Divergence and Reticulation among Montane Populations of a Jumping Spider (*Habronattus pugillis* Griswold)

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Abstract.—Populations of the jumping spider *Habronattus pugillis* Griswold isolated on nearby mountain ranges in southern Arizona are differentiated in many features of the males (color, shape, and orientation of setae on face; shape of carapace; markings of palpi and legs; motions during courtship behavior). These features are (mostly) consistent within a range and different between ranges. The concentration of differences in male courtship behavior and body parts exposed to the female during courtship and correlations between form and courtship behavior suggest sexual selection was involved in the differentiation. A phylogenetic analysis of the populations yields a tree that for the most part groups geographic neighbors, but the history of *H. pugillis* populations may not be adequately described by a tree. Geographic proximity of apparent convergences suggests that populations from at least some of the mountain ranges acquired characteristics through introgression. Lowering of the woodland habitat during the last glacial period probably brought some populations into contact, but it is not clear whether the interrange woodlands would have provided corridors for extensive mixing. [Differentiation; geographic variation; homoplasy; hybridization; phylogeny; Salticidae; sexual selection; speciation; spiders.]

Phylogenetic diversifications that occur rapidly and in small geographical areas may be particularly difficult to reconstruct. When phylogenetic branches are short (in time), not only might the novel characters evolving be too few to mark them, but also ancestral polymorphisms are more likely to be retained through several speciation events and then to sort to monomorphism variously in the descendants (Pamilo and Nei, 1988; Takahata, 1989). This sorting can generate character distributions that are discordant with one another and with the phylogenetic relationships of the species (Throckmorton, 1965; Arnold, 1981), leading to the "gene tree–species tree" problem (Avise et al., 1983; Pamilo and Nei, 1988; Doyle, 1992; Page, 1993; Maddison, 1997). Among closely related forms that are geographic neighbors, hybridization and introgression can also yield character discordance (Arnold, 1981; McDade, 1990, 1995; Reiseberg and Morefield, 1995). Although discordant character distributions are usually interpreted to imply convergence or reversal, hybridization and retention of polymorphisms allow discordance to arise even when there is no convergence (i.e., when the instances of a character state are homologous to one another, for every state of every char-

acter). The problem is that each character might have followed its own unique history of descent (de Queiroz et al., 1995).

The availability of DNA sequence data has recently focused attention on the discordant character distributions that can result from hybridization (Reiseberg and Morefield, 1995; Arnold, 1997) and the retention and sorting of ancestral polymorphisms (Avise et al., 1983; Pamilo and Nei, 1988; Takahata, 1989; Doyle, 1992). For genetic data, it is becoming well recognized that different characters may have followed different histories (Goodman et al., 1979; de Queiroz et al., 1995; Doolittle, 1999). Awareness of the phylogenetic complications of these processes is not new, however. Especially among botanical phylogeneticists, hybridization has long been a concern (Stebbins, 1950; Wagner, 1983; McDade, 1990, 1995). The phylogenetic patterns generated by retention and subsequent sorting of ancestral polymorphisms have been discussed for decades (Throckmorton, 1965; Farris, 1978; Felsenstein, 1979; Arnold, 1981) and are implicitly considered in the use of gene frequencies to reconstruct phylogeny (Cavalli-Sforza and Edwards, 1967). The concept of a gene phylogeny distinct from, and to some extent independent of, a species phylogeny is implicit in early work on polytene chromosome inversion phylogenies (Dobzhansky and Sturtevant, 1938). However, although these concerns are old,

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they have only recently begun to affect how most phylogeneticists treat their data. Moreover, perhaps these concerns have been too little discussed for phenotypic characters (Throckmorton, 1965; Arnold, 1981; McDade, 1990; Maddison, 1995; Doyle, 1996).

With these concerns in mind, we here report a remarkable diversification that has occurred at a small spatial scale, and possibly a small temporal scale. The jumping spider *Habronattus pugillis* Griswold occurs in the woodland habitats of mountain ranges of southeastern Arizona. These mountain ranges, along with other satellite ranges of the Sierra Madre of northwestern Mexico, have been nicknamed "sky islands" because their peaks stand high above the desert lowlands, forming an archipelago of isolated woodlands (Warshall, 1995). In both structure and behavior, specimens of *H. pugillis* are remarkably distinct from range to range in Arizona. They are little separated by space and time: Different forms can be found in woodlands isolated by <10 km, and the spiders' habitats were probably contiguous between at least some of the now-isolated ranges <10,000 years ago.

Our primary purpose here is to describe the phenotypic differentiation of *H. pugillis*. However, we will also begin to examine the history and processes of its diversification. We will explore what can be discovered from phenotypic data alone; molecular data will be presented elsewhere (Masta, 1999; Masta and Maddison, in prep.). Because the isolated populations differ in many scorable characters of form and behavior, *H. pugillis* offers an opportunity to attempt phylogenetic analysis at small spatial and temporal scales using phenotypic traits. We will ask whether the differences among populations in *H. pugillis* are readily explicable by a branching phylogenetic tree.

We will also explore what factors may have promoted the phenotypic differentiation of *H. pugillis*. Sexual selection has been proposed as a force not only in the evolution of extreme male traits but also in diversification (Lande, 1981, 1989; West-Eberhard, 1983; Schluter and Price, 1993; Barraclough et al., 1995). Interpopulational differentiation of secondary sexual characteristics has been attributed to divergent sexual selection in other organisms (e.g., Claridge et al., 1985;

Young et al., 1994). The differentiation in *H. pugillis* also is mostly in secondary sexual characteristics of males, and we will suggest that sexual selection was involved in its origin.

MATERIALS AND METHODS

Study Organisms

H. pugillis was described by Griswold (1987) on the basis of specimens from the Mexican states of Sinaloa and Nayarit. In this paper we will refer to the Arizonan populations as *H. pugillis*, although it is unclear whether they should be considered conspecific with those described by Griswold or, for that matter, with each other. We will intentionally avoid the issue of formal taxonomic rank (species or subspecies) of different populations because it is not material to our analysis. The genus *Habronattus* is restricted to the New World, and most of its nearly 100 species are North American (Griswold, 1987). Species of *Habronattus* exhibit a great variety of male courtship behaviors and associated morphological ornaments (Peckham and Peckham, 1889, 1890; Griswold, 1987). Which of the other *Habronattus* species is most closely related to *H. pugillis* is uncertain (Griswold, 1987), although *H. pugillis* clearly is derived within a major clade and is not the sister to the rest of the genus (Griswold, 1987; Hedin and Maddison, unpubl.).

Jumping spiders of the genus *Habronattus* are typically ground dwellers, living on rocks, leaf litter, and other debris. They are best collected by scanning the substrate visually. We sampled various habitat types throughout southern Arizona, from the lower Sonoran desert through riparian habitats, oak woodlands, and the high-elevation pine and fir forests. In seeking *H. pugillis*, we sampled not only the mountain ranges labeled in Figure 1, but also the Pinal Mountains and parts of the Mogollon Rim.

Characters

To score most morphological characters, alcohol-preserved specimens were examined by dissecting microscope. For a few characters, such as the form of setae clothing the face, scanning electron microscopy was used. In addition, these setae were examined with a compound microscope
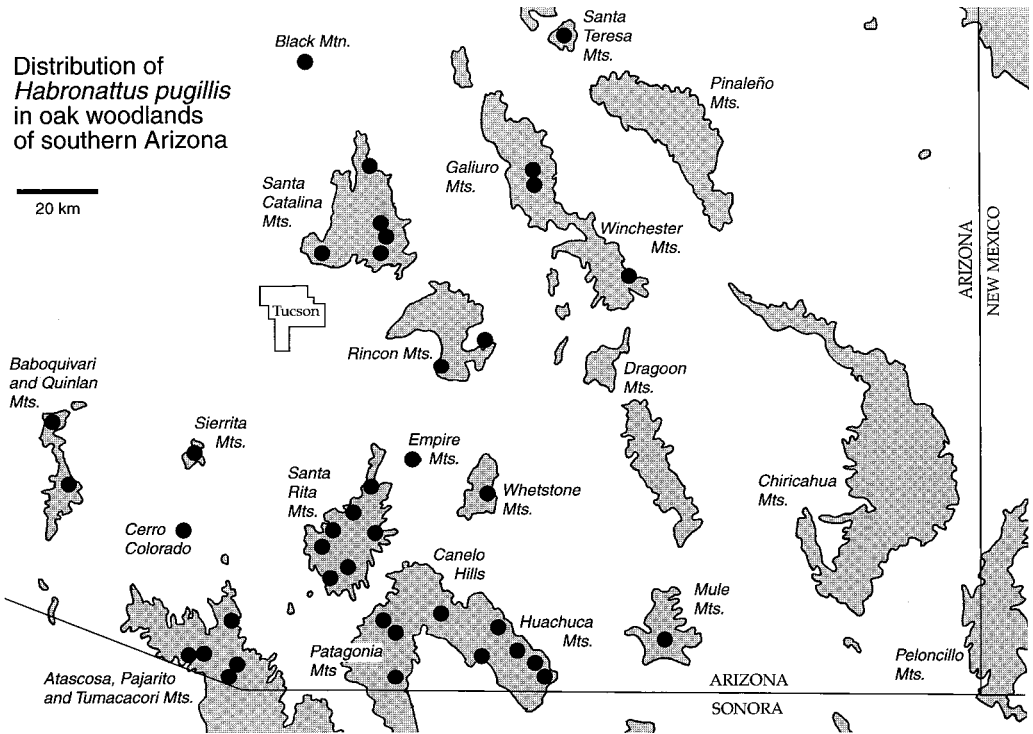
FIGURE 1. Map of southern Arizona. Outlined on each mountain range is the lower limit of oak woodland habitat according to Brown and Lowe (1982), corresponding to an elevation of ~1,300–1,500 m. Dots show collecting localities for *H. pugillis*.

(incident illumination with whole specimens or transmitted light with cleared cuticle) for one or two specimens from most of the ranges.

Courtship behavior was observed by placing a male and female together on graph paper, and videotaping with a NEC color Charge-coupled device camera with attached 100-mm Nikon macro lens (yielding a 10- to 15-mm-diameter field of view). Specimens were occasionally prodded or relocated to ensure that males and females remained in proximity and, as much as possible, facing each other. When the male began his display, intervention ceased. Whereas the frequent intervention used in this procedure would be inappropriate for studies of acceptance rates and other aspects of male–female interaction, it is adequate to characterize male courtship behavior, which is remarkably consistent regardless of how the female responds or of the source mountain range of the female. (Indeed, in *Habronattus* in general, the basic form of a male's courtship behavior does not seem to depend on the female being of the same species, or even alive; Maddison, unpubl.). For the most part,

wild-caught adult males and females were used, and their ages past maturity are not known.

Twenty-two morphological and behavioral characters were scored in undertaking a phylogenetic analysis of the populations. Characters selected for scoring are those that differed among ranges and could be scored with confidence. The characters and definitions of states are given in Tables 1 and 2. Four characters (7, 11, 18, and 22) were particularly difficult to score, three (7, 11, 22) because they varied more or less continuously, the other because in some populations the behavior was expressed infrequently. Because the close relatives of *H. pugillis* are unknown and the genus *Habronattus* includes ~100 species, outgroup species were not included individually. Instead, a single outgroup taxon was included to summarize states occurring in other species of *Habronattus* (W. Maddison, unpubl. data). If all other *Habronattus* species shared the same state, so far as known, the outgroup taxon was coded with that state. If the condition in other *Habronattus* was variable, the outgroup taxon was assigned missing data.

TABLE 1. Morphological characters for *Habronattus pugillis* from 16 mountain ranges. Outgroup is the composite of all other *Habronattus* species. & = individuals vary and both states are seen on the mountain range; / = uncertainty ("or"). Characters and their states are listed below the table. Sample sizes from each mountain range are indicated in the Appendix.

Taxon	Characters														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Outgroup	0	?	0	?	?	0	?	0	?	0	?	?	0	?	?
Santa Rita Mts.	2	0	1	0	2	0	1	1	0	0	0	0&1	0	1	0
Empire Mts.	2	0	1	0	2	0	1	1	0	0	?	?	0	1	0
Santa Catalina Mts.	1	0	0	0	4	0	1	0	1	0	0	0	0	1	0
Rincon Mts.	1	0	0	0	4	0	1	0	1	0	1	?	0	1	0
Sierrita Mts.	1	0	0	0	4	0	0	0	0	1	0	0	0	1	0
Cerro Colorado	1	1	0	0&1	3	0	0	1	0	1	0	0	0	1	1
Baboquivari Mts.	0	1	0	1	1	1	0	0	0&1	0	0	0	1	0	0
Atascosas Mts.	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0
Tumacacori Mts.	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0
Whetstone Mts.	2	0	1	0	3	0	1	0	1	0	1	1	0	1	0
Canelo Hills	2	0	1	0	3	0	1	0	1	0	1	?	0	1	0
Huachuca Mts.	1&2	0	1	0	3	0	?	0	1	0	1	1	0	1	0
Patagonia Mts.	0&1	1	1	0	3	0	?	0	0&1	0	?	1	0	0	0
Mule Mts.	0	0	0	0	2/3	0	0	0	1	0	1	0	0	1	0
Winchester Mts.	0	1	1	0	2	0	?	0	0	0	1	1	1	0	0
Galiuro Mts.	0	1	1	0	2/3	0	?	0	0	0	0	1	1	0	1

1. *Eye streak*: 0 = no white band; 1 = half (band is below lateral eyes but does not extend above median eyes); 2 = full (narrow band of white scales extending horizontally, from below the lateral to above the median eyes, like eyebrows). Treated as ordered. 2. *White or translucent band on lower part of clypeus*: 0 = narrow (height less than one-sixth height of clypeus); 1 = broad (height greater than or equal to one-fourth that of clypeus). This is scorable even on those with a silver grey face, because of a change in texture of scales marking the lower band. 3. *Scale flow transition on clypeus*: 0 = gentle (white scales below anterior lateral eyes point dorsally, but toward the median the white scales gradually turn, and over the chelicerae they are pointing obliquely ventrally or horizontally); 1 = abrupt (toward the median, the white scales turn abruptly to be pointing ventrally, and over the chelicerae they are pointing more or less directly down). The states are distinct; the most problematical form is the Santa Rita, with a somewhat intermediate condition. 4. *Orientation of white or translucent scales on clypeus*: 0 = primarily oblique below median eyes; 1 = primarily horizontal. While in some males scored "oblique" a small fraction of the setae may be horizontally oriented, in those scored "horizontal" most are oriented horizontally. 5. *Type of setae just below anterior median eyes*: 0 = leaflike (flattened, broad, transparent scale on a petiole-like stalk); 1 = unstalked leaflike (flattened, broad but not stalked; brown); 2 = blade-shaped (brown flattened scale with smooth rimmed edge); 3 = barbed scale (blade-shaped flattened brown scale with barbs along edges); 4 = barbed hair (narrow brown hair with barbed edges). Treated as ordered, this might have been equivalently divided into several characters (petiole present, width, barbs). Widths are distinctly different, and ordered 0 > 1 > 2, 3 > 4. We could not confidently score barb presence in some populations and therefore have treated it as uncertain (2/3). 6. *Prominent cheek spots*: 0 = absent (bare patches very small or absent); 1 = present (two or three large bare patches of integument, without covering of setae, beneath anterior lateral eyes among white scales). 7. *Type of setae on chelicerae*: 0 = hairs (setae on chelicerae are entirely hairlike, possibly flattened slightly, but at least 10 times as long as wide); 1 = scales (numerous broad, flattened white or cream-colored setae present on chelicerae, possibly mixed with fine hairs). This character is in general easily scored, except for males from the Huachucas, Galiuros, and Winchesters, which have an intermediate condition of flattened hairs. 8. *Integument of cymbium*: 0 = matte (finely rugose, so as to reflect light diffusely); 1 = shiny (smooth and reflective). 9. *White scales on cymbium*: 0 = absent (few or no white scales); 1 = present (10 or more, generally many more than 10, white scales on basal half of cymbium). 10. *Tibial hair spike*: 0 = absent (no tuft); 1 = present (narrow tuft of white hairs extending from lateral edge of palp tibia over the cymbium). 11. *White scales on tibia of palpus*: 0 = none to several scattered scales; 1 = a dense fringe of white scales. The distinction between "several" and "dense" was clear except for males from the Empire and Patagonia mountains. 12. *Bare patch on anterior lateral face of palp femur*: 0 = short (bare patch no more than one-half the length of femur); 1 = long (at least two-thirds the length of the femur). 13. *Swollen carapace sides ("cheeks")*: 0 = normal (no prominent bulge); 1 = swollen (prominent bulge on side of carapace beneath posterior eyes [Figs. 2i–l], such that lateral distance from inner edge of back eye to carapace side is greater than longitudinal distance from small eye to back of back eye). Although the carapace varies in width even among those without bulges, the categorization of some populations as having a prominent bulge is not problematical. 14. *Vertical fringes of first leg*: 0 = weak (few or no white hairs); 1 = strong (relatively dense fringe of long white hairs beneath patella and tibia). This character was subjectively scored. Although all populations have some white hairs, they can be easily broken down into those with stronger and those with weaker white fringes. 15. *Black tip, telotarsus of first leg*: 0 = small (black area no more than one-fourth the length of the telotarsus); 1 = large (black area at least one-third the telotarsus length).

More than 300 adult specimens from 20 mountain ranges were examined. For the males, it was confirmed that the easily observed features (e.g., appearance of clypeus [face below eyes], eye streak, clothing of palpus) are consistent with those described for their range. In addition, 179 males were examined carefully and scored for the morphological characters in Table 1. Courtship behaviors of 78 males were videotaped and then scored for the characters in Table 2. A more detailed accounting of the specimens examined is given in the Appendix.

Phylogenetic Analysis

The characters of Tables 1 and 2 were analyzed by using PAUP* 4.0b1 (Swofford,

TABLE 2. Characters of male courtship behavior in *Habronattus pugillis* from 16 mountain ranges. Outgroup is the composite of all other *Habronattus* species; state is listed where uniform as far as known. & = individuals vary and both states are seen on the mountain range. Characters and their states are listed below the table.

Taxon	Characters						
	16	17	18	19	20	21	22
Outgroup	?	0	?	?	0	0	?
Santa Rita Mts.	0	0	1	0	0	1	0&1
Empire Mts.	0	0	1	0	0	1	1
Santa Catalina Mts.	0	1	1	0	0	0	0
Rincon Mts.	0	1	0	0	0	0	1
Sierrita Mts.	0	0	?	1	0	0	1
Cerro Colorado	0	0	0	1	0	0	1
Baboquivari Mts.	1	0	0	0	0	0	0
Atascosas Mts.	1	0	0	0	0	0	0
Tumacacori Mts.	?	0	0	0	0	0	1
Whetstone Mts.	0	0	1	0	0	0	?
Canelo Hills	0	0	1	0	0	0	1
Huachuca Mts.	0	0	1	0	0	0	1
Patagonia Mts.	1	0	0	0	0	0	1
Mule Mts.	0	0	0	0	0	0	?
Winchester Mts.	0	0	0	0	1	0	1
Galiuro Mts.	?	0	?	?	1	0	1

16. *Approach*: 0 = direct (approaching female more or less directly straight forward), 1 = sidling (approaching female in indirect arcs, sidling left then right, and so on). 17. *Body shake*: 0 = no shake; 1 = shake (body shaken side to side during early courtship). 18. *Semaphore wave*: 0 = absent; 1 = present (a single first leg is slowly lifted high, almost to vertical, then lowered, followed by the other first leg). 19. *Femur pull*: 0 = absent; 1 = present (first legs are held forward and waved in a peculiar pushing and pulling motion two to three times per second, accomplished by pushing and pulling the end of the femur forward and backward). 20. *First leg wavy circle*: 0 = absent; 1 = present (first legs are held forward, and their tips are moved in circles simultaneously, rising medially, then laterally and down to complete the circle; in the lower and medial part of the circle, the tip is waved up and down with fairly high amplitude). 21. *Palp motion*: 0 = not circled (held down and to side; if moved, flickered quickly up and down with small amplitude); 1 = circled alternately (first one palp, then other—each is raised to the side while being shaken, then moved medially and down to complete the circle). 22. *Late-display leg flick*: 0 = double (both left and right legs flicked together, although usually with one leg flicked more strongly); 1 = single (one leg motionless while other is flicked downward, then the other is flicked downward).

1998). Parsimony was used as the criterion for branch-and-bound searches. Characters 1 and 5 were treated as ordered, the others as unordered. Although we might have excluded the four difficult-to-score characters (7, 11, 18, and 22) because they are likely to contain errors, we included them for the main analysis but gave them half the weight of the other characters. Trees were reconstructed primarily to help explore patterns of character-state distributions, not to obtain the definitive phylogenetic history of these populations. A simple phylogenetic tree may not exist for these populations, given the possibility of gene flow or retention of polymorphisms.

Phylogenetic methods typically constrain lineages to branch (not anastomose), characters to be monomorphic within the lineages, and all characters to follow the same branching history. Methods that relax these restrictions include those that allow hybridization or horizontal transfer (e.g., Wagner, 1983; Reiseberg and Morefield, 1995; Alroy, 1995; Dickerman, 1998; Charleston, 1998), those that allow retained polymorphisms (Cavalli-Sforza and Edwards, 1967; Farris, 1978; Felsenstein, 1979; Swofford and Berlocher, 1987; Page, 1993; Maddison, 1997), and those that detect recombination (Sneath et al., 1975; Hein, 1990; Maynard Smith and Smith, 1998). Reconstructing the history of lineages requires a balance of costs. For instance, under the parsimony criterion, a proposed history containing a reticulation (hybridization) is more complex than a simple branching phylogeny, but the complication would be balanced against the parsimony savings in character steps gained by avoidance of convergence (Alroy, 1995; Dickerman, 1998). The more steps saved by allowing a reticulation, the more compelling the case for hybridization.

Although studies of discordant histories of different genes are becoming commonplace, relatively little attention has been devoted to methods for phenotypic data. The methods of Alroy (1995) and Dickerman (1998) both assess the ability of a reticulate graph to explain characters parsimoniously.

Dickerman's method considers the reticulate graph as a composite of alternative branched trees and allows individual characters to choose which path of inheritance they followed. Unfortunately, no program is currently available to implement the method (Dickerman, pers. comm.). Alroy's (1995) Continuous Track Analysis (CTA) seeks to minimize the number of disjunct patches of character states on a reticulate graph. We used version 1.2.3 of CTA (Alroy, 1999) to explore reticulate histories. For this, four populations were trimmed from the data set (Empire, Rincon, Canelo Hills, and Tumacacori) so as to parallel the simulations discussed later. The two multistate characters (eye streak, 1; scale type, 5) were recoded additively as binary characters; polymorphic taxa were recoded as having missing data. Both complementary coding and polarized connections were used, as is appropriate when the results are to be interpreted as evolutionary history of lineages (Alroy, 1995).

CTA can best detect hybridization when some whole lineages are the products of hybridization affecting many characteristics. If, however, there were no major lineage fusions, but only occasional gene flow resulting in the introgression of a few characteristics scattered around the phylogeny, a method that focuses more directly on individual discordant character patterns might better detect reticulation. Accordingly, we have developed a test for hybridization that takes into account the geographic patterns of homoplasy for individual characters. We asked whether the convergences suggested by the reconstructed population tree tended to occur in populations that were geographical neighbors. Geographic proximity might suggest that the apparent convergence is not convergence at all, but rather the result of gene flow among neighbors.

To determine geographic patterns in apparent convergence, ancestral states were reconstructed by parsimony on the tree, using the same ordering assumptions as for tree reconstruction. A character showing homoplasy, whether apparent convergence or reversal to the ancestral state, was counted as having convergence in geographic neighbors if the distribution of one state in the reconstruction was separated into two portions of the tree, such that one portion included populations that are geographic neighbors of populations in the other portion. If so, then the one portion could be interpreted as having obtained the state from the other portion by introgression between those neighbors. Otherwise, the character was counted as having convergence in nonneighbors. If the ancestral state reconstruction was ambiguous but alternative resolutions agreed on the interpretation, the character was scored accordingly. If alternative resolutions disagreed or there was too much homoplasy to be readily interpreted, the character was not counted at all. Mountain ranges were defined to be neighbors as follows (with abbreviations; see Fig. 1): Santa Catalina (SC) with Galiuro (G), Winchester (Wi), Whetstone (Wh), Santa Rita (SR), and Sierrita (Si); Huachuca (Hu) with Mule (M), Wh, SR, and Patagonia (Pa); SR with Pa, Atascosa (At), Si, and Wh; Cerro Colorado with Si, SR, At, and Baboquivari (Bq); Wi with G and Wh; M with Wh; Bq with Si, and At; and At with Pa. Four ranges (Empire, Rincon, Canelo, Tumacacori), the forms of which are nearly identical to those of nearby ranges, were excluded from the tree for purposes of scoring the geographic proximity of homoplasy, to make the tree comparable with that used in the simulations described below.

The amount of geographically proximate homoplasy must be judged against a null expectation. Perhaps it is easy to invent an ad hoc explanation of hybridization between neighbors with these populations—there are few enough populations, and they are close enough together that most convergent characters will occur in clades with points of geographic contact. To be sure, many patterns of homoplasy would not concord with hybridization, such as derived states shared between distant ranges (e.g., Huachucas and Sierritas). Therefore, a simple simulation of character evolution was performed to test whether geographically proximate homoplasy was more common than expected by chance. One of the parsimonious trees was used (the most symmetrical, to minimize differences in branch lengths), but pruned to include only 12 populations. Excluded were the outgroup and four mountain ranges (Tumacacori, Empire, Rincon, and Canelo Hills) because they are nearly identical to their sister ranges and may represent very short branches; including them as separate taxa would artificially expand the size of the model tree. Two-state characters were

evolved by using the "Evolve Characters" feature of MacClade 3.07 (Maddison and Maddison, 1992) with a probability of change of 0.05 per branch segment (branch lengths minimally adjusted by adding segments to make the tree ultrametric). The simulation was concluded when 200 simulated characters were obtained that showed the most common level of homoplasy observed in our data (two steps = character-state changes) and that could be scored as to whether or not they showed convergence in geographic neighbors, using the same scoring as described above for our data. Characters with three or more steps were excluded because, with so many changes on a tree this small, they could not in general be confidently scored as to whether homoplasy was geographically proximate or not. The proportion of simulated characters showing geographically proximate convergence was compared with that among characters in the actual data, and significance was tested by a *G* test (likelihood ratio chi-square test).

RESULTS

Distribution and Habitat

H. pugillis was found in montane habitats between 1,200 and 2,600 m elevation, mostly in xeric oak woodland. The spiders were typically found below 2,000 m, on rocks or sun-struck leaf litter where rocks and grasses are intermixed on well-drained slopes with a scattered to dense covering of oaks. At higher elevations they could be found in pine woodlands, but usually near oak trees. Adult males were most commonly found from February through April, coinciding with the spring season, and August through September, coinciding with the summer wet season. Despite extensive collecting at lower elevations, *H. pugillis* was never found below the oak woodland. Lower-elevation habitats are occupied by other species of *Habronattus* (e.g., *H. virgulatus*, *H.* cf. *fallax*, *H. ustulatus*, *H. conjunctus*, and *H. clypeatus*).

H. pugillis was found on all the mountain ranges of southern Arizona sampled (Fig. 1) except the easternmost (Chiricahuas, Dragoons, Peloncillos, and Pinaleños), where *H. clypeatus* occupies the same microhabitats, and the northernmost (Pinals, Mogollon Rim). The literature provides no further information regarding its distribution in Arizona for, before our collecting, it was known only from three specimens collected many years ago in Sinaloa and Nayarit, Mexico (Griswold, 1987). Given its habitat and its occurence in the satellite ranges of the Sierra Madre, *H. pugillis* may be broadly distributed throughout the Sierra Madre Occidental of Mexico.

Common Features

Specimens of *H. pugillis* are generally grayish tan to brown, ~5–7 mm long. Structures and behaviors are illustrated in Figures 2–5. Males are brown without prominent markings as viewed from above, with the abdomen paler than the carapace. Females are pale grayish tan except for two darker longitudinal bands on the abdomen. A combination of characters serves to diagnose *H. pugillis* from other *Habronattus*: unmarked abdomen (most *Habronattus* males have prominent stripes or bars of white and black), ventral fringe of pale hairs on the first leg, black tip on the first leg, pale setae on the male chelicerae (jaws) organized in bundles, stridulatory organ between the carapace and abdomen (weaker than that present in the *H. agilis* group; Maddison and Stratton, 1988), simple male courtship behavior with little movement of first leg during approach followed by periodic downward flicking before mounting, and genitalia with characteristic form. The genitalia (Griswold, 1987), which are usually concordant with other evidence of species and clade boundaries in salticids (e.g., Griswold, 1987; Maddison, 1996), are consistent across populations and distinct from those of most other *Habronattus*. More details on the species, including photographs, can be found at http://spiders.arizona.edu/salticidae/habronattus/pugillis.html.

The courtship behavior of *H. pugillis* varies by population, but there is a common theme throughout. The courtship can be divided into two main stages. In the first stage, which often begins several centimeters from the female, the male raises and spreads the first pair of legs, and lowers and spreads the palpi (Fig. 3). In that position he approaches the female, either directly or in a sidling motion, waving or flickering his appendages in a characteristic manner. The first pair of legs may be waved or held still, but in none of the forms do they engage in
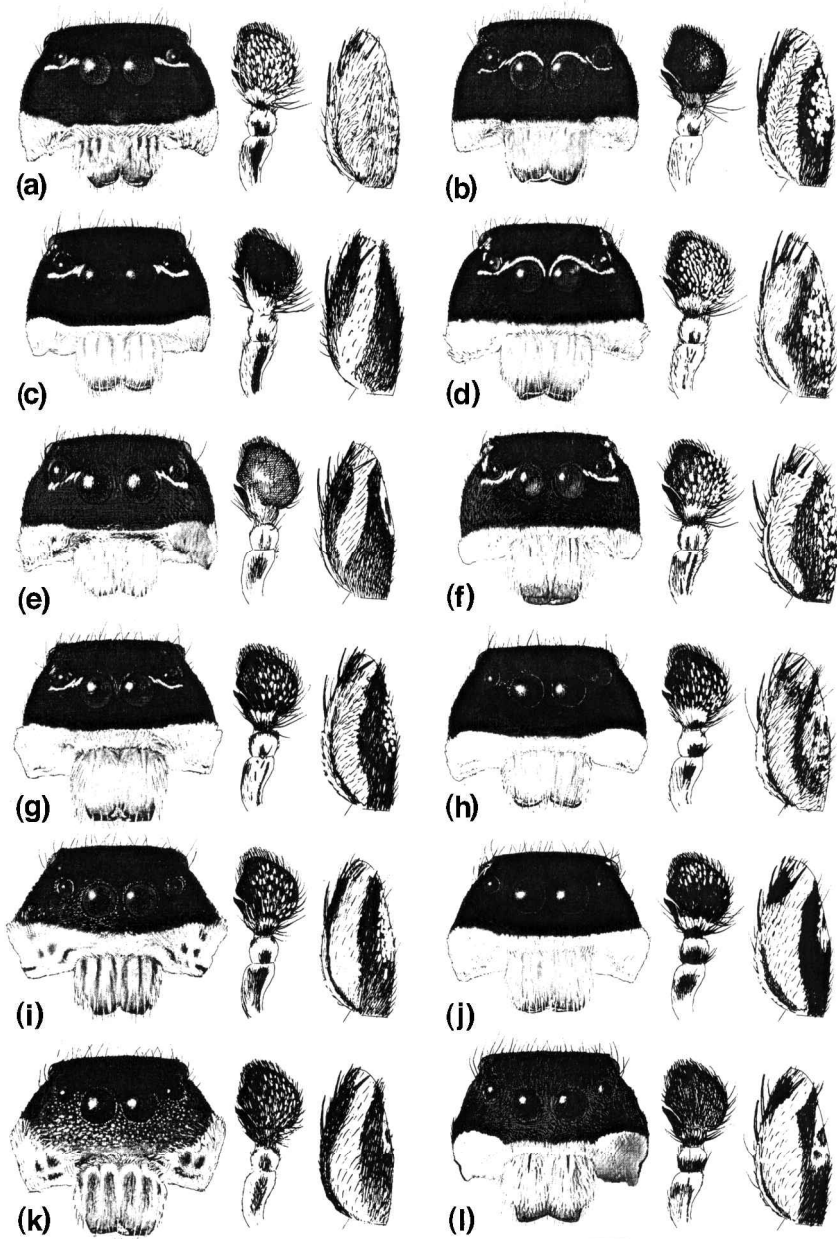
FIGURE 2.   Males of *H. pugillis* from different mountain ranges. Shown for each are face, dorsal view of palpus, and anterolateral side of first leg femur. (a) Santa Catalina Mountains, (b) Santa Rita Mountains, (c) Sierrita Mountains, (d) Whetstone Mountains, (e) Cerro Colorado, (f) Huachuca Mountains, (g) Patagonia Mountains, (h) Mule Mountains, (i) Baboquivari Mountains, (j) Winchester Mountains, (k) Atascosa Mountains, and (l) Galiuro Mountains.

the complex motions seen in other species groups of *Habronattus* such as the *coecatus* or *viridipes* groups (Peckham and Peckham, 1889, 1890; Maddison and Stratton, 1988). As he gets within one or two body lengths of the female, the second stage begins. The male slows his approach and periodically flicks the first legs quickly downward, simultaneous with a grinding of the abdomen against the carapace (presumably, stridulation). If
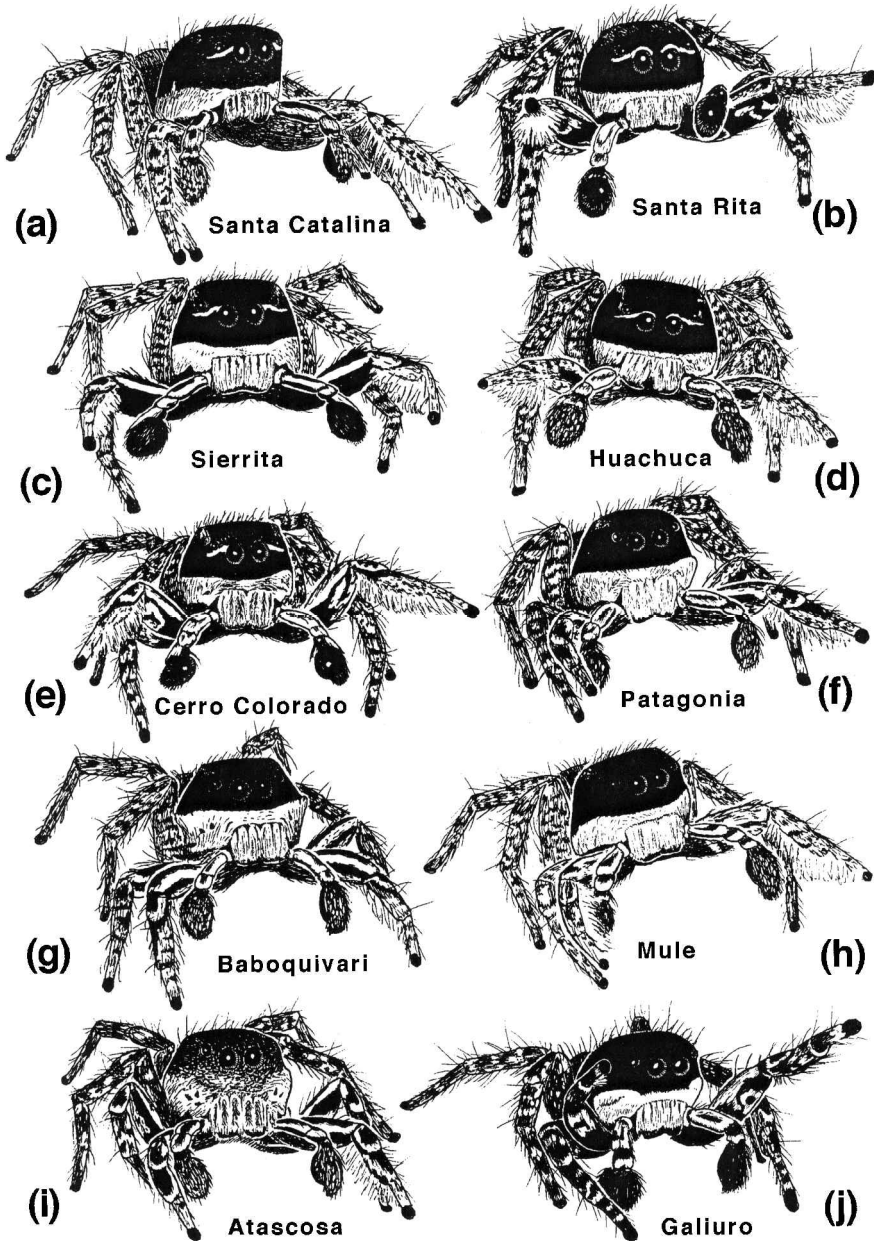
FIGURE 3.   Males of *H. pugillis* from different mountain ranges. Shown in courtship pose, traced from video images. (a) Santa Catalina Mountains, (b) Empire Mountains (Santa Rita form), (c) Sierrita Mountains, (d) Huachuca Mountains, (e) Cerro Colorado, (f) Patagonia Mountains, (g) Quinlan Mountains (Baboquivari form), (h) Mule Mountains, (i) Tumacacori Mountains (Atascosa form), and (j) Galiuro Mountains.

the female has remained in place, he then attempts to mount and copulate.

Geographic Variation

The features showing geographic variation in *H. pugillis* primarily involve the colors and form of the male face and anteriormost appendages (Fig. 2), which are exposed to the female during courtship display, and in the display behavior itself (Fig. 3). The male abdomen, top of the carapace, and posterior appendages vary, but only in a few features: The overall darkness varies, as does the distinctness of the paler longitudinal bands on the thoracic region. Females show little
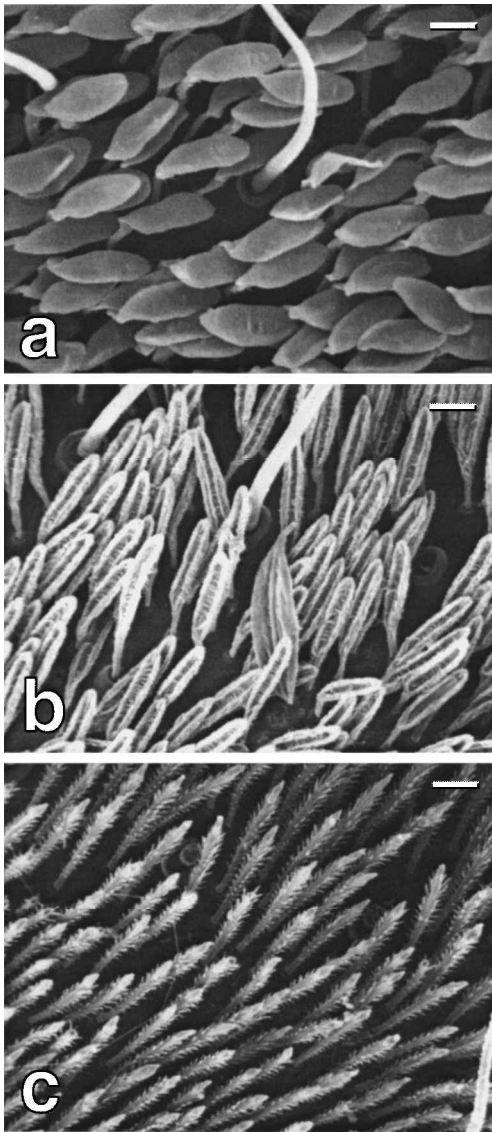
FIGURE 4. Setae on male face just below anterior median eyes. Scale bars 10 μm. (a) Atascosa Mountains, (b) Santa Rita Mountains, and (c) Sierrita Mountains.

distinction between populations except in the distinctness of the longitudinal bands on the abdomen.

Relative to differences among ranges, there is little variation among the males collected at a locality or within the same mountain range, and thus the differences between mountain ranges are consistent for most described characters.

Among some neighboring mountain ranges, the differences in *H. pugillis* are slight. For instance, specimens from the Santa Rita and Empire Mountains are more or less indistinguishable. For convenience, these two ranges are grouped together in descriptions and discussions as if they contained a single "form" of *H. pugillis*. The same is done for several other groups of ranges (see Appendix). We sometimes refer to a form by its largest mountain range (thus, the form from the Santa Rita and Empire Mountains is called simply the "Santa Rita form").

We present here an overview of the variation. Descriptions of the populations on each mountain range are given in the Appendix, including any known variation within a range. Figure 6 summarizes geographic distributions of character states.

Face.—The male face (Fig. 2) in most populations is bicolored—dark brown with white along the lower margin—but in the southwesternmost ranges (Atascosas, Pajaritos, and Tumacacoris) males have silvery grey faces. The brown or dark grey setae vary in orientation (erect, recumbent; oriented dorsally, medially) and in form (barbed, smooth; wide [scales], narrow [hairs]; stalked on a petiole, or not; Fig. 4). The white marginal band varies in width, and its setae vary in orientation, translucence, yellowness, and density. Some populations have white streaks beside the anterior eyes ("white eye streaks"), which can be either complete, extending from beneath the lateral eyes to above the median eyes, or incomplete, being restricted to beneath the lateral eyes. (Females have a white face but have some dark setae around the eyes. They show a hint of this eye streak in parallel with their local males.) Males of some forms have swollen carapace sides below the posterior eyes, others narrow.

Appendages.—The chelicerae are clothed in setae that can take the form of thin hairs, flattened hairs, scales, or a mixture; they vary in orientation and density to produce such patterns as vertical bundling. The cymbium (expanded terminal segment of male palpus; Fig. 2) may be clothed with dark hairs only, or with white scales as well; in some populations, it has few hairs and its integument is shiny. The first leg in some populations has the patella and tibia fairly pale with a heavy fringe of long white or yellow hairs beneath, but in others the leg has dark maculations dorsally and little fringe beneath (Fig. 5). The first leg femur can be emphatically striped, spotted, or uniformly dusted with pale scales
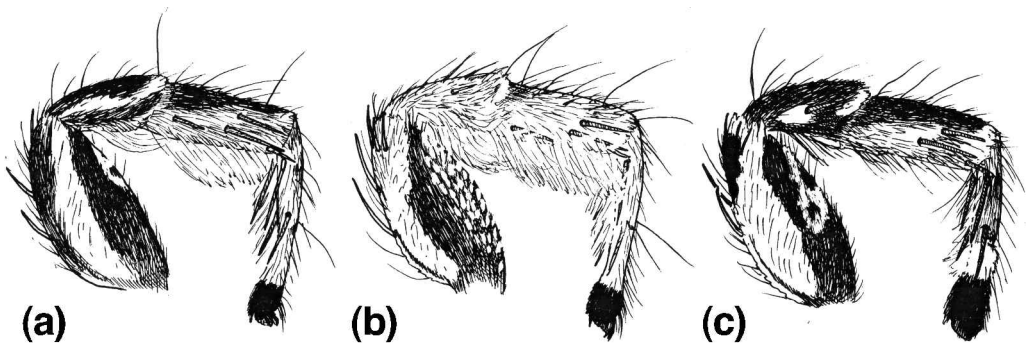
FIGURE 5. Left first leg of males from (a) Atascosa Mountains, (b) Huachuca Mountains, and (c) Galiuro Mountains.

(Fig. 2). The only differences among populations noted in the posterior legs are in darkness and contrast between dark and pale maculations.

Courtship behavior (Fig. 3).—Some forms have unique elements, including palp circling (Santa Rita), body shakes (Santa Catalina), and leg circling (Galiuro). The southwestern mountain ranges have a zigzag approach (sidling) to the female during the first stage of courtship (Atascosa, Baboquivari, and Patagonia). Others proceed more directly to the female. In general those that

sidle perform this first stage very quickly (5 seconds or less); those that approach directly spend much longer in the first stage (up to a few minutes). Several forms (Huachuca, Whetstone, Santa Rita, and Santa Catalina) pause occasionally during the first stage and raise and lower one first leg slowly, then the other, in a semaphore-like motion.

We did not perform controlled measurements of female response to males, but in our observations to record male courtship behavior we often paired the male with a female from a different mountain range. In seven
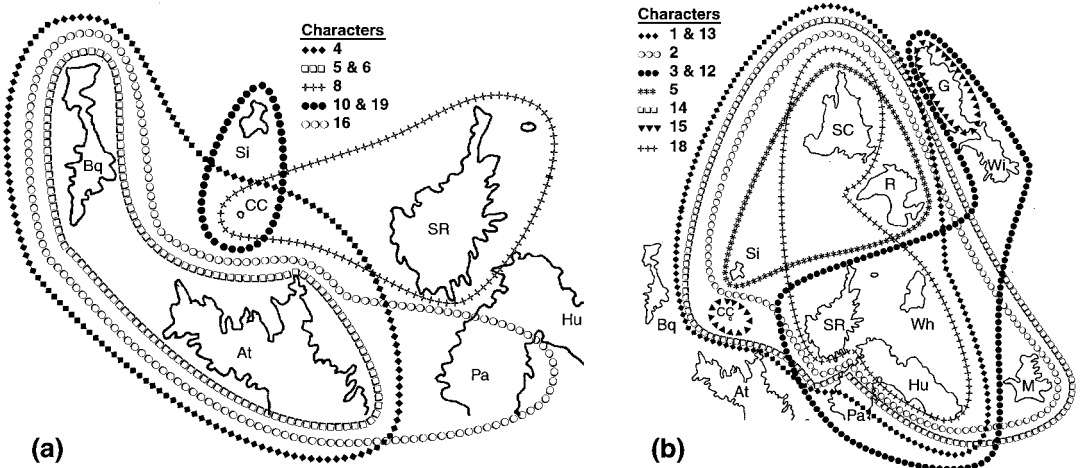

FIGURE 6. Distributions of character states. Abbreviations for mountain ranges as in Methods. For two-state characters, the distribution of only one state is shown, chosen for graphical simplicity (not necessarily the state interpreted as derived). For the ordered multistate characters 1 and 5, several states are combined. (a) Selected states of characters 4 (horizontal clypeal scales), 5 (bladelike setae, states 0 and 1), 6 (cheek spots), 8 (shiny cymbium), 10 (palp hair spike), 16 (sidling), and 19 (femur pull). (b) Selected states of characters 1 (eye streak present, states 1 and 2), 2 (narrow white clypeal band), 3 (abrupt clypeal transition), 5 (setae hairlike, state 4), 12 (long bare patch palp femur; polymorphic in SR), 13 (narrow carapace), 14 (strong leg fringes), 15 (black leg tip), and 18 (semaphore wave). Characters not shown: 7 (too many uncertainties in data); 9, 11, and 22 (too homoplasious); 17, 20, and 21 (simple distributions, with one state restricted to two very similar neighboring ranges).

cases females copulated with males from other ranges (females from the Atascosas accepted males from the Winchesters, Catalinas, Canelo Hills, Whetstones, and Quinlans; a female from the Patagonias accepted a male from the Whetstones; and a female from the Santa Ritas accepted a male from the Galiuros). Because these observations were not controlled we do not know if females have a relative preference for males from their own range.

Phylogenetic Analysis

The results of detailed character-scoring for phylogenetic analysis are summarized in Tables 1 and 2. Not all ranges are included. Many more features than these differ from range to range, as indicated above and in the Appendix, but we did not obtain clear data for them. The problem with scoring many features was not within-range variation but rather the subtlety of more-or-less continuous variation in a character (e.g., translucence of white scales on clypeus). All of the characters scored were parsimony-informative.

Fifteen most-parsimonious trees were obtained by a branch-and-bound search (tree length 33.5 excluding steps in terminal polymorphisms; consistency index 0.62; retention index 0.80). Their consensus is given in Figure 7a, which also shows the percentage

of bootstrap replicates (if >50%; total: 500) that yielded the various clades. The 15 trees differ primarily in the rooting and in the arrangement of the Huachuca–Canelo Hills–Whetstone clade. The tree in general groups by geographic proximity, with one notable exception being the grouping of the extreme northeastern (Galiuro and Winchester) and southwestern (including Atascosa) populations. The northeastern and southwestern populations are in general darker, with weak leg fringes and wider carapaces. The central populations have eye streaks and well-fringed first legs. Alternative analyses that excluded the characters considered difficult to score (7, 11, 18, and 22), or that gave them the same weight as other characters, resulted in trees that were largely similar to the tree presented, except that with equal weighting the position of the root of *H. pugillis* became unresolved.

CTA (Alroy, 1995) resulted in graphs (Figure 7b) that are fairly concordant with the standard parsimony analysis. The CTA score was 73 when no reticulations were allowed, 68 with one reticulation. The graph with one reticulation differs from the graph with none by the addition of a link between the Santa Rita and Sierrita forms. Graphs with 2 through 13 reticulations had scores of 67, 64, 61, 57, 54, 52, 50, 47, 49, 48, 47, and 47, respectively (the 49 and 48 apparently reflect search inefficiencies).
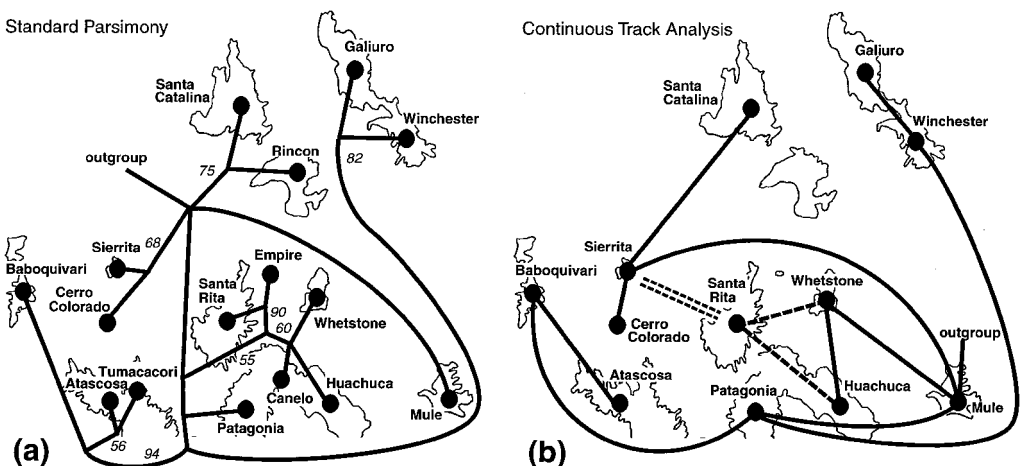

FIGURE 7. Results of phylogenetic analyses. (a) Standard parsimony tree. Strict consensus of 15 most-parsimonious trees, with percentage of 500 bootstrap replicates that show particular clades (if >50%). (b) Graph from Continuous Track Analysis. 0-reticulation graph represented by solid lines and single dashed lines. Single dashed lines represent uncertainty in links (Santa Rita connecting either directly to Whetstone or indirectly by way of Huachuca). Double dashed line shows link added by allowing one reticulation (Santa Rita to Sierrita by way of Whetstone and Huachuca).

Patterns of Homoplasy

On the reconstructed trees, 8 of the 22 characters showed no homoplasy: 6, 10, 13, 14, 17, and 19–21. Of the remaining 13, three (9, 11, 22) show high homoplasy (four to five changes) and no obvious interpretation has been found for the "convergence." One (character 15) has a derived state in the Galiuros and Cerro Colorado, two distant ranges for which convergence is a reasonable explanation.

However, for characters 1–5, 7, 8, 12, 16, and 18, homoplasy occurs in geographic proximity. That is, independent "derivations" on the tree occur in neighboring ranges. A wide white clypeus band (character 2) and horizontally directed white setae (character 4) are derived states in the Cerro Colorado but occur "independently" in the neighboring ranges to the south and west. The shiny cymbium (character 8) appears convergent in the Cerro Colorado and the neighbor to the east, the Santa Ritas. The tree interprets a gradual scale flow transition (character 3) and short bare patch on palp femur (character 12) as ancestral, occurring in the Sierritas and Cerro Colorado (along with the Santa Catalina form), but these traits are shared as an apparent reversal by the nearby southwestern ranges. A group of central populations (including the Santa Ritas and Whetstones) shares apparent convergence in wide scales on the chelicerae (character 7), semaphore display (character 18), and eye streak (character 1) with the Santa Catalinas form just to the north. (The eye streak could equally parsimoniously have been lost independently, in which case its absence in many Patagonias males would be convergent with the neighboring Atascosas.) Sidling in the Patagonias (character 16) also occurs in their neighbors to the west. The Sierritas shares with its neighbors to the north (Santa Catalinas and Rincons) the thin barbed hairs on the face (character 5).

In total, eight two-state characters show homoplasy with two steps (2–4, 7, 8, 15, 16, and 18). Of these, seven (2–4, 7, 8, 16, and 18) were scored as having homoplasy in geographic neighbors by the criteria discussed in Methods.

Of the 200 simulated characters that showed homoplasy with two steps, 113 were scored as having homoplasy in geographic neighbors (56.5%). We used this as a null expectation. A 2×2 contingency test comparing 113:87 (from simulation) against 7:1 (observed) shows the abundance of observed cases of geographically proximate homoplasy approaches significance ($G = 3.51$; df $= 1$, $P = 0.06$).

Also contributing to the geographic pattern of homoplasy are the observed polymorphisms within populations. The polymorphisms in Table 1 for characters 1 (Patagonias), 4, and 12 all represent within-locality variability. In each case the polymorphic mountain range has monomorphic neighbors with each state. For instance, the eye streak being polymorphic in the Patagonias generates a phylogenetic character conflict: The eye streak is shared with the ranges immediately north and east, but other characters in the Patagonias (dark legs, sidling approach, wide carapace, translucent clypeal band) are like those in the streakless ranges just to the west. Some, but not all, males from the Santa Catalinas and Santa Ritas have the white clypeal border abruptly broader just lateral to the chelicerae (a character not formally scored), reminiscent of the more pronounced cheek patches of the nearby Galiuro form.

DISCUSSION

Although it is tempting to imagine the Arizonan sky islands as a continental Galapagos with waves of desert heat lapping against the oak woodland, in fact few of their species are known to show a phenotypic diversification comparable with that of *H. pugillis*. By "comparable" we mean a mosaic of closely related forms, differing from one sky island to the next, whether this differentiation is currently considered intraspecific or interspecific. The differentiation of *H. pugillis* appears to be endemic to these sky islands. The fact that many of the forms of *H. pugillis* are unique, as far as known, to individual mountain ranges suggests that they differentiated in situ. The alternative, that they differentiated elsewhere and then moved in and settled down one each to a range, is implausible, especially because it appears that they can interbreed. To be sure, other groups of organisms have different forms or species on the different sky islands, but many such examples would not be considered endemic radiations. For instance,

we would not consider comparable a clade with two more broadly distributed parapatric forms for which the range boundary just happens to fall among the Arizonan sky islands.

A mosaic of phenotypically differentiated forms among the Arizonan sky islands has been reported in the gastropod genus *Sonorella* (Miller, 1967; Bequaert and Miller, 1973; McCord, 1995), the snail-eating beetle *Scaphinotus petersi* Roeschke (Ball, 1966), and the angiosperm *Castilleja austromontana* (Slentz et al., 1999). Unpublished examples exist, including some other salticid spiders that show more subtle differentiation than *H. pugillis* (*Ha. altanus*, *H. oregonensis*, and *Phidippus tyrrellii*). In contrast, no morphological differentiation has been detected in the many other species of salticids from these woodlands (including 10 species of *Pelegrina* [Maddison, 1996] and species of at least 8 other genera [Maddison, unpubl.]). We have asked many biologists familiar with the flora and fauna (vertebrate and invertebrate) of these mountain ranges, and none knew of differentiations of the magnitude of *H. pugillis*, other than those discussed here. Thus, the extent of differentiation of *H. pugillis* is rare among its fellow sky island inhabitants. Clearly, different species have reacted differently to their fragmentation on the sky islands.

In exploring the differentiation of *H. pugillis*, we will examine four issues: the geographic patterning of homoplasy, whether hybridization or sorting of retained polymorphisms are indicated, the possibility of sexual selection driving the differentiation, and the age of the differentiation.

Geographic Patterning of Homoplasy

We sought to answer whether in general homoplasy was geographically patterned, that is, whether apparent convergences were more often between geographic neighbors than expected by chance. Our answer is a qualified "yes." The statistical test was suggestive but not compelling. The evidence for a geographic pattern is fairly strong, however, in connection with a few mountain ranges.

An intuitive sense of the geographic patterning of homoplasy can be obtained from Figure 6, which shows many character distributions that are necessarily discordant, regardless of tree chosen (see LeQuesne, 1969). For instance, in Figure 6a, characters 4, 8, and 10 are necessarily discordant with one another, and yet states in each character act to delimit sets of geographic neighbors. Many other such discordances can be found (e.g., 19 vs. 2; 16 vs. 3).

Statistical test.—In the statistical test of geographic proximity of apparent convergences, we scored proximity in characters homoplasious on the reconstructed trees (Fig. 7a), and compared these characters with the simulated characters. The proportion of observed characters with two steps showing geographically proximate convergence (7 of 8, 87%) was greater than in our simulations (56%), a difference that was close to significant at the 5% level ($P = 0.06$).

Just as with the significance of the result, our statistical approach was promising but not quite satisfying to us. It has the advantage of focusing on individual characters and using geographic information, thus possibly being more effective at detecting scattered introgression than previous phylogenetic methods. Although the approach was inconvenient (we scored simulated characters by eye, because we lacked an automated way to score geographic proximity of homoplasy), it may be a reasonable approach given current methods and our knowledge of the spiders. However, several concerns about the approach and its application to these data warrant discussion.

There were, as always, difficulties with scoring of and assumptions about characters. The interpretation of character 18 as showing geographically proximate convergence could be questioned, given the fact that the Rincon specimens did not show semaphore waving (Fig. 6b). This behavioral character was difficult to score, because the characteristic waving was rarely performed in some populations. On the other hand, five to six additional cases of convergence in neighbors might have been counted but were not: lack of barbs in character 5 (a multistate character), hair vs. scale in character 5, polymorphisms in eye streak (character 1), white femoral band (not scored; scoring ambiguous in several populations), and translucence of setae (not scored; continuously variable). But even if these were included, statistical problems would remain. There are hints of functional correlations among the characters, as discussed below concerning sexual

selection. Nonindependence of the characters would detract from an argument for significance.

A general concern with our approach is the difficulty of assigning parameter values in the simulation. For example, our test is sensitive to the branches on which changes occur. If changes tend to occur deep in the tree, convergences will be between large clades, making it more likely that they will be judged geographically proximate. Thus, different assignments of branch lengths in our simulations would likely affect the results of the test.

Another concern with our method is its use of a particular phylogenetic tree. The null hypothesis should be that there existed a tree, of unknown form, on which convergence generated homoplasy. Our test specifies a particular tree and asks whether convergence on it could explain the pattern. Could a significant result merely reflect an inappropriately chosen tree? For instance, if these populations had a true, branching phylogeny that is more strongly concordant with geographic proximity than that of Figure 7a, then our tree could be incorrectly splitting apart populations that are geographically and phylogenetically close. This would cause homologies to appear falsely as convergences among geographically close populations. We would have preferred a method that did not depend on a choice of tree but instead considered all possible trees, either explicitly or implicitly, in the style of compatibility analysis (LeQuesne, 1969; Estabrook et al., 1976). Because the scoring of the simulated characters was done by hand, we were unable to examine all possible trees.

However, although our choice of tree may have some effect, that is unlikely to explain most of the pattern. Our tree is mostly concordant with geography and thus would seem to minimize false convergences among neighbors. We examined implicit homoplasy on two alternative trees. The first tree was based on that in Figure 7a, but modified to be more concordant with geography by moving the northeasternmost populations (Galiuros and Winchesters) from being sister to the southwesternmost populations, to being sister to the Mules. This tree shows only a slight decrease in the pattern, with a net loss of one example of geographically linked homoplasy. The second alternative tree was based on a new parsimony search. We excluded characters that were perfectly concordant with

our tree (4, 6, 10, 13, 14, 17, 19–21), and let the remaining characters choose the most-parsimonious trees. 1102 trees resulted from the PAUP branch-and-bound search. We examined trees 1, 201, 401, 601, 801, and 1001. For tree 1, the number of characters with two steps was 11, of which 10 were scored as showing homoplasy among neighbors. For the other trees the proportions were 7/8, 9/10, or 10/11. The geographic pattern is as strong as or stronger than with our original tree. The results from alternative trees give us confidence that at least some of the pattern is independent of choice of tree.

Concentration of discordance.—Our statistical test does not pay attention to the geographic concentration of character discordance. In fact, many discordant distributions center around one mountain range, Cerro Colorado (Fig. 6). This small range has apparently derived states that it shares with neighboring ranges in each direction: east (Santa Ritas, character 8), north (Sierritas, characters 10 and 19), south and west (characters 2 and 4), and north and east (character 1). In addition, other traits not scored formally are shared with different neighbors. The narrow, centrally placed white band on the first femur (Fig. 2c, e, k) is shared to the north and south (Sierritas and Atascosas), and translucence of setae on the clypeal margin occurs also to the south and southeast (Atascosas and Patagonias) and in the more distant Galiuros. These characters hint that Cerro Colorado has received genes from neighboring ranges. The Patagonias also show signs of a mixed heritage, with the bicolored face and (polymorphically) eye streaks being shared with the ranges to the north and east, but the reduced leg fringes, partly translucent clypeal scales, broad clypeal band, and sidling being shared with the ranges to the west.

Hybridization versus Polymorphisms versus Convergence

There appears to be an abundance of geographically proximate homoplasy, at least surrounding a few ranges such as Cerro Colorado, if not in general. If we accept this, how is it to be explained? We will here consider three alternatives: convergence, retention and sorting of ancestral polymorphisms, and introgression by way of hybridization.

Convergence.—Adaptation to similar environments in neighboring ranges, directly or

by influencing sexual selection, could yield geographically proximate convergence. One possible scenario would invoke geographically patterned selection based on female preference. If female preference is based on sensory biases (Ryan and Rand, 1993) that have evolved differently in response to differing environments, then geographically patterned differences in the environments may result in differences among the male traits as observed. However, at the scale of a spider, the variation in habitat (forest type, slope, substrate) experienced within a range is probably far greater than that between ranges, given that within a range they are present in varied elevations and woodland types.

Even if differing environments have provoked differences in female preference, it seems unlikely that female preferences would convergently demand the same detailed male trait. If, for example, females' senses are stimulated by a highlighted eye or by a brown-white contrast, it appears unlikely that different populations would just happen to produce the same solution—a curved streak of white just over and beside the eye. There are many other ways such contrast could be achieved, as indicated by the diversity of ornaments seen in *Habronattus* in general (see Griswold, 1987). Similar arguments could be made about the tibial spike (character 10), shiny cymbium (character 8), and translucent horizontal pale setae on clypeus (character 4). On the other hand, perhaps the same solution to female preference might arise repeatedly because of a common developmental background, causing some phenotypes to be accessible through fewer genetic changes than others (and thus more likely to be available for selection). A combined ecological–developmental explanation of convergence may therefore suffice, although it seems to us unnecessarily complex with current data.

Retention and sorting of polymorphisms.—If an initially broad range of a polymorphic *H. pugillis* were fragmented, random fixation of the polymorphism in isolated populations could leave an eventual pattern of discordant characters. This might appear to imply an initial population much more polymorphic than any seen today. However, the polymorphism would not need to have been expressed phenotypically: Genetic polymorphisms could have existed but failed to yield

the allele combinations to produce differing phenotypes (Throckmorton, 1965), especially if epistasis were involved. Perhaps what makes this explanation doubtful is that it is not clear why it should generate a clear geographic pattern. Successive range fragmentation into smaller and smaller populations with partial lineage sorting (fixation of polymorphisms) in intermediate stages could cause neighboring populations to be somewhat more likely to have fixed to the same state. We expect, however, that any geographically proximate homoplasy generated by such a process would be isolated to small clades of populations. This seems not to be the case with our data because the apparently convergent populations differ in many features and do not appear to be particularly close relatives. We are inclined to doubt sorting of polymorphisms as an explanation of the homoplasy, but we realize that distinguishing between this hypothesis and that of hybridization is difficult.

Hybridization and introgression.—Geographic proximity of convergence is most readily explained by introgression between neighbors. Hybridization and introgression are also consistent with hints that the forms are not reproductively isolated (cross-range matings and lack of sympatry, discussed in the following section), and with the expectation that there would have been contact between the forms in the last 10,000 years (discussed in the section on Age of the Differentiation).

The drop in score from 73 to 68 when a reticulation is allowed in the CTA might be taken to indicate that the data prefer a non-branching history. The place chosen by CTA for the first reticulation—between the Sierrita and the Santa Rita forms—is intriguing, for these are geographic neighbors. However, this is only a single reticulation, and its geographic placement could be mere luck. The statistical significance of such a drop in score is not yet known. It is a far smaller percentage decrease than was yielded by reticulations in the example figured by Alroy (1995:Fig. 9)

To distinguish better among the possible causes of homoplasy in this system, better methods and data would both help. We have already suggested that a tree-independent method of gauging geographic patterns in homoplasy would have been useful. In addition, neither our method nor those of Alroy and Dickerman pay attention to the form

that introgressed characters are likely to take (intermediate between parentals, or not?— see McDade, 1990). Whereas the methods could work either if hybrid character states were scorably intermediate or if hybrids contained a mix of pure states of the parental lineages, any more sophisticated phylogenetic method would do well to consider these issues (McDade, 1990, 1995). However, better methods of analysis will help only to a certain extent. New sources of data are at least as important. A morphometrics approach may give us many more phenotypic characters, and a better assessment of their variation. Genetic complementation tests could allow us to assess homology of the discordant character states.

Sexual Selection and Reproductive Isolation

Lacking controlled experiments on female choice and hybridization, we cannot make definitive statements about sexual selection and reproductive isolation. However, the involvement of sexual selection in the differentiation is suggested by the fact that numerous consistent differences among the ranges were found in male secondary sexual characteristics that are visible to the female during courtship behavior, but few differences were found in females or other aspects of male morphology. For instance, it is unlikely that the posterior legs are under substantially different developmental or ecological constraints than the anteriormost legs (in female salticids they tend to vary in parallel), and yet the former are much more uniform across populations than the latter. Masta (1999) and Masta and Maddison (in prep.) have found population genetic evidence pointing to the involvement of selection in this differentiation.

Another indication of sexual selection comes from correlations between behavior and form. Peckham and Peckham (1889, 1890) used this same argument of behavior–form correlation in *Habronattus* courtship to argue, more than a century ago, for sexual selection. The palp circling of the Santa Ritas is accompanied by an unusually dark and shiny palpus. The Sierrita and Cerro Colorado forms have striking longitudinal markings on their legs and palpi (Fig. 3c, e) and hold their appendages stretched to the side, giving a coherent impression of long

horizontal stripes. The Galiuro form, with annulate appendages, holds them forward, likewise yielding horizontal banding. The ranges with strong pale fringes on the front legs are also those that hold the legs to the side and engage in the "semaphore" display. Because it seems unlikely that pleiotropy could explain these correlations, a signaling function for the ornaments is suggested.

Several facts point to a lack of complete reproductive isolation among the forms: matings between forms in the lab, the indications of introgression from the phylogenetic analysis, and a lack of sympatry of alternative forms. Currently, in no known mountain ranges do two distinct forms live sympatrically. Were this simply a group of reproductively isolated species, one would expect that as the habitat fragmented, at least one mountain range would have received and maintained more than one "species," unless there was intense competitive exclusion. Selection for reinforcement of reproductive isolation is another possible mechanism by which differences could have arisen (and is consistent with the evidence presented here for sexual selection), but because we do not see sympatry currently, we have no strong reason to suspect it.

Although reproductive isolation could result from divergent sexual selection, it is not a necessary outcome (Claridge et al., 1985, Schluter and Price, 1993). In fact, sensory exploitation (Basolo, 1990; Ryan, 1990; Ryan and Rand, 1993) or chase-away sexual selection (Holland and Rice, 1998) could even promote introgression, if females were particularly susceptible to the wiles of immigrant males (e.g., Basolo, 1990). Chase-away selection, in particular, could drive both diversification and introgression. Not only could traits be introduced from other populations, but by these models they might spread quickly to fixation. Hybridization would be neither a conservative force nor a dead end but rather a means to introduce novel traits (Arnold, 1997). This could yield a pattern like that observed: most features monomorphic within populations but with discordant distributions among populations. To explore this possibility in *H. pugillis*, studies of female choice would be valuable. An intriguing but unquantified observation is that *H. pugillis* females appear unusually willing to watch quietly the courtship displays of males of

different species (other *Habronattus* females tend to decamp quickly).

AGE OF THE DIFFERENTIATION

Before 9,000 years ago, woodland habitats ranged lower in elevation and would have filled many of the valleys, thus bridging mountain ranges (Van Devender, 1990). Those woodlands were dominated by juniper and pinyon (Van Devender, 1990), unlike the xeric oak woodland in which *H. pugillis* is common today. It is unclear whether this would have provided suitable habitat for *H. pugillis*, and thus an opportunity for contact of now-isolated populations. *H. pugillis* can be found today in high-elevation habitats dominated by pine as long as a few oaks are present, although it is less common in these habitats than in the xeric oak woodland. Even if the tree composition were suitable, some of the alluvial plains between the mountain ranges may have been unsuitable because of insufficient rocks or slopes (we found *H. pugillis* primarily on rocks on slopes). However, at least some ranges are linked by terrain with enough ridges and hills to have provided corridors of suitable habitat if the woodland had been slightly lower in elevation (e.g., especially the Patagonias and Santa Ritas, but also between these and the Canelo Hills, Pajaritos, and Rincons).

Thus, at least some corridors between at least some of the ranges were probably available ~10,000 years ago. It is tempting to conclude that the differentiation of *H. pugillis* has happened over this time span. However, the differentiation could be much older. More than 10,000 years ago, repeated expansions and contractions of the woodlands presumably took place with each glacial cycle, and some of the differentiation may have occurred during earlier contractions. Even were the currently isolated populations in contact within the last 10,000 years, this contact may have failed to homogenize them completely. The Huachuca form shows within-range differentiation, albeit milder than that seen between ranges, despite a continuous habitat. As well, the Huachucas and Patagonias are probably linked by a more or less continuous habitat at present, yet the forms are clearly distinct morphologically and behaviorally. It would be particularly valuable to survey the Sierra Madre Occidental of northwestern Mexico, with large areas of continuous habitat, to determine whether differentiation can be seen there. Isolation of populations may not have been needed to establish the initial differentiation (Lande, 1982).

Perhaps most important to help assess the age of the differentiation would be data from genetic markers. The scenario of explosive diversification from a uniform, contiguous population 10,000 years ago would predict that such markers would show little differentiation among the mountain ranges, unless population bottlenecks have been severe. In fact, the genetic differences found by Masta (1999) suggest the differentiation is considerably older than 10,000 years.

CONCLUSIONS

We suggest the remarkable differentiation found among the sky-island populations of *H. pugillis* is driven by diverging sexual selection. The differentiation could be only a few tens of thousands of years old, since the last contact of oak woodlands, or it could be much older, having persisted despite interpopulation contact. The population history appears to have involved not only divergence but also reticulation. Although our statistical test supports a geographic pattern of homoplasy only tentatively, hybridization remains the most likely explanation for at least some of the apparent character convergence. Paradoxically, the process underlying the divergence could very well be the same as that promoting reticulation. Sexual selection, if following a model such as chase-away (Holland and Rice, 1998), could drive continual change within a population and yet could encourage introgression of courtship traits when populations came into contact.

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APPENDIX DESCRIPTIONS

Detailed accounts are given here of the populations, emphasizing unique and notable features. Mountain ranges are grouped according to whether their contained populations are similar enough to be easily described as one form. The total numbers of males and females examined from a mountain range are indicated, followed by the number of males scored for the characters in Tables 1 and 2 and the descriptions. For the males scored, three numbers are listed in the format m, v(b): the number of males examined for morphological characteristics (m), the number of males whose courtship behavior was videotaped (v), and the number of bouts of courtship observed (b). Localities within a mountain range are listed in order from north to south (see Fig. 1).

Santa Catalina and Rincon Mountains, and Black Mountain (Figs. 2a, 3a).—Brown setae on clypeus barbed, thin, and standing more erect than in most other forms. In many Santa Catalinas localities the brown is also more reddish and paler than usual. White eye streak incomplete. Palpi and first legs thoroughly clothed with white scales and hairs, chelicerae more thinly clothed with white than in other ranges such as the Santa Ritas. The most distinctive feature is in courtship: The male holds the first legs and palpi down and spread (Fig. 2a), and shakes his entire body side to side. In the Rincon Mountains, a southern locality (Posta Quemada) has specimens much like those of the Santa Catalinas, except that the white scales on the chelicerae and overhanging the chelicerae are denser and perhaps more yellowish. However, a single male from the eastern Rincons (Miller Creek Trail) has a complete eye streak.

Specimens examined: *Santa Catalina Mountains*: ~30 ♂, ~20 ♀; males scored: Peppersauce Canyon 1m, 0v; Rose Canyon Lake 4m, 4v(9b); Bear Canyon 5m, 8v(19b); Molino Basin 0m, 3v(5b); Finger Rock Canyon 2m, 0v. *Rincon Mountains*: 13 ♂, 5 ♀; males scored: Posta

Quemada Canyon 12m, 3v(7b); Miller Creek 1m, 0v. *Black Mountain*: 3 ♂, 1 ♀; males scored: Jewell Well 0m, 3v(4b).

Santa Rita and Empire Mountains (Figs. 2b, 3b, 5b).— Cymbium dark and shiny, with few setae. Eye streak complete, extending above main eyes (out of ~60 males seen from the Santa Ritas, a single male had an incomplete eye streak). Brown scales on clypeus canoe-shaped and barbless (Fig. 5b). Chelicerae thickly clothed with cream-colored scales. Prominent fringe of pale hairs on first leg. During courtship, the palpi are circled alternately, a unique behavior (Fig. 3b). First, one palp is raised near the first leg femur as it is shaken, then moved medially and down to complete the circle. Then, the other palp is moved in a circle. This left–right alternation continues throughout most of the display.

Specimens examined: *Santa Rita Mountains*: ~60 ♂, 20 ♀; males scored: Box Canyon 5m, 1v(13b); Florida Canyon 1m, 1v(1b); Madera Canyon 6m, 1v(3b); Gardner Canyon 1m, 0v; Mount Hopkins 4m, 0v; Piper Gulch 1m, 0v; Squaw Gulch 3m, 2v(6b). *Empire Mountains*: 9 ♂, 5 ♀; males scored: 9m, 4v(6b). In addition, male courtship behavior was observed to be in general as expected in an additional 15 males from Mt. Hopkins, Santa Rita Mountains (palps circled, no sidling).

Sierrita Mountains (Figs. 2c, 3c, 5c).—First femur with distinct white band against a dark background, and palp with spike of white hairs extending from the tibia over cymbium. These markings, along with the pose the male takes during courtship, contribute to an overall lineate appearance (Fig. 3c). Brown setae on clypeus narrow and barbed (Fig. 5c) as in the Santa Catalinas. White eye streak incomplete. Chelicerae clothed in vertical fine white hairs bundled into bands (like the Baboquivari form). Cymbium black, well clothed with black hairs; integument not shiny.

Specimens examined: 11 ♂, 3 ♀; males scored: Fresnal Canyon 11m, 5v(6b).

Cerro Colorado (Figs. 2e, 3e).—White band on clypeus translucent; setae mostly oriented horizontally. White eye streak incomplete. Cymbium shiny, as in the Santa Rita form, but even more devoid of setae and somewhat swollen. Palpi not circled during courtship. Palp tibia with spike of white projecting over the cymbium, but smaller and not so dense as in Sierrita form. Prominent black tip of first leg, nearly half the telotarsus length, as in the Galiuros.

Specimens examined: 3 ♂, 6 ♀; males scored: 3m, 2v(8b).

Whetstone Mountains and Canelo Hills (Fig. 2d).—Male well clothed with yellowish scales on the palpi, first legs, and chelicerae. White eye streaks prominent and complete. Ventral fringe of pale hairs on first legs dense. The slow alternate waving of the first legs in courtship ("semaphore") is particularly pronounced. In the few displays observed of Whetstone males, leg flicks during the second stage of courtship were rare.

Specimens examined: *Whetstone Mountains*: 8 ♂, 2 ♀; males scored: French Joe Canyon 8m, 5v(14b). *Canelo Hills*: 4 ♂, 0 ♀; males scored: Canelo Pass 4m, 4v(12b).

Huachuca Mountains (Figs. 2f, 3d, 4b).—Little different from Whetstone/Canelo form. Brown setae on clypeus dark and contrast strongly with vertically-oriented white setae above the chelicerae. Tibia and patella of first legs pale, their fringe of pale yellowish hairs dense. During courtship, the chelicerae are periodically moved open and shut, more consistently than in any other range. Males vary from site to site, especially

in the extent of the white eye streak, being complete in the north (Garden Canyon) and incomplete in the south (Miller, Ash, and Carr Canyons). Because there is almost continuous oak woodland from the Huachucas across to the Patagonias by way of the Canelo Hills, future collecting could show a cline from a Whetstone-like form in the Canelo Hills to the Patagonia form in the west and Huachuca forms to the southeast.

Specimens examined: *Huachuca Mountains*: 29 ♂, 9 ♀; males scored: Garden Canyon 5m, 5v(20b); Ramsey Canyon 1m, 0v; Miller Canyon 1m, 1v(4b); Parker Canyon 2m, 2v(10b); Carr Canyon 5m, 0v; Ash Canyon 15m, 0v.

Patagonia Mountains (Figs. 2g, 3f).—Dark brown of upper clypeus contrasts strongly against broad band of brilliant blue-white scales along clypeus margin (Galiuros and Santa Teresas have similar coloration). Carapace relatively swollen, first leg and cymbium relatively dark, and sidling is used in the display, in which respects it resembles the more westerly forms (Atascosa, Baboquivari). In other respects, such as the dark brown face and occasional eye streaks, it resembles the ranges to the east (Huachucas). White eye streaks in some specimens absent, in others incomplete (even from the same locality).

Specimens examined: 14 ♂, 4 ♀; males scored: Patagonia 8m, 7v(13b); Harshaw Creek 4m, 3v(16b); San Antonio Canyon 2m, 0v.

Mule Mountains (Figs. 2h, 3h).—Similar to the nearby Huachuca form but lacks white eye streak, and white marginal band on clypeus is broad and with obliquely-oriented setae. The annulate nature of markings on palp is reminiscent of Winchester and Galiuro form, but first leg is well fringed, as in the Huachucas.

Specimens examined: 2 ♂, 0 ♀; males scored: Mule Pass 2m, 1v(4b).

Winchester Mountains (Fig. 2j).—Dark, with broad white marginal band on clypeus, lacking eye streaks. Pale markings on palpi and first legs are organized into annulate bands, so that when the first legs are held vertically during courtship the dominant appearance is of white lateral bands against a vertical background (contrast with Sierrita form). White ventral fringe on first leg is present but weak. Much like Galiuro form but without prominent expansion of the white band into cheek patches and also lacking the extended black on the first leg tip. Courtship includes the waving circle of the first legs, as in the Galiuros, but does not emphasize the second stage nearly so much.

Specimens examined: 13 ♂, 0 ♀; males scored: Adobe Canyon 13m, 3v(5b). '

Galiuro and Santa Teresa Mountains (Figs. 2l, 3j, 4c).—A dark, annulate-marked form. White marginal band on clypeus is broad, vertical, and translucent bluish above chelicerae; beneath anterior lateral eyes the band expands dorsally to make a striking cheek patch. Black on tip of first leg much extended, occupying almost half of the length of the telotarsus. White ventral fringe of first leg nearly absent, restricted to tarsal segments. (Santa Teresa males differ from Galiuros in having cheek patches slightly less prominent, less black on the first telotarsus, and a weak white fringe on the first leg's patella and tibia.) Males rarely performed the first stage of courtship, and instead concentrated on a tediously long second stage with the tips of the first legs moving in waving circles. The tips of the first legs move synchronously in large circles, rising medially, then moving laterally and descending. On the lower and medial part

of the circle, the legs are in addition waved up and down several times alternately (left leg moving up while right leg moving down, and so on). The downward flick of the first leg typical of second stage display is given when the leg is high and to the side, though flicks are not done on each circle.

Specimens examined: *Galiuro Mountains*: 3 ♂, 0 ♀; males scored: High Creek 3m, 3v(6b). *Santa Teresa Mountains*: 4 ♂, 0 ♀; males scored: Cottonwood Mountain 4m, 3v(6b).

Baboquivari and Quinlan Mountains (Figs. 2i, 3g).— A form with brown and white male face but showing many features in common with the nearby gray-faced Atascosa / Pajarito / Tumacacori form. In particular, it shares the swollen carapace sides, and bare spots on the "cheeks." White band across clypeus is broad, its setae narrow and horizontally directed. Courtship similar to that of the Atascosa form.

Specimens examined: 6 ♂, 5 ♀; males scored: Kitt Peak 2m, 2v(8b); Sabino Canyon 4m, 0v.

Atascosa, Pajarito, and Tumacacori Mountains (Figs. 2k, 3i, 4a, 5a).—Clypeus covered with silvery gray scales stalked on petioles beneath the main eyes (Fig. 5a); white and yellow scales near the lateral margins. Cheeks with two or three prominent dark barren spots, and strongly swollen carapace sides. Chelicerae covered with fine hairs obliquely oriented in alternating bands so as to give a bundled appearance. The first stage of courtship is short (usually <5 seconds), with the male walking toward female in large arcs (sidling). He then engages in a second stage with vigorous leg flicking.

Specimens examined: *Atascosa and Pajarito Mountains*: ~30 ♂, ~15 ♀; males scored: Warsaw Canyon 1m, 0v; Ruby 4m, 3v(12b); Atascosa Peak 7m, 0v; Sycamore Canyon 6m, 0v. *Tumacacori Mountains*: 5 ♂, 3 ♀; males scored: Tumacacori 5m, 2v(2b). In addition, male courtship behavior was observed to be in general as expected in an additonal eight males from Atascosa Peak, Atascosa Mts. (palps not circled, sidling approach to female).