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Paul D. Klawinski  
*Stephen F Austin State University*

R. Kathryn Vaughan  
*Texas A & M University - College Station*

Daniel Saenz  
*Stephen F Austin State University*

William Godwin  
*Stephen F Austin State University*

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## Comparison of Dietary Overlap between Allopatric and Sympatric Geckos

PAUL D. KLAWINSKI,<sup>1,3</sup> R. KATHRYN VAUGHAN,<sup>2</sup> DANIEL SAENZ,<sup>1,4</sup> AND  
WILLIAM GODWIN<sup>1,5</sup>

<sup>1</sup>Department of Biology, Stephen F. Austin State University, Nacogdoches, Texas 75962, USA, and

<sup>2</sup>Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843, USA

**ABSTRACT.**—Two gecko species, *Hemidactylus turcicus* and *Cyrtopodion scabrum*, have been introduced into the Port of Galveston, Texas. While *H. turcicus* has been established for a longer period of time, the relatively recent introduction of *C. scabrum* near the entrance of the Port has apparently led to the displacement of *H. turcicus* in that area. This has resulted in a distribution in which the two populations are largely allopatric except for a narrow band of sympatry at the periphery of each of their ranges. We examined stomach contents of both species in allopatry and sympatry in order to determine if dietary overlap in sympatry is less than that in allopatry. We calculated Pianka's (1973) symmetric overlap for geckos occupying sympatric areas (0.55) and allopatric areas (0.81). We found significant differences between the resource utilization distributions of the two species in sympatry but not in allopatry. In addition, we compared overlap between allopatric and sympatric populations within each species and found that the differences in resource utilization between the two species in sympatry was due to a dietary shift exhibited in *H. turcicus* but not *C. scabrum*. Observed differences in resource utilization may be a response to competition between these two species in sympatry which may have led to the exclusion of *H. turcicus* on areas of the docks occupied by this species prior to the introduction of *C. scabrum*.

Interspecific competition is the interaction between individuals of two or more species which utilize the same limiting resource (Pianka, 1988). Competition can be mediated either by direct interaction (interference) or by resource depression or depletion (exploitative) (Pianka, 1988). A great deal of effort has been expended towards detecting and measuring competition in the field (reviewed by Connell, 1983; Schoener, 1983). Field observations of proportional resource utilization, which may be affected by resource availability, have been converted into indices of overlap (MacArthur and Levins, 1967), similarity (Sale, 1974), or competition coefficients (MacArthur, 1968) and used as indicators of interspecific competition.

A number of studies have used proportional utilization of resources as indicators of the presence or absence of competition between lizard species. Huey et al. (1974) showed that sympatric populations of *Typhlosaurus lineatus* and *T. garipeensis* exhibited lower dietary overlap than allopatric populations. Pianka and Pianka (1976) and Huey and Pianka (1978) documented

food resource partitioning in two communities of nocturnal geckos. Pianka et al. (1979) used similarity measures to demonstrate that resource partitioning occurred in three lizard guilds. Dunham (1983) showed that as prey availability increased, dietary overlap increased, a result that is consistent with the hypothesis of increased competition during time periods when food was limiting.

A serious criticism of these methods has been that a high degree of overlap in resource utilization did not prove the existence or nonexistence of competition (Colwell and Futuyma, 1971). Further, demonstration of a low degree of overlap was not necessarily attributable to an evolutionary response to past competition (Colwell and Futuyma, 1971; Connell's, 1980, "ghost of competition past"). Colwell and Futuyma (1971) distinguished between the resource utilization of a species in the absence of competitors and the resource utilization of a species in the presence of competitors and concluded that, to demonstrate competition using overlap or similarity measures, it is necessary to measure the overlap of these two types of resource utilization patterns of the species in question. Competition can then be inferred if the overlap in resource utilization between two species in allopatry is greater than the overlap in resource utilization between two species in sympatry (Colwell and Futuyma, 1971).

Measurement of these types of resource utilization can be accomplished by (1) removing

Present Address: <sup>3</sup>Department of Biology, University of Texas at Arlington, Arlington, Texas 76019, USA; <sup>4</sup>Wildlife Habitat and Silviculture Lab, Southern Forest Experiment Station, USDA Forest Service, Nacogdoches, Texas 75962, USA; and <sup>5</sup>Department of Entomology, Texas A&M University, College Station, Texas 77843, USA.

competitors, (2) finding natural situations where competitors are absent, or (3) creating an oversupply of resources so that competition is removed (Colwell and Futuyma, 1971; reviews in Connell, 1983; Schoener, 1983). Condition (2) above occurs in Galveston, Texas, where two species of introduced geckos, *Cyrtopodion scabrum* and *Hemidactylus turcicus*, occupy areas adjacent to the docks of the Port of Galveston. Both of these species are nocturnal, scansorial, insectivorous lizards of the family Gekkonidae which inhabit the walls of brick, stucco, and wooden buildings on the study area. *Hemidactylus turcicus* have been established in Galveston since the 1960s (Davis, 1974) while *C. scabrum* were first reported in Galveston in 1983 (Selcer and Bloom, 1984). Since the introduction of *C. scabrum*, probably at the fruit warehouses of the Port, a breeding colony has been established (Bloom et al., 1986) and the population has extended inland, gradually displacing *H. turcicus*. This displacement has resulted in a distributional pattern in which both species are largely allopatric except for a narrow band of sympatry at the periphery of each species' distribution. The inadvertent introduction of these two species provides an opportunity to examine interspecific interactions between the resident species and the recent invader as these interactions progress. The purpose of our research was to compare dietary overlap of allopatric *H. turcicus* and *C. scabrum* with that of sympatric *H. turcicus* and *C. scabrum* in order to determine if competition for food resources may be responsible for the displacement of *H. turcicus* by *C. scabrum* in Galveston.

#### METHODS AND MATERIALS

We collected all specimens between 2100 and 0200 h on a single night (21–22 June 1991) in Galveston, Galveston Co., Texas. This time period corresponds to the reproductive season of both species and the peak activity period of *H. turcicus* (Klawinski, 1991). Although the activity period of *C. scabrum* is unknown, Pianka and Pianka (1976), Selcer (1986), and Frankenberg (1978) have all recorded similar patterns of peak activity in a number of distantly related gekkonid taxa. Of the 60 specimens collected, 16 were *C. scabrum* from an allopatric area (mean SVL = 47.6 mm, SD = 3.7), 13 were *C. scabrum* sympatric with *H. turcicus* (mean SVL = 46.1 mm, SD = 3.4), 13 were *H. turcicus* sympatric with *C. scabrum* (mean SVL = 48.8 mm, SD = 5.3) and 18 were *H. turcicus* from an allopatric area (mean SVL = 50.1 mm, SD = 6.5). We judged gecko populations to be sympatric or allopatric based upon repeated observations over a three year period.

Upon capture, we placed each gecko in a sep-

arate plastic bag with a tag upon which was noted the building where it was collected and the perch height of the specimen. We stored all geckos in a chilled ice chest for transport to the laboratory the following morning. At that time, we sacrificed all geckos by chloretone injection and preserved them in 10% buffered formalin. Following preservation, we removed the stomachs and intestines and transferred these to 70% ethanol. Subsequently, we removed all prey items from the stomachs, identified the contents to Order, and counted them. Because *C. scabrum* finely chews and fragments prey prior to swallowing, we were unable to measure the volume of the prey items. As a result, we present only data on the frequency of prey taxa. All *C. scabrum* were processed at Texas A&M University (TAMU) by RKV while all *H. turcicus* were processed by DS and WG at Stephen F. Austin State University (SFASU).

We calculated overlap separately for allopatric and sympatric geckos using Pianka's (1973) symmetric version of the MacArthur-Levins (1967) overlap index. This overlap index compares the proportion of a resource utilized by each species, and yielded a single overlap value for each comparison, i.e., allopatric *C. scabrum* vs. allopatric *H. turcicus*. Because we did not believe that we could accurately estimate total prey availability from patterns of resource utilization of only two species, we elected to use proportional utilization coefficients. Proportional utilization coefficients were calculated by dividing the number of prey of a particular taxon across all stomachs of one type of gecko (i.e., the number of isopods in all allopatric *C. scabrum*) by the total number of prey of all taxa found in all stomachs of that type of gecko (i.e., all insects in all allopatric *C. scabrum*). The resulting resource utilization distributions were compared using Chi-square analysis (Daniel, 1990). Categories of prey with expected values less than one were deleted prior to analysis, yielding a conservative Chi-square test (Daniel, 1990).

We did not measure relative abundance of the different prey taxa; however, we did attempt to assess whether the geckos in the different localities were experiencing differences in overall prey availability by performing Mann-Whitney U tests on the number of prey per stomach in both species in allopatry and sympatry. In addition, Chi-square tests were performed on the prey utilization of both species combined in sympatry and both species combined in allopatry in order to determine whether allopatric and sympatric geckos were experiencing similar prey communities. The transition from areas with allopatric *C. scabrum* to areas of sympatry and then to areas with

allopatric *H. turcicus* occurs over a linear distance of less than 400 m. Within the entire study area the dominant habitat is warehouses with limited but consistent vegetation and relatively uniform lighting conditions. For this reason, we did not expect prey availabilities to vary significantly among the sites sampled. The potential effects on our results of varying prey availabilities across the study area are addressed in the Discussion.

Saenz (1992) found that the diet of *H. turcicus* is related to the height at which they forage, whereas Vaughan (1991) reported that *H. turcicus* and *C. scabrum* may partition habitat space when housed together in captivity. Therefore, any differences found in resource utilization may be a result of differences in perch height rather than food resource partitioning (Vaughan, 1991). We performed Mann-Whitney U tests on perch height data to compare perch height of both species in sympatry and allopatry to detect any perch height differences between the two species that might affect interpretation of any observed overlap. Because differences in gecko size might have an effect on diet (Pianka and Pianka, 1976; Huey and Pianka, 1978), Mann-Whitney U tests were performed on the SVL of the two gecko species in allopatry and sympatry to test for size differences. Nonparametric tests were used because the data for SVL (skewed left), number of prey per stomach (skewed right) and perch height (skewed right) failed to meet the assumptions of parametric tests.

In addition to comparing overlap between the two species in allopatry and sympatry, we analyzed differences within each species' diet between allopatric and sympatric populations. We calculated Pianka's (1973) overlap index and compared resource utilization distributions (Chi-square analysis) between allopatric and sympatric populations within each species to assess changes in food resource utilization with and without the presence of the supposed competitor.

## RESULTS

Both species of geckos combined consumed a total of 17 different prey taxa. The average number of prey per stomach for allopatric and sympatric *C. scabrum* were 3.09 and 4.77, respectively, while the average number of prey per stomach for allopatric and sympatric *H. turcicus* was 3.10 and 3.04, respectively. The number of prey per stomach were not significantly different between species either in allopatry (Mann-Whitney U = 212;  $P > 0.06$ ) or in sympatry (Mann-Whitney U = 263;  $P > 0.07$ ). The percentage of geckos with food present in the stomach was 90%. These figures correspond well to another study on gekkonid diet where the

TABLE 1. Proportional utilization of prey by allopatric and sympatric *C. scabrum* and *H. turcicus* from Galveston, Texas. Prey taxa are ranked in descending order, by occurrence across all geckos.

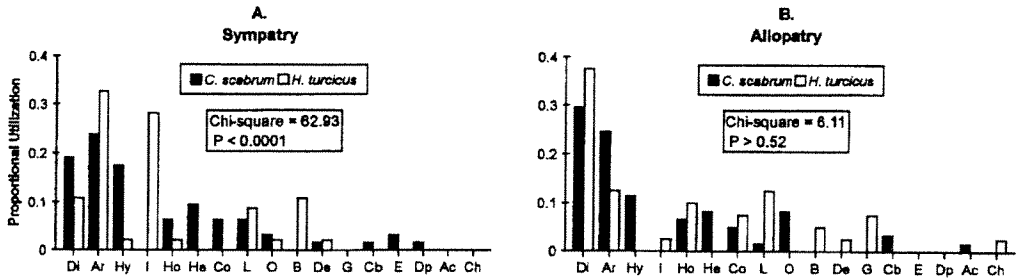
	Allopatric		Sympatric	
	<i>C. scabrum</i>	<i>H. turcicus</i>	<i>C. scabrum</i>	<i>H. turcicus</i>
Diptera	0.30	0.38	0.19	0.11
Araneae	0.25	0.13	0.24	0.33
Hymenoptera	0.11	—	0.17	0.02
Isopoda	—	0.03	—	0.28
Homoptera	0.07	0.10	0.06	0.02
Hemiptera	0.08	—	0.10	—
Coleoptera	0.05	0.08	0.06	—
Lepidoptera	0.02	0.13	0.06	0.09
Orthoptera	0.08	—	0.03	0.02
Blattoidea	—	0.05	—	0.11
Dermoptera	—	0.03	0.02	0.02
Gastropoda	—	0.08	—	—
Collembola	0.03	—	0.02	—
Embiidina	—	—	0.03	—
Diplopoda	—	—	0.02	—
Acari	0.02	—	—	—
Chilopoda	—	0.03	—	—

average number of prey per stomach was 3.65 (range = 1.15–6.48 for 12 species of geckos) and the percentage of geckos with food in the stomach was 72% (range = 38.2–100%) (data calculated from Tables 5 and 7 in Pianka and Pianka, 1976).

Proportional utilization by each category of gecko for each prey taxon are shown in Table 1 and Fig. 1. The arthropod Orders are ranked in order of occurrence across all groups of geckos; the top five arthropod Orders composed over 70% of the total prey consumed. Observed dietary overlap between the two species in allopatry is 0.81; overlap between the two species in sympatry is 0.55. Resource utilization distributions between the two species were significantly different in sympatry ( $\chi^2 = 62.93$ ,  $P < 0.0001$ , Fig. 1A), but not in allopatry ( $\chi^2 = 6.11$ ,  $P > 0.52$ , Fig. 1B). This result indicates that the two species feed on similar prey in allopatry, but that there is a dietary shift by one or both species in sympatry. Comparisons of the prey utilization of both species combined in allopatry was not different from the prey utilization of both species combined in sympatry ( $\chi^2 = 17.26$ ,  $P > 0.05$ ). This result indicates that allopatric geckos and sympatric geckos were experiencing similar prey communities and that the observed differences in proportional utilization in sympatry were not caused by differences in prey availability.

*Hemidactylus turcicus* were not significantly different in size compared to *C. scabrum* either

## Between Species



## Within Species

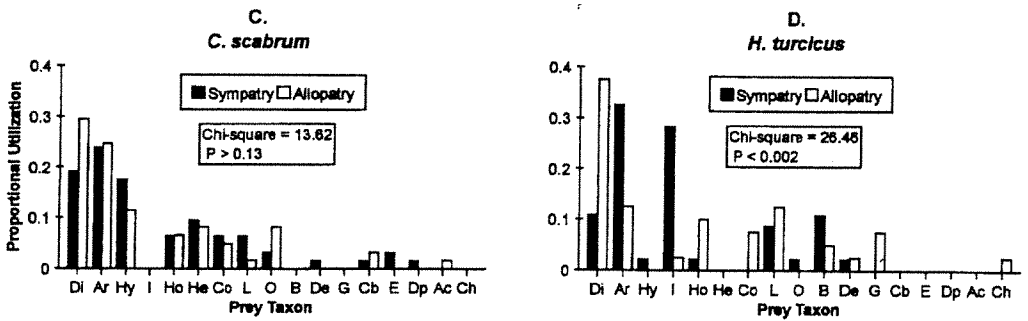


FIG. 1. Comparisons of proportional utilization of prey taxa by *C. scabrum* and *H. turcicus* in sympatry (A) and allopatry (B). Within species comparisons of proportional prey utilization for *C. scabrum* in allopatry and sympatry (C) and for *H. turcicus* in allopatry and sympatry (D). Symbols are Di = Diptera, Ar = Araneae, Hy = Hymenoptera, I = Isopoda, Ho = Homoptera, He = Hemiptera, Co = Coleoptera, L = Lepidoptera, O = Orthoptera, B = Blattoidea, De = Dermaptera, G = Gastropoda, Cb = Collembola, E = Embiidina, Dp = Diplopoda, Ac = Acarina, and Ch = Chilopoda. See text for statistics.

in allopatry (Mann-Whitney  $U = 224$ ;  $P > 0.05$ ) or in sympatry (Mann-Whitney  $U = 209$ ;  $P > 0.09$ ). Thus, the differences in resource utilization were not attributable to differences in size. The heights at which *H. turcicus* were collected did not differ significantly from the heights at which *C. scabrum* were collected in either allopatry (*H. turcicus* = 1.73 m; *C. scabrum* = 2.85 m; Mann-Whitney  $U = 123$ ;  $P > 0.45$ ) or sympatry (*H. turcicus* = 0.96 m; *C. scabrum* = 1.10 m; Mann-Whitney  $U = 82.5$ ;  $P > 0.90$ ). Thus, the observed reduction in overlap in sympatry was not attributable to differences in perch heights of sympatric geckos. Both species occur at lower heights in sympatry but only *H. turcicus* increased its proportional utilization of ground dwelling invertebrates (Araneae, Isopoda, and Blattoidea; Table 1).

Dietary overlap between allopatric and sympatric *C. scabrum* was high (0.93) and proportional prey utilization was not different be-

tween the two populations ( $\chi^2 = 13.62$ ,  $P > 0.13$ ; Fig. 1C). Dietary overlap between allopatric and sympatric *H. turcicus* was low (0.52) and proportional prey utilization was significantly different between the two populations ( $\chi^2 = 26.46$ ,  $P < 0.002$ ). This result indicates that the observed differences in diet between the two species in sympatry is caused by a dietary shift exhibited by *H. turcicus* and not *C. scabrum*.

## DISCUSSION

Ecological shifts in sympatry have been demonstrated for lizards in the past. Huey et al. (1974) reported that for females and immature blind skinks, dietary overlap was lower between sympatric populations than between allopatric populations of the same species. Similar examples in the lizard literature are uncommon. Our data show a reduction in dietary overlap between *H. turcicus* and *C. scabrum* in sympatry when compared to allopatry, due primarily to

a shift in the food resource utilization of *H. turcicus* when in sympatry.

Although a number of studies with lizards have used overlap measures as indicators of competition, our study and Huey et al. (1974) are, to our knowledge, the only ones that compare resource utilization between species in sympatry and allopatry (see a review in Dunham, 1983). If demonstrating lower resource utilization overlap between sympatric populations of two species, compared to allopatric populations, is indicative of competition, then our data are consistent with the hypothesis that competition exists between *H. turcicus* and *C. scabrum* where they occur in sympatry.

An alternative to the competition hypothesis is that the availability of prey varies across the transition from allopatric populations of one species, to the sympatric populations, to the allopatric populations of the other species, a distance of approximately 400 m. Intrinsically similar species may not appear alike if they occur in different environments and intrinsically different species may appear similar if they occur in similar environments (Lawlor, 1980). However, there is no a priori reason to expect wide variations in prey availability in a habitat that has been effectively homogenized by human activities. The comparison of proportional utilization of both species in sympatry to the proportional utilization of both species in allopatry indicate that allopatric and sympatric geckos were exposed to similar prey communities but were partitioning the available prey differently in the two areas.

Dietary shifts caused by changes in perch height might explain the observed differences in resource utilization (Saenz, 1992). However, the perch height data of our study do not support this alternative. Klawinski (1991) found that of 337 *H. turcicus* sighted in a habitat similar to that in Galveston, over 60% occurred within 3 m of the ground and this pattern is corroborated for both species by our data. Also, no differences were found in the sizes of the two species of gecko. The two species sampled in our study share a common period of activity, a common microhabitat, similar sizes, and similar prey populations; thus, dietary overlap should be high. We found high overlap between allopatric populations but not between sympatric populations.

The distributional patterns of these two species in Galveston has allowed us to measure overlap in resource utilization between two species in the presence and absence of suspected competitors. Based on these overlaps, we conclude that competition for food appears to exist between *C. scabrum* and *H. turcicus* where

they occur in sympatry. In addition, the reduction in overlap seems to be due to a shift in resource utilization by *H. turcicus*, but not by *C. scabrum*. This asymmetric shift in dietary niche is consistent with the observed displacement of *H. turcicus* by *C. scabrum* although our data cannot address such a causality. Long term study of these two species in Galveston is warranted as opportunities to study the trajectories of species interactions as they evolve are exceedingly rare. Clearly, this system and others where inadvertent introductions permit these types of observations should be exploited by ecologists as fertile ground for the study of interspecific interactions in vertebrate species where manipulative experiments are not practical.

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