

Parapatry and Niche Complementarity of Peruvian Desert Geckos (*Phyllodactylus*): the Ambiguous Role of Competition

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Abstract. The Sechura Desert of Peru is among the most arid, barren regions of South America. Four species of nocturnal geckos (*Phyllodactylus*) are parapatric in part of the desert. By comparing niche associations of these species in allopatry and parapatry, I attempt to determine whether the observed parapatric distributions and niche dimension complementarity are related to competition— as is frequently assumed. While parapatry suggests a role for competition, distributional patterns can alternatively be related to adaptations of geckos to different physical environments (sandy desert and rocky foothill) that abut in the study area. Niche complementarity might also be a result of competition, but potentially contradictory evidence suggests that niche complementarity might instead be the result of adaptations developed in allopatry and having no relationship to competition. The ambiguity of these interpretations sets limits on the significance of this kind of evidence: in the absence of attempts to falsify alternative explanations, observations of parapatry or of niche dimension complementarity do not demonstrate conclusively the impact of competition as a force structuring communities.

Introduction

Interspecific competition is often believed to be the predominant organizing force in ecological communities. First-level field descriptions of competition document interspecific differences in niche associations. These procedures are inconclusive and potentially misleading, because particular niche differences may well be unrelated to competitive interactions (Andrewartha and Birch, 1954). Second-level descriptions, developed in response to this limitation, examine possible character displacement (Brown and Wilson, 1956), niche-dimension complementarity (high overlap along one dimension tends to be associated with low overlap along another dimension; Rosenzweig and Winakur, 1969), and parapatric distributions (Schoener, 1974). Yet, even these richer

data can be reinterpreted within alternative conceptual frameworks such as predation (Connell, 1975; Dayton, 1973; Huey and Pianka, 1977).

Here I examine ecological interactions among four species of nocturnal geckos (*Phyllodactylus*) at Bayovar in the Sechura Desert of northern Peru, among the most arid, botanically depauperate regions of South America (Tosi, 1960). Even though only three species of woody shrubs commonly occur, this area supports more nocturnal geckos than any other known locality in western South America (Dixon and Huey, 1970). By analyzing patterns of niche differences in sympatry and by making limited comparisons with patterns in allopatry, I show that the observed parapatric distributions and niche complementarity at Bayovar can be related either to adaptations developed prior to sympatry or to interspecific competition or both. Thus, parapatry and niche complementarity may sometimes be indicated by insufficient indicators of the impact of competition on the structure of ecological communities.

Methods

I gathered these data by first-sighting methods using headlamps or lanterns in July 1967 and in July and August 1968. For each undisturbed lizard collected or observed, I generally recorded habitat, microhabitat, time of activity, snout-to-vent (SVL) length, and plant species association. When possible I also determined body (cloacal) and air (1 cm above substrate) temperatures with a quick-reading Schultheis thermometer. Prey in stomachs were later classified by taxa (usually at ordinal level) and by size (length).

To estimate overlap along particular niche dimensions, I used the symmetrical formula of Pianka (1973). Overlap values from this equation vary from zero (no overlap) to one (complete overlap).

Frequency data are analyzed statistically with *G*-tests for overall heterogeneity among species and *STP*-tests for paired comparisons between species; interval data are analyzed by analysis of variance (Sokal and Rohlf, 1969).

Background

Environmental Setting at Bayovar, Peru

Bayovar is a small mining camp on the western edge of the Sechura Desert (a northern part of the Peruvian-Atacama Desert) in northern, coastal Peru. Adjacent to the camp is Cerro Illescas, a rocky hill (c. 500 m), separated from the Andes to the east by 125 km of sandy desert. In essence, the cerro is an andeanlike foothill in a sand sea. I recognize four habitats along a transect from the desert proper onto the cerro.

Habitat I. The Sechura Desert is topographically subdued. Barchane dunes are present, but more typically the sandy terrain is flat or pocked with hummock dunes stabilized by *Capparis scabrida*, subjectively judged to be the dominant shrub in this habitat. Total plant cover is very low (Tosi, 1960, see photograph in Huey, 1969b). Gecko data for this habitat are pooled from several localities with the desert.

Habitat II. Within about 2 km of the cerro, surface sands of the desert become coarse grained, and the land is void of barchane or hummock dunes. By counting plants in 32 randomly placed quadrats (each 230 m², see Pianka, 1967), I determined that 79.1% of all plants (134 total) were *Capparis avicennifolia*, 11.9% were *C. scabrida*, and 9.0% were *Prosopis* sp.

Habitat III. This narrow habitat (generally less than 50 m wide) is defined as the base and washes of Cerro Illescas. Substrates are gravel and small rocks on moderate slopes. A linear transect along the habitat showed that 48.9% of all plants (131 total) were *C. scabrada*, 34.3% were *C. avicennifolia*, and 16.8% were *Prosopis*. Total plant cover is subjectively intermediate between Habitats I and II.

Habitat IV. The cerro proper has rocky, relatively steep slopes. *Capparis scabrada* is virtually the only shrub observed, and total plant cover is extremely low.

Distributions and Natural History of Phyllodactylus from Bayovar

Ecological relations of species in sympatry must be interpreted with reference to geographic distributions, habitat occurrences, and microhabitat associations at other localities. For the four geckos at Bayovar, these data are readily summarized from the systematic revision of Dixon and Huey (1970).

Phyllodactylus microphyllus inhabits only the sandy, coastal deserts of the north half of Peru. At most localities *microphyllus* is exclusively an open-ground forager. Dorsal coloration is a sandy, yellowish tan.

Phyllodactylus kofordi occurs in the Andean foothills of northwestern Peru. In northern Tumbes Province, however, *kofordi* replaces *microphyllus* in the beach dune communities (Dixon and Huey, 1970, p. 42). *Kofordi* generally forages on the ground near shrubs, trees, or rocks, but occasionally forages on shrubs as well. Color varies from medium to dark brown.

Phyllodactylus reissi is also an Andean foothill species. This large gecko is scansorial, foraging on rocks, on trees, and on shrubs. Color is medium gray.

Phyllodactylus clinatus is known from only four specimens, all from near Bayovar. This rare gecko is closely related to *P. lepidopygus*, a scansorial, foothill species from central Peru (Dixon and Huey, 1970). *Clinatus* also appears to be scansorial. Because of small samples, I briefly discuss *clinatus* in the text.

Of the four species of *Phyllodactylus*, only *microphyllus* is typically a species of the sandy deserts. The remaining species, absent from the surrounding Sechura desert, probably invaded the cerro from the Andean foothills.

Results

Habitat Associations

Habitat associations of the four geckos near Bayovar (Table 1) mirror overall geographic distributional patterns. *Microphyllus* is associated primarily with sandy habitats (I and II), whereas the remaining species are found only near or on Cerro Illescas (II to IV). Similarly, the dominant ground substrates (sand, gravel, small rocks, or large rocks) in the immediate vicinity of geckos in Habitats II to IV emphasize the association of *microphyllus* with sandy substrates (Table 2). That substrate associations appear important to these geckos is further emphasized by data from Habitat II where a large patch of gravel penetrated this normally sandy habitat: substrate associations of *microphyllus* (54 on sand, 4 on gravel) and of *kofordi* (25 sand, 18 gravel) differ significantly ($P < 0.001$). Overlap values for habitat and ground substrate associations (Table 8) summarize the relative distinctiveness of *microphyllus* from *kofordi* and *reissi*. (Signifi-

Table 1. Relative representation (% total) of species of *Phyllodactylus* in habitats at Bayovar: Habitats I (flatland desert), II (flatland adjacent to Cerro Illescas), III (base and washes of Cerro Illescas), and IV (Cerro Illescas). *N*= within-habitat sample size

Species (total sample)	Habitat			
	I	II	III	IV
<i>P. microphyllus</i> (161)	100	55.2	13.7	0
<i>P. kofordi</i> (140)	0	41.0	61.1	86.7
<i>P. reissi</i> (30)	0	1.9	24.2	11.1
<i>P. clinatus</i> (4)	0	1.9	1.1	2.2
N (for habitat)	90	105	95	45

Table 2. Percentage of *Phyllodactylus* associated with particular ground substrates in Habitats II to IV (*N*=total sample for a species)

Species (<i>N</i>)	Ground substrates			
	Sand	Gravel	Small rock	Large rock
<i>microphyllus</i> (74)	74.3	21.6	4.1	—
<i>kofordi</i> (133)	19.5	18.8	24.1	37.6
<i>reissi</i> (30)	6.7	16.7	26.7	50.0

Table 3. Percentage of *Phyllodactylus* associated with particular microhabitats in Habitats II to IV

Species (<i>n</i>)	Microhabitats			
	Ground		Arboreal	
	open	litter	plant	rock
<i>microphyllus</i> (71)	18.3	23.9	57.7	—
<i>kofordi</i> (134)	0.7	62.7	26.1	10.4
<i>reissi</i> (29)	3.4	13.8	58.6	24.1

cance levels adjacent to overlap values in Table 8 refer to statistical significance of differences between species pairs in that niche dimension as determined by ANOVA or *G*-test, not to the significance of the overlap value itself.)

Microhabitat Associations

Microhabitat associations (on shrubs or trees, in leaf litter, on open ground, or on rocks: categories selected from personal experience with *Phyllodactylus* elsewhere in Peru) of geckos in Habitats II to IV (Table 3) document that

Table 4. Percentages of *Phyllodactylus* associated with plant species in Habitats II to IV

Species (N)	Plant species		
	<i>C. avicennifolia</i>	<i>C. scabrida</i>	<i>Prosopis</i>
<i>microphyllus</i> (55)	63.6	12.7	23.6
<i>kofordi</i> (128)	20.3	75.8	3.9
<i>reissi</i> (21)	38.1	23.8	38.1

both *reissi* and *microphyllus* were observed primarily on plants, whereas *kofordi* occurred predominantly on leaf litter beneath shrubs and trees. All species pairs differ significantly in microhabitat associations (Table 8).

By grouping microhabitats into ground (open + leaf litter) or arboreal (plant + rock) categories, the greater arboreality of *reissi* (82.7%) and of *microphyllus* (56.7%) than of *kofordi* (36.5%) is evident. The relative arboreality of *reissi* and the terrestriality of *kofordi* is consistent with patterns at an Andean foothill locality (see also Dixon and Huey, 1970). For example, *reissi* does not differ significantly ($P > 0.1$) in degree of arboreality between Bayovar and Las Lomas (92.0%, $N = 25$) in the Andean foothills; although *kofordi* is slightly less arboreal ($P < 0.05$) at Las Lomas (19.5%, $N = 36$). *Microphyllus* is, however, strikingly less arboreal in Habitat I (2.2%, $N = 90$) where it is allopatric than in Habitats II and III (57%). Indeed, 96.7% of all *microphyllus* in Habitat I were observed on the open ground and thus not associated with plants at all! Huey (1969a) speculated that this dramatic shift by *microphyllus* (that greatly increases its overlap in microhabitat with other geckos) might have occurred because sands in Habitats II and III, partially derived from the cerro, are darker than the sands of Habitat I, such that an open ground *microphyllus* might be very conspicuous to known predators (Huey, 1969b) in Habitats II and III.

Plant Species Associations

Plant species associations of *Phyllodactylus* in Habitats II to IV are presented in Table 4. *Kofordi* differed significantly ($P < 0.001$) from the other species in being found primarily on or under *C. scabrida*, whereas *microphyllus* and *reissi* were mainly found on or under *C. avicennifolia* and *Prosopis*.

Plant species associations might be artifacts of differential representation of plant species and geckos among habitats (see *Environmental Setting at Bayovar, Peru* and *Habitat Associations*). To check this possible bias, I compared the number of geckos on *C. avicennifolia* and *Prosopis* or on *C. scabrida* in Habitat II and in Habitat III against the number of plants of these species observed in each habitat. *Kofordi* were significantly more often (P 's < 0.01) on *C. scabrida* than expected in both habitats. *Microphyllus* and *reissi* were significantly more frequent (P 's < 0.05) on *C. avicennifolia* and *Prosopis* than expected only in Habitat III (recall, however, that only two *reissi* were observed in Habitat II).

Table 5. Body sizes (SVL) of adult *Phyllodactylus* at Bayovar and in Peru (mean adult SVL's and SVL_{max} from Dixon and Huey 1970)

Species	Bayovar			Peru	
	N	$\bar{X} \pm s.e$	SVL_{max}	\bar{X}	SVL_{max}
<i>kofordi</i>	52	38.6 ± 0.57	45	38.3	46
<i>clinatus</i>	4	37.5 ± 3.88	46	—	—
<i>microphyllus</i>	41	47.6 ± 0.88	57	46.6	58
<i>reissi</i>	17	57.7 ± 2.70	71	58.3	75

Hence, plant species associations appear real for *kofordi* and may also be real for *microphyllus* and *reissi*. Plant species associations might relate to background color matching through selection by predators: *microphyllus* and *reissi*, relatively light colored geckos, associate primarily with shrubs and trees having light or medium colored bark (*Prosopis* and *C. avicennifolia*) whereas *kofordi*, a much darker gecko, is associated mainly with shrubs having darker bark (*C. scabrida*).

Body Length

Body length (SVL) of these geckos is presented in Table 5. *Kofordi* and *clinatus* are small geckos, *microphyllus* is intermediate, and *reissi* is large. Mean SVL and maximum known SVL at Bayovar are very similar to corresponding values for these species throughout Peru (Table 5), documenting that character displacement in SVL has not occurred.

Time of Activity, Body and Air Temperatures

Average times of activity of these geckos (*microphyllus* = 20.9 ± 0.21 h, $N=29$; *kofordi* = 20.9 ± 0.13 h, $N=38$; *reissi* = 20.5 ± 0.20 , $N=8$) do not differ significantly ($P > 0.25$). Average body (*microphyllus* = 20.3 ± 0.19 C, $N=30$; *kofordi* = 21.5 ± 0.38 C, $N=15$; *reissi* = 20.3 ± 0.38 C, $N=4$) and average air (20.0 ± 0.30 C, 19.9 ± 0.41 C, and 20.2 ± 0.58 C, respectively) temperatures do not differ significantly among species (both $P > 0.25$). Times of activity and temperatures of Australian geckos (Pianka and Pianka, 1976) and of Kalahari geckos (Pianka and Huey, 1978) are also very similar, suggesting that active geckos generally do not differ greatly in times of activity or thermal relations (except potentially late at night).

Prey

Percentages of prey items in different length categories are presented in Table 6. *Kofordi* takes more small (1 to 5 mm) prey than the other species (P 's < 0.001),

Table 6. Percentages of prey items in different length categories

Prey length (mm)	Species		
	<i>microphyllus</i>	<i>kofordi</i>	<i>reissi</i>
1 to 5	69.8	86.4	55.0
6 to 10	20.1	11.3	18.3
11 to 15	6.7	2.3	23.3
> 15	3.3	—	3.3
N (items)	149	177	60

Table 7. Percentages (by number) of prey items in different taxa

Prey taxa	<i>microphyllus</i>	<i>kofordi</i>	<i>reissi</i>
Coleoptera: adults	27.1	21.4	35.0
Lepidoptera: larvae	9.6	7.7	20.0
Formicidae	14.5	22.5	8.3
Diptera	6.0	9.3	5.0
Homoptera-Hemiptera	7.2	11.0	3.3
Pseudoscorpiones	4.8	9.9	6.7
Araneidae	6.6	2.7	5.0
Miscellaneous	18.2	12.3	13.4
Unidentified	6.0	3.8	3.3
N (items)	166	182	60

and *microphyllus* takes significantly smaller prey than *reissi* ($P < 0.001$). Prey size differences directly parallel body size differences among these geckos.

Percentages of prey items in different taxa are presented in Table 7. (Twelve minor prey taxa are lumped into Miscellaneous – complete prey lists are available in Huey, 1969a). Overall, the three geckos differ significantly in prey taxa ($P < 0.05$), but none of the paired tests is significant. All three geckos eat a variety of prey taxa.

Discussion

Parapatry and niche complementarity are often used as evidence of the importance of competition as an influence on both distributions and niches of animals (Cody, 1974; Schoener, 1974, 1977; Selander and Giller, 1963). I first use the results presented above to demonstrate parapatry and niche dimension complementarity in some Peruvian geckos. Then, by comparing habitat and microhabitat associations between allopatry and parapatry, I show that factors other than competition could have been involved in establishing both parapatry and niche complementarity.

Cerro Illescas near Bayovar is in effect an insular Andean foothill flanked by the sandy Sechura Desert and the Pacific Ocean. The geckos on the cerro

proper (*reissi*, *kofordi*, *clinatus*) are typical elements of localities on the Pacific slope of the Andes (with *clinatus* represented by its close relative, *lepidopygus*, see Dixon and Huey, 1970). The fourth gecko, *microphyllus*, is allopatric in the sandy Sechura Desert (Habitat I), does not occur on the cerro proper (Habitat IV), and is thus narrowly sympatric (=parapatric) with the other geckos in Habitats II and III near and at the base of Cerro Illescas.

Parapatric distributions may result if interspecific competition is too intense to permit coexistence of species over broad geographic areas. Parapatry can, however, also result from extensive hybridization (Hall and Selander, 1973; Mayr, 1963) or from adaptation of species to different habitats that abut geographically (Pianka, 1969; Huey and Pianka, 1977). Determining which of these possibilities is (are) involved in a particular case of parapatry is non-trivial (Huey and Pianka, *ibid*). Hybridization can be disregarded if hybrids are not detected in the zone of parapatry (this decision could, however, be inappropriate if hybrid offspring were totally inviable). Differential habitat adaptations can be supported by documenting that the zone of parapatry coincides with a change in habitat, that species in parapatry occur in habitats typical of their occurrence in allopatric areas, and that the species show some adaptations to those typical habitats. As Rosenzweig (1974) has warned, however, similar patterns do not necessarily exclude the role of competition in differential habitat occupancy. Competition is more difficult to support directly, but would be suggested if hybridization and differential habitat adaptations were found unlikely and if patterns of niche overlap in parapatry were consistent with predictions based on competition theory (see below).

Despite substantial samples of most species, no hybrids (as judged by external morphological characters) among these geckos have been discovered (Dixon and Huey, 1970). Therefore, hybridization is an unlikely cause of parapatry of these geckos.

The zone of parapatry does coincide exactly with a major habitat change – sandy desert abutting rocky foothill. Moreover, in the zone of habitat change, the geckos occur in exactly those habitats characterizing their distributions in Peru: *microphyllus* in sandy habitats and the other species in rocky foothill habitats, Dixon and Huey (1970) related habitat associations of these and other Peruvian *Phyllodactylus* to particular functional morphological adaptations, most importantly in toepad structure and in nostril shape. Parapatry may partially be related to differential adaptation of the geckos to habitats that merely abut sharply near Bayovar.

Whether competition is also involved in maintaining parapatry is problematical. Competition probably does not influence parapatric distributions of *microphyllus* and *reissi* because these species never occur in habitats other than sandy desert and rocky foothills, respectively, anywhere in Peru (Dixon and Huey, 1970). *Kofordi* does, however, occur in beach dunes in extreme northern Peru (Dixon and Huey, *ibid*). Thus the absence of *kofordi* from the Sechura Desert (Habitat I) could potentially be attributed to competition with *microphyllus*. The curious convergence of *microphyllus* on *kofordi* in microhabitat associations suggests that competition may not be a dominant factor affecting microhabitat selection by *microphyllus*. Nevertheless, under conditions of high

Table 8. Overlap values for niche dimensions using data from Habitats II to IV, except habitat associations, which contain data from Habitat I. Body length overlaps computed for geckos >30 mm SVL, using 5 mm-length classes. Significance levels (* = $p < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) computed for paired comparisons by ANOVA or *G*-tests with *STP*-tests, see Methods, using data in Tables 1 to 7

Niche dimension	Species pair		
	<i>microphyllus</i> vs. <i>kofordi</i>	<i>reissi</i> vs. <i>microphyllus</i>	<i>reissi</i> vs. <i>kofordi</i>
Habitat	0.438 ***	0.163 ***	0.833 *
Ground substrate	0.483 ***	0.310 ***	0.955
Microhabitat	0.663 ***	0.893 ***	0.593 ***
Plant species	0.433 ***	0.892	0.589 ***
Body length	0.435 ***	0.509 ***	0.388 ***
Prey length	0.662 ***	0.709	0.547 ***
Prey taxa	0.927	0.903	0.800

Table 9. Analysis of niche complementarity. Number of niche dimensions (excluding body size) of each species pair for which overlap is highest, intermediate, or lowest relative to overlaps for other species pairs (from Table 8). See text. Relative overlap in habitat, which is equivalent to ground substrate, is indicated

Species pair	Habitat <i>overlap</i>	Relative niche overlap		
		<i>lowest</i>	<i>intermediate</i>	<i>highest</i>
<i>kofordi</i> vs. <i>reissi</i>	highest	3	1	—
<i>microphyllus</i> vs. <i>kofordi</i>	intermediate	1	2	1
<i>microphyllus</i> vs. <i>reissi</i>	lowest	—	1	3

resource availability, some theories predict that competitors should actually converge (MacArthur, 1972). Whether food near shrubs is more abundant in allopatry is unknown. If, however, *microphyllus* were that sensitive to fluctuations in food availability, one might expect to find at least one other population that was exposed to high food abundance and hence be largely arboreal. The lack of association of *microphyllus* with plants in all other populations (Dixon and Huey, 1970) makes the hypothesis of competition-induced convergence unlikely.

Niche complementarity is used as evidence that competition has been important in the evolution or structuring of niche differences (Rosenzweig and Winakur, 1969; Schoener, 1974, 1977). Table 9 lists species pairs by decreasing overlap in habitat occupancy (or equivalently in ground substrate associations, see Table 8). Then I determined the number of remaining niche dimensions (excluding body size, which is associated with prey size) for which each pair had highest, intermediate, or lowest overlap using values in Table 8. If niches are complementary, then the species pair with highest overlap in habitat should have the lowest overlap in the remaining niche dimensions, and vice versa. This trend

is clearly evident (Table 9). Therefore, niche dimensions appear complementary in these geckos.

Inferring that competition is or was involved in the evolution of niche complementarity is risky in the absence of information on niche patterns in allopatry, primarily because niche patterns might have evolved in allopatry and simply be "preadapted" to sympatry. For these *Phyllodactylus*, in fact, character displacement in body size has not occurred (Table 5), and microhabitat associations of most species in parapatry are very similar to those in allopatry. The exception is the shift in microhabitat by *microphyllus*. Because this shift increases rather than decreases its overlap with *kofordi* and *reissi*, however, the assertion that competition is severe for these geckos may be contradicted (but see above). Therefore, niche complementarity among these geckos need not be related to competition but instead might merely be a fortuitous accident of adaptations developed in allopatry.

In conclusion this analysis emphasizes that the phenomena of parapatry and of niche dimension complementarity can result from causes other than or in addition to competition. As the particular Peruvian data demonstrate, attempts to delineate which of the potential causes is most important may frequently yield ambiguous results. This inability to interpret patterns cleanly re-emphasizes an important (Dayton, 1973) but often overlooked dilemma for field studies: while competition can seemingly be invoked to explain almost any pattern in nature, a particular pattern need not be the result of competition.

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