tiere 10: 576-675.

Gertsch, W. J. 1934. Further notes on American spiders. American Mus. Novit. 726: 1-26.

_____. 1979. American Spiders. Van Nostrand Reinhold Co., New York, 274 p.

Gertsch, W. J. and W. L. Jellison. 1939. Notes on a collection of spiders from Montana. American Mus. Novit. 1032: 1-13.

Gertsch, W. J. and S. E. Riechert. 1976. The spatial and temporal partitioning of a desert spider community, with descriptions of new species. American Mus. Novit. 2604: 1-25.

Gertsch, W. J. and L. A. Woodbury. 1930. Spiders found in the stomachs of Sceloporus graciosus graciosus (B. & G.) (Araneina). Ent. News 41: 318.

Gisbon, W. W. 1947. An ecological study of the spiders of a river-terrace forest in western Tennessee. Ohio J. Sci. 47: 38-44.

Glick, P. A. 1939. The distribution of insects, spiders, and mites in the air. USDA Tech. Bull. 673, U. S. Dept. Agric., Washington, D. C., 150 p.

_____. 1960. Collecting insects by airplane with special reference to dispersal of the potato leafhopper. U. S. Dept. Agric. Tech. Bull. 1222: 1-16.

Hartman, C. 1905. Observations on the habits of some solitary wasps of Texas. Bull. Univ. Texas. Sci. Ser. 6: 1-72.

Hentz, N. M. 1835. VII. Araneids Latr. The Spiders, in, A catalogue of the animals and plants of Massachusetts. Report on the Geol. Mineral. Bot. and Zool. of Massachusetts. Amherst, 1835: 550-552.

_____. 1845. Descriptions and figures of the Araneides of the United States. Boston J. Natur. Hist. 5: 189-202.

_____. 1846. Descriptions and figures of the Araneides of the United States. Boston J. Natur. Hist. 5: 352-370.

_____. 1850. Descriptions and figures of the Araneides of the United States. Boston J. Natur. Hist. 6: 18-35.

Hermann, H. R. 1969. The hymenopterous poison apparatus: Evolutionary trends in three closely related subfamilies of ants (Hymenoptera: Formicidae). J. Georgia Ent. Soc. 4: 123-141.

Highton, R. 1956. Systematics and variation of the endemic Florida snake genus Stilosoma. Bull. Florida St. Mus. Biol. Serv. 1: 73-96.

Hill, D. E. 1977a. The mating of Phidippus princeps. Peckhamia 1: 5-7.

_____. 1977b. The pretarsus of salticid spiders. Zool. J. Linnean Soc. 60: 319-338.

_____. 1977c. Field observations on the behavior of immature *Phidippus princeps* in Minnesota. Peckhamia 1: 44-50.

_____. 1978. The behavior of *Eris marginata* (Araneae: Salticidae). Peckhamia 1: 63-70.

_____. 1979. Orientation by jumping spiders of the genus *Phidippus* (Araneae: Salticidae) during the pursuit of prey. Behav. Ecol. Sociobiol. 5: 301-322.

Hoelldobler, B. 1969. *Steatoda fulva* (Theridiidae), a spider that feeds on harvester ants. Psyche 77: 202-208.

Hollis, J. H. and B. A. Branson. 1964. Laboratory observations on the behavior of the salticid spider *Phidippus audax* (Hentz). Trans. Kansas Acad. Sci. 67: 131-148.

Horner, N. V. 1974 (1975). Annual aerial dispersal of jumping spiders in Oklahoma (Araneae, Salticidae). J. Arachnol. 2: 101-105.

Horner, N. V. and J. H. Klein, Jr. 1979. Spider prey of two mud dauber wasp species in Comanche County, Oklahoma (Hymenoptera: Sphecidae). Environ. Ent. 8: 30-31.

Howard, L. O. 1890. U.S.D.A. Insect Life 2: 270.

_____. 1892. Hymenopterous parasites of spiders. Proc. Ent. Soc. Washington 2: 290-303.

Howell, J. O. and R. L. Pienkowski. 1971. Spider populations in alfalfa, with notes on spider prey and effect of harvest. J. Econ. Ent. 64: 163-168.

Hubbell, T. H. 1954. Relationships and distribution of *Mycotrupes*, in, A. L. Olsen. The burrowing beetles of the genus *Mycotrupes*. Misc. Publ. Univ. Michigan Mus. Zool. 84: 1-59 (39-51).

_____. 1956. Some aspects of geographic variation in insects. Ann. Rev. Ent. 1: 71-88.

Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67-77.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22: 415-427.

_____. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Natur. 93: 145-159.

Jackson, R. R. 1976. The evolution of courtship and mating tactics in a jumping spider, Phidippus johnsoni (Araneae, Salticidae). Ph.D. Thesis, University of California, Berkeley, 271 p.

_____. 1977a. Courtship versatility in the jumping spider, Phidippus johnsoni (Araneae: Salticidae). Anim. Behav. 25: 953-957.

_____ 1977b. Prey of the jumping spider Phidippus johnsoni (Araneae: Salticidae). J. Arachnol. 5: 145-149.

_____. 1978a. An analysis of alternative mating tactics of the jumping spider Phidippus johnsoni (Araneae, Salticidae). J. Arachnol. 5: 185-230.

_____. 1978b. The life history of Phidippus johnsoni (Araneae: Salticidae). J. Arachnol. 6: 1-29.

_____. 1979. Nests of Phidippus johnsoni (Araneae, Salticidae): characteristics, pattern of occupation, and function. J. Arachnol. 7: 47-58.

Judd, W. W. 1965. Studies of the Byron Bog in southwestern Ontario. Canadian Ent. 95: 327-333.

Jung, A. K. S. and V. D. Roth. 1974. Spiders of the Chiricahua Mountain area, Cochise Co., Arizona. J. Arizona Acad. Sci. 9: 29-34.

Kagan, M. 1943. The Araneida found on cotton in central Texas. Ann. Ent. Soc. America 36: 257-258.

Kaston, B. J. 1936. The senses involved in the courtship of some vagabond spiders. Entomologica americana 16: 97-166.

_____. 1938a. New spiders from New England with notes on other species. Bull. Brooklyn Ent. Soc. 33: 173-191.

_____. 1938b. Checklist of the spiders of Connecticut. Bull. Connecticut Geol. Natur. Hist. Surv. 60: 175-201.

_____. 1945. New spiders in the group Dionycha with notes on other species. American Mus. Novit. 1290: 1-25.

_____. 1948. Spiders of Connecticut. Connecticut State Geol. & Natur. Hist. Bull. 70: 1-874.

_____. 1972. How to Know the Spiders. Wm. C. Brown Co., Dubuque, Iowa, Second Edition, 289 p.

_____. 1978. Ibid. Third Edition, 271 p.

Keyserling, E. 1884. Neue Spinnen aus Amerika. VI. Verh. Zool.-bot. Ges. Wien 34: 489-534.

Koch, C. L. 1837. Uebersicht des Arachnidensystems Nurnberg, 39 p.

_____. 1846. Die Arachniden. Dreizehnter Band. Nurnberg, 234 p.

_____. 1851. Uebersicht des Arachnidensystems. Heft 5. Nurnberg, 104 p.

Kohn, A. 1971. Diversity, utilization of resources, and adaptive radiation in shallow water marine invertebrates of tropical oceanic islands. Limnol. Oceanography 16: 332-345.

Krombein, K. V. 1955. Miscellaneous prey records of solitary wasps. I. (Hymenoptera: Aculeata). Bull. Brooklyn Ent. Soc. 50: 13-17.

_____. 1959. Biological notes on some ground-nesting wasps at Kill Devil Hills, North Carolina, 1958, and additions to the faunal list (Hymenoptera, Aculeata). Proc. Ent. Soc. Washington 61: 193-199.

_____. 1961. Miscellaneous prey records of solitary wasps. IV. (Hymenoptera: Aculeata). Bull. Brooklyn Ent. Soc. 56: 62-65.

_____. 1967. Trap-nesting wasps and bees - life histories, nests, and associates. Smithsonian Press, Washington, D. C., 576 p.

Kuenzler, E. J. 1958. Niche relations of three species of lycosid spiders. Ecology 39: 494-500.

Kurczewski, F. E. and E. J. Kurczewski. 1968. Host records for some North American Pompilidae (Hymenoptera). First Supplement. J. Kansas Ent. Soc. 41: 367-382.

Laessle, A. M. 1942. The plant communities of the Welaka area. Publ. Univ. Florida Biol. Sci. Ser. 4: 1-143.

Lamore, D. H. 1958. The jumping spider, Phidippus audax Hentz, and the spider Conopistha trigona Hentz, as predators of the basilica spider, Allepeira lemniscata Walckenaer, in Maryland. Proc. Ent. Soc. Washington 60: 286.

Land, M. F. 1969a. Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. J. Exp. Biol. 51: 443-470.

_____. 1969b. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. J. Exp. Biol. 51: 471-493.

_____. 1971. Orientation by jumping spiders in the absence of visual feedback. J. Exp. Biol. 54: 119-139.

_____. 1972. Stepping movements made by jumping spiders during turns mediated by the lateral eyes. J. Exp. Biol. 57: 15-40.

LeSar, C. D. and J. D. Unzicker. 1978. Soybean spiders: species composition, population densities, and vertical distribution. Illinois Natur. Hist. Survey 107: 1-14.

Levi, H. W. 1957. The spider genera Crustulina and Steatoda in North America, Central America, and the West Indies (Araneae: Theridiidae). Bull. Mus. Comp. Zool. 117: 367-424.

Levi, H. W. and H. M. Field. 1954. The spiders of Wisconsin. American Midl. Natur. 51: 440-467.

Levi, H. W. and L. R. Levi. 1951. Report on a collection of spiders and harvestmen from Wyoming and neighboring states. Zoologica 36: 219-237.

Levi, H. W. and L. R. Levi. 1968. Spiders and Their Kin. Golden Press, New York, 160 p.

Levi, L. R. and H. W. Levi. 1955. Spiders and harvestmen from Waterton and Glacier National Parks. Canadian Field-Naturalist 69: 32-40.

Levi, H. W. and L. J. Pinter. 1970. Attus audax Hentz, 1845 (Araneae): Proposed preservation under the plenary powers and designation as type-species of Phidippus Koch, 1846. Bull. Zool. Nomencl. 27: 103.

Levins, R. 1968. Evolution in Changing Environments: Some Theoretical Explanations. Princeton Univ. Press, Princeton, New Jersey, 120 p.

Lincoln, C., J. R. Phillips, W. H. Whitcomb, G. C. Dowell, W. P. Boyer, K. O. Bell, Jr., G. L. Dean, E. J. Matthews, J. B. Graves, L. D. Newsom, D. F. Clower, J. R. Bradley, Jr., and J. L. Bagent. 1967. The bollworm-tobacco budworm problem in Arkansas and Louisiana. Agr. Exp. Sta. Div. Agr. Univ. Ark. Bull. 720: 1-66.

Lloyd, M., J. H. Zar, and J. R. Karr. 1968. On the calculation of information - theoretical measures of diversity. American Midl. Natur. 79:257-272.

Locket, G. H. 1939. A case of crossing in spiders. Ann. Mag. Natur. Hist. 11: 629-631.

Lowrie, D. C. 1942. The ecology of the spiders of the xeric dunelands in the Chicago area. Bull. Chicago Acad. Sci. 6: 161-189.

_____. 1948. The ecological succession of spiders of the Chicago area dunes. Ecology 29: 334-351.

Lucas, H. 1833. Memoire sur plusieurs Arachnides nouvelles appartenant au genre Atte de M. de Walckenaer. Ann. Soc. Ent. France 2: 476-482.

_____. 1857. Aragnides, in Ramon de la Sagra, Historia fisica, politica y natural de la Isla de Cuba. Secunda parte, tomo VII, Paris 1857: xxiv-xxx.

Luczak, J. 1963. Differences in the structure of communities of web spiders in one type of environment (young pine forest). Ekol. Polska A. 11: 159-221.

_____. 1966. The distribution of wandering spiders in different layers of the environment as a result of interspecies competition. Ekol. Polska A. 14: 233-244.

Luczak, J. and T. Wierzbowska. 1959. Analysis of the likelihood of material in relation to the length of a series in the sweep method. Bull. Acad. Pol. Sci. Cl. 2. 7: 313-318.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.

MacArthur, R. H. and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Natur. 101: 377-385.

MacNeil, F. S. 1950. Pleistocene shorelines in Florida and Georgia. U. S. Geol. Surv. Prof. Pap. 221-F: 95-107.

Malas, D. and J. B. Wallace, 1977. Strategies for coexistence in three species of net-spinning caddisflies (Trichoptera) in second-order southern Appalachian streams. Canadian J. Zool. 55: 1829-1840.

Martin, J. L. 1966. The insect ecology of red pine plantations in central Ontario. IV. The crown fauna. Canadian Ent. 98: 10-27.

Marx, G. 1890. Catalogue of the described Araneae of temperate North America. Proc. U. S. Nat. Mus. 12: 497-594.

May, R. M. 1975. Patterns of species abundance and diversity, in M. L. Cody and J. M. Diamond (eds.). Ecology and Evolution of Communities. Belknap Press, Cambridge, Massachusetts, pp. 81-120.

_____. 1976. Models for two interacting populations, in R. M. May (ed.). Theoretical Ecology: Principles and Applications. W. B. Saunders and Co., Philadelphia, pp. 49-70.

Mayr, E. 1954. Change of genetic environment and evolution, in J. S. Huxley (ed.). Evolution as a Process. Geo. Allen and Unwin Ltd., London, pp. 157-180.

McCaffrey, J. P. and R. L. Horsburgh. 1980. The spider fauna of apple trees in central Virginia. Environ. Ent. 9: 247-252.

McCrone, J. D. 1963. Taxonomic status and evolutionary history of the Geolycosa pikei complex in the southeastern United States (Araneae, Lycosidae). American Midl. Natur. 70: 47-73.

Mittal, O. P. 1964. Karyological studies on the Indian spiders VI. Res. Bull. Panjab Univ. Sci. (NS) 5: 67-80.

Moulder, B. C. and D. E. Reichle. 1972. Significance of spider predation in the energy dynamics of forest floor arthropod communities. Ecol. Monogr. 42: 473-498.

Muma, M. H. 1944. A report on Maryland spiders. American Mus. Novit. 1257: 1-14.

_____. 1945. New and interesting spiders from Maryland. Proc. Biol. Soc. Washington 58: 91-102.

_____. 1975. Spiders in Florida citrus groves. Florida Ent. 58: 83-90.

Muma, M. H. and W. F. Jeffers. 1945. Studies of the spider prey of several mud-dauber wasps. Ann. Ent. Soc. America 38: 245-255.

Muma, M. H. and K. E. Muma. 1949. Studies on a population of prairie spiders. Ecology 30: 485-503.

Murrill, W. A. 1942. Spiders of Alachua County, Florida. Florida Ent. 25: 7-9.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164: 262-270.

Oehler, C. M. 1980. Jumping spiders (Araneae: Salticidae) in the Cincinnati region of Ohio. Ohio Biol. Surv. Biol. Notes 13: 1-36.

Oliver, A. D. 1964. Studies on the biological control of the fall webworm, *Hyphantria cunea*, in Louisiana. J. Econ. Ent. 57: 314-318.

Painter, T. S. 1914. Spermatogenesis in spiders. I. Zool. Jahrb., Anat. 38: 509-576.

Patrick, R. and D. Strawbridge. 1963. Variation in the structure of natural diatom communities. American Natur. 97:51-57.

Patterson, J. T. and W. S. Stone. 1952. Evolution in the genus *Drosophila*. MacMillen, 610 p.

Peck, W. B. 1966. The population composition of a spider community in west central Missouri. American Midl. Natur. 76: 151-168.

Peck, W. B., L. O. Warren, and I. L. Brown. 1971. Spider fauna of shortleaf and loblolly pines in Arkansas. J. Georgia Ent. Soc. 6: 87-94.

Peckham, G. W. and E. G. Peckham. 1883. Descriptions of new or little known spiders of the family Attidae from various parts of the United States of North America. Milwaukee 1883: 1-35.

_____. 1888. Attidae of North America. Trans. Wisconsin Acad. Sci. Arts Let. 7: 1-104.

_____. 1889. Observations on sexual selection in spiders of the family Attidae. Occ. Pap. Natur. Hist. Soc. Wisconsin 1: 1-60.

_____. 1896. Spiders of the family Attidae from Central America and Mexico. Occ. Pap. Natur. Hist. Soc. Wisconsin 3: 1-101.

_____. 1901. Spiders of the *Phidippus* group of the family Attidae. Trans. Wisconsin Acad. Sci. Arts Let. 13: 282-358.

_____. 1909. Revision of the Attidae of North America. Trans. Wisconsin Acad. Sci. Arts Let. 16: 355-646.

Petrunkevitch, A. 1911. A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands, etc. Bull. American Mus. Natur. Hist. 29: 1-791.

Pianka, E. R. 1974. Niche overlap and diffuse competition. Proc. Nat. Acad. Sci. U.S.A. 71: 2141-2145.

Platnick, N. I. and M. U. Shadab. 1975. A revision of the spider genus *Gnaphosa* (Araneae, Gnaphosidae) in America. Bull. American Mus. Natur. Hist. 155: 1-66.

_____. 1975. Niche relations of desert lizards, in M. L. Cody and J. M. Diamond (eds.). Ecology and Evolution of Communities. Belknap Press, Cambridge, Massachusetts, pp. 292-314.

Pielou, E. C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. J. Theoret. Biol. 10: 370-383.

_____. 1975. Population and Community Ecology. Principles and Methods. Gordon and Breach Science Publ., New York, 424 p.

Pinter, L. J. and D. M. Walters. 1971. Karyological studies I. A study of the chromosome numbers and sex-determining mechanism of three species of the genus Phidippus (Aranea: Salticidae, Dendryphantinae). Cytologia 36: 183-189.

Price, P. W. 1975. Insect Ecology. John Wiley & Sons, New York, 514 p.

Randall, J. R. 1978. The use of femoral spination as a key to instar determination in the Green Lynx spider, Peucetia viridans (Hentz) (Araneida, Oxyopidae). J. Arachnol. 6: 147-153.

Rathcke, B. J. 1976. Competition and coexistence within a guild of herbivorous insects. Ecology 57: 76-87.

Rau, P. 1926. The ecology of a sheltered clay bank; a study in insect sociology. Trans. Acad. Sci. St. Louis 25: 158-260.

_____. 1928. The nesting habits of the wasp Chalybion caeruleum. Ann. Ent. Soc. America 21: 25-35.

_____. 1935. The spider prey of the mud wasp, Sceliphron caementarium (Araneae, Hymen.: Sphegidae). Ent. News 46: 267-270.

Reiskind, J. 1969. The spider subfamily Castianeirinae of North and Central America (Araneae, Clubionidae). Bull. Mus. Comp. Zool. 138: 163-325.

_____. 1970. Multiple mimetic forms in an ant-mimicking clubionid spider. Science 169: 587-588.

Reiskind, J. and H. W. Levi. 1967. Anatea, an ant-mimicking theridiid spider from New Caledonia (Araneae: Theridiidae). Psyche 74: 20-23.

Richman, D. B. 1977. The relationship of epigamic display to the systematics of jumping spiders (Araneae: Salticidae). Ph.D. Thesis, University of Florida, 162 p.

_____. 1978. Some thoughts on Walckenaer's names for salticids after an examination of Abbot's drawings. Peckhamia 1: 57-61.

Richman, D. B. and B. Cutler. 1978. A list of the jumping spiders (Araneae: Salticidae) of the United States and Canada. Peckhamia 1: 82-110.

Riley, C. V. 1887. Our shade trees and their insect defoliators. U.S. Dept. Agric. Div. Ent. Bull. 10: 1-69.

Roewer, C. F. 1954. Katalog der Araneae. 2. Band, Abt. b. Brussels, pp. 927-1751.

Ross, H. H. 1957. Principles of natural coexistence indicated by leaf hopper populations. Evolution 11: 113-129.

Rovner, J. S. 1967. Acoustic communication in a lycosid spider (Lycosa rabida Walckenaer). Anim. Behav. 15: 273-281.

_____. 1975. Sound production by Nearctic wolf spiders: A substratum-coupled stridulatory mechanism. Science 190: 1309-1310.

_____. 1980. Vibration in Heteropoda venatoria (Sparassidae): A third method of sound production in spiders. J. Arachnol. 8: 193-200.

Sailer, R. I. 1954. Interspecific hybridization among insects with a report on crossbreeding experiments with stink bugs. J. Econ. Ent. 47: 377-383.

Scheffer, T. H. 1904. A preliminary list of Kansas spiders. Industrialist 30: 371-386.

_____. 1905. A preliminary list of Kansas spiders. Trans. Kansas Acad. Sci. 19: 182-193.

_____. 1906. Additions to the list of Kansas Arachnida. Trans. Kansas Acad. Sci. 20: 121-130.

Schlinger, E. I. 1960. A revision of the genus Ogcodes Latreille with particular reference to species of the western hemisphere. Proc. U. S. Nat. Mus. 111: 227-336.

Schoener, T. W. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704-726.

_____. 1969. Models of optimum size for solitary predators. American Natur. 103: 277-313.

_____. 1970. Non-synchronous overlap of lizards in patchy habitats. Ecology 51: 408-418.

_____. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

_____. 1975. Competition and the niche, in D. W. Tinkle and W. W. Milstead for C. Gans (eds.). Biology of the Reptilia. Academic Press, New York.

Shannon, C. E. 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27: 379-424; 623-656.

Simon, E. 1864. Histoire naturelle des Araignées (Aranéides). Paris 1864: 1-540.

_____. 1901. Histoire naturelle des Araignées. Tome 2, fascicule 3. Paris 1901: 381-668.

Snetsinger, R. 1955. Observations on two species of Phidippus. Ent. News 66:9-15.

Specht, H. B. and C. D. Dondale. 1960. Spider populations in New Jersey apple orchards. J. Econ. Ent. 53: 810-814.

Taylor, B. B. and W. B. Peck. 1975. A comparison of northern and southern forms of Phidippus audax (Hentz) (Araneida, Salticidae). J. Arachnol. 2: 89-99.

Thorell, T. 1891. Spindlar fran Nikobarerna och andra delar af Sodra Asien, etc. Kongl. Svenska Vet.-Akad. Handl. 24: 1-149.

Tikader, B. K. 1974. Studies on some jumping spiders of the genus Phidipppus from India (Family-Salticidae). Proc. Indian Acad. Sci. 79: 120-126.

Tolbert, W. W. 1975. Predator avoidance behaviors and web defensive structures in the orb weavers Argiope aurantia and Argiope trifasciata (Araneae, Araneidae). Psyche 82: 29-52.

Townes, H. 1957. Nearctic wasps of the subfamilies Pepsinae and Ceropalinae. Bull. U. S. Nat. Mus. 209: 220-237.

Tullgren, A. 1901. On the spiders collected in Florida by Dr. Einar Lonnberg 1892-93. Bih. Svenska Vet.-Akad. Handl. 27: 1-29.

Turnbull, A. L. 1964. The search for prey by a web-building spider, Acheaearanea tepidariorum (C. L. Koch) (Araneae: Theridiidae). Canadian Ent. 96: 568-579.

_____. 1973. Ecology of the true spiders (Araneomorphae). Ann. Rev. Ent. 18: 305-348.

Turner, M. 1979. Diet and feeding phenology of the green lynx spider, Peucetia viridans (Araneae: Oxyopidae). J. Arachnol. 7: 149-154.

Turner, M. and G. A. Polis. 1979. Patterns of co-existence in a guild of raptorial spiders. J. Anim. Ecol. 48: 509-520.

Uetz, G. W. 1975. Temporal and spatial variation in species diversity of wandering spiders (Araneae) in deciduous forest litter. Environ. Ent. 4: 719-724.

_____. 1977. Coexistence in a guild of wandering spiders. J. Anim. Ecol. 46: 531-541.

Vachon, M. 1957. Contribution a l'etude du developpement postembryonaire des araignees. Premier Note. Generalities et nomenclature des stades. Bull. Soc. Zool. France 82: 337-354.

Valerio, C. E. 1974. Feeding on eggs by spiderlings of Achaearanea tepidariorum (Araneae: Theridiidae), and the significance of the quiescent instar in spiders. J. Arachnol. 2: 57-63.

Vandermeer, J. H. 1972. Niche theory. Ann. Rev. Ecol. Syst. 3: 107-132.

Van Hook, R. I., Jr. 1971. Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. Ecol. Monogr. 41: 1-26.

Walckenaer, C. A. 1805. Tableau des Araneides ou Caracteres essentials des tribus, genres, familles et races que renferme le genre Aranea de Linné, avec la designation des especes comprises dans chacune de ces divisions. Paris 1805: 1-88.

_____. 1837. Histoire naturelle des Insectes. Apteres. Tome I. Paris 1837: 1-549.

_____. 1947. Histoire naturelle des Insectes. Apteres. Tome IV. Paris 1847: 1-623.

Wallace, H. K. 1942. A revision of the burrowing spiders of the genus Geolycosa (Araneae, Lycosidae). American Midl. Natur. 27: 1-62.

_____. 1950. On Tullgren's Florida spiders. Florida Ent. 33: 71-83.

Warren, L. O., W. B. Peck, and M. Tadic. 1967. Spiders associated with the fall webworms, Hyphantria cunea (Lepidoptera: Arctiidae). J. Kansas Ent. Soc. 40: 382-395.

Wheeler, A. G., Jr. 1973. Studies on the arthropod fauna of alfalfa V. Spiders (Araneida). Canadian Ent. 105: 425-432.

Whitcomb, W. H. 1967. Field studies on predators of the second-instar bollworm, Heliothis zea (Boddie) (Lepidoptera: Noctuidae). J. Georgia Ent. Soc. 2: 113-118.

_____. 1973. Natural populations of entomophagous arthropods and their effect on the agroecosystem. Proc. Mississippi Symp. Biol. Contr. 1973: 150-169.

Whitcomb, W. H., H. Exline, and R. C. Hunter. 1963. Spiders of the Arkansas cotton field. Ann. Ent. Soc. America 56: 653-660.

Whitcomb, W. H. and M. Tadic. 1963. Araneida as predators of the fall webworm. J. Kansas Ent. Soc. 36: 186-190.

Wickler, W. 1968. Mimicry in Plants and Animals. World Univ. Libr., McGraw-Hill Book Co., New York.

Wiens, J. A. 1977. On competition and variable environments. American Scientist 65: 259-267.

Williams, S. C. 1970. Coexistence of desert scorpions by differential habitat preference. Pan-Pacific Ent. 46: 254-267.

Woodwell, G. M. 1974. Variation in the nutrient content of leaves of Quercus alba, Quercus coccinea, and Pinus rigida in the Brookhaven Forest from bud-break to abscission. American J. Bot. 61: 749-753.

Yeargan, K. W. 1975. Prey and periodicity of Pardosa ramulosa (McCook) in alfalfa. Environ. Ent. 4: 137-141.

Zug, G. R. and P. B. Zug. 1979. The marine toad, Bufo marinus: A natural history resume of native populations. Smithsonian Contr. Zool. 284.

BIOGRAPHICAL SKETCH

G. B. Edwards, Jr., was born November 24, 1948,at Aberdeen, Maryland, the oldest child of Glavis B., Sr., and Margaret P. Edwards. He graduated from Northwestern Senior High in 1967, having participated on the varsity baseball and basketball teams; the basketball team won the Maryland state highschool championship his senior year. He then enrolled at the University of Maryland, where he played on the freshman basketball team, graduating with a Bachelor of Science degree in 1971. He enrolled as a graduate student in the Entomology and Nematology Department of the University of Florida in 1972, and earned a Master of Science degree in 1975. Between undergraduate and graduate school, he married C. Sue Williams on the 3rd of April, 1972; they have no children.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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December, 1980

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