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# Comparative Ecology, Resource Utilization and Niche Segregation Among Gekkonid Lizards in the Southern Kalahari

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**Varied aspects of the general ecology of little-known gekkonid lizards from the southern Kalahari semi-desert of Africa are documented. Four to seven species of geckos coexist on ten study areas. Six of the seven species are nocturnal: three species are ground-dwellers, three climb (of these, one is diurnal) and one is semiarboreal. The percentage of climbing species in various areas is positively correlated with plant height diversity. Body temperatures of nocturnal geckos are very similar and these lizards thermoregulate less carefully than diurnal Kalahari lizards. Pairs of species differ in habitat, microhabitat and/or diet. Resource utilization patterns among Kalahari geckos are compared with those of an independently-evolved, but otherwise ecologically similar, nocturnal saurofauna: the geckos of the western Australian desert. Microhabitat utilization is similar on both continents, but Australian geckos eat a greater variety of prey taxa than Kalahari geckos. Pairs of morphologically similar species on the two continents do not necessarily converge ecologically in diet and microhabitat. The frequency of pairs with high overlap in both diet and microhabitat is greater among intercontinental comparisons than it is among intracontinental ones, suggesting a limit to the similarity of potentially competing species.**

GECKOS are an important component of many desert lizard faunas, particularly in Africa and Australia (Pianka, 1973, 1975). In the southern Kalahari semi-desert of southern Africa, geckos comprise from 31% to 44% (mean 36%) of the total saurofauna on ten selected study areas differing in topography, vegetation, and climate (Pianka, 1971; Pianka and Huey,

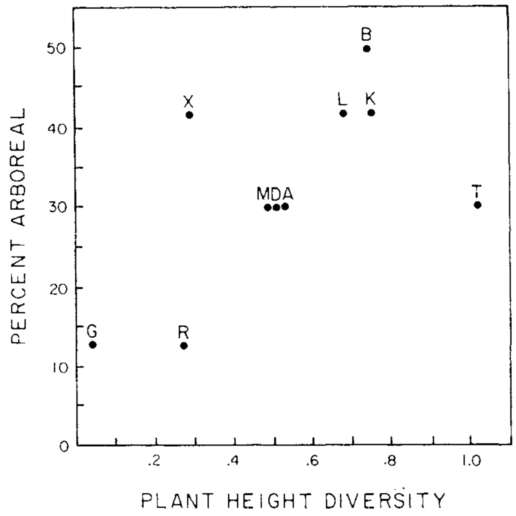

Fig. 1. Plot of the percentage of gecko species that was arboreal versus plant height diversity for ten study areas in the Kalahari ($r_s$ = .59, P < .05). Letters designate particular study sites as listed in Pianka (1971).

1971). During the course of a year-long field investigation of the ecology and diversity of lizards on these study areas, we gathered ecological data on most of the seven species of previously little-known but widespread geckos. Our data provide important new information on the comparative ecology, reproduction, broken tail frequencies, thermal relations, diet, habitat and microhabitat associations, and niche segregation of these lizards. Moreover, these data permit informative comparisons with similar data on geckos from an independently-evolved, yet ecologically very similar, nocturnal saurofauna: the geckos of the Great Victoria Desert of Western Australia (Pianka and Pianka, 1976). Our approach is somewhat eclectic but intentionally designed to help fill a variety of gaps in knowledge about the general ecology of nocturnal geckos.

Elsewhere we have evaluated overall niche relationships of these geckos in the context of analyses of entire saurofaunas (Pianka, 1973, 1974, 1975; Pianka, Huey and Lawlor, 1978), without presenting data on the geckos per se. Haacke (1975, 1976a,b) recently described systematics and briefly discussed aspects of the natural history of the three ground-dwelling lizards (*Colopus*, *Chondrodactylus* and *Ptenopus*).

Leistner (1967) described the vegetation, topography and climate of the southern Kalahari in detail. Stabilized sandridges cover most of the southwestern region and grade into extensive areas of sandplain to the east. Vegetation is predominantly grassy, somewhat savanna-like, with many scattered shrubs and some small trees (important to climbing geckos) including *Acacia mellifera* (a sprawling low shrubby plant), *A. haemotoxylon* (a small tree with dense foliage), *A. giraffae* (a large tree with rough bark and dense foliage) and *Boscia albitrunca* (a moderate-sized tree with relatively smooth pale bark and hollows). Fallen logs are common in some areas.

## METHODS

Active nocturnal geckos were spotted by eye shine or body shine using head lamps. We re-

TABLE 1. OCCURRENCES OF DIFFERENT GECKO SPECIES ON THE VARIOUS STUDY AREAS. See Fig. 1 in Huey and Pianka (1974) for localities coded by letters.

| | L | K | M | B | A | X | G | D | R | $T_s$ | $T_f$ | T | Microhabitat | Retreat |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Colopus wahlbergi* | x | x | x | x | x | x | x | x | e | x | x | x | terrestrial | burrow |
| *Chondrodactylus angulifer* | x | x | x | x | x | x | x | x | x | x | x | x | terrestrial | burrow |
| *Ptenopus garrulus* | x | x | x | x | x | x | x | x | x | x | x | x | terrestrial | burrow |
| *Pachydactylus capensis* | x | e | x | x | x | x | x | x | x | x | x | x | semiarboreal | termite mounds under bark, log |
| *Pachydactylus rugosus* | x | x | x | x | x | x | | x | | | | | arboreal | under and in log or bunch grass |
| *Pachydactylus bibroni* | x | x | | x | | x | | | | | x | x | arboreal | under bark, logs, rocks |
| *Lygodactylus capensis* | | | | x | | | | | | | | | arboreal | under bark, logs |

x = collected, e = highly expected.

TABLE 2. MICROGEOGRAPHICAL ASSOCIATIONS OF GECKOS IN SANDRIDGE LOCALITIES (PERCENTAGES).

| | *Colopus* | *Chondrodactylus* | *Ptenopus* | *P. capensis* | *P. rugosus* | *P. bibroni* | *Lygodactylus* |
|---|---|---|---|---|---|---|---|
| Flat | 12.8 | 70.9 | 79.2 | 93.8 | 22.2 | 83.0 | 96.3 |
| Base | 12.8 | 7.8 | 9.4 | 6.3 | 11.1 | 5.3 | 0 |
| Slope | 59.0 | 8.6 | 7.5 | 0.0 | 61.1 | 8.5 | 0 |
| Crest | 15.4 | 12.7 | 3.8 | 0.0 | 5.6 | 3.2 | 3.7 |
| N | 39 | 268 | 106 | 16 | 18 | 94 | 27 |

corded microhabitat, habitat and time of activity, as well as body (cloacal) and air temperatures at capture with Schultheis thin-bulb thermometers. To obtain an indication of the general ambient thermal conditions, air temperatures were recorded at chest height rather than at the point of capture (other studies have shown that body temperatures correlate better with chest height air temperatures than with ground-level air temperatures, e.g., Schall, 1977).

Techniques of analysis of reproductive traits and stomach contents using preserved material parallel those of Pianka and Pianka (1976).

## RESULTS

*Occurrences on study sites.*—Gecko censuses on ten study areas, microhabitat associations while active, and diurnal retreat of each species are presented in Table 1. The number of sympatric gecko species varies from 4 to 7 and is significantly correlated with plant height diversity at the site ($r_s = .59$, $P < .05$; plant data in Pianka, 1971).

The three ground-dwelling species are nearly ubiquitous, but the occurrence of climbing species is spotty (Table 1). This distributional difference presumably reflects the greater sensitivity of arboreal species to vegetation structure. The percentage of gecko species on an area that is arboreal is significantly correlated with plant height diversity ($r_s = .71$, $P < .05$; Fig. 1). Thus areas with high vegetative diversity support more species of arboreal geckos, a pattern that holds as well for numbers of bird species (Pianka and Huey, 1971) and for number of species of diurnal lizards in the Kalahari ($r_s = .71$, $P < .05$).

TABLE 3. HABITAT ASSOCIATIONS OF TERRESTRIAL GECKOS IN SANDPLAIN LOCALITIES (PERCENTAGES). Scrub, edge includes *Rhigozum* flats.

| | Gecko species | | |
|---|---|---|---|
| Habitat | *Colopus* | *Chondrodactylus* | *Ptenopus* |
| Forest | 64.8 | 20.7 | 26.1 |
| Scrub, edge | 26.8 | 71.8 | 68.3 |
| Savanna | 8.5 | 7.5 | 5.6 |
| N | 71 | 174 | 268 |

*Microgeographic distributions on sandridge sites.*—We recognize four microgeographic subdivisions of dunes (Huey and Pianka, 1974) in sandridge areas: street, base, slope, and crest (Table 2). While most species are found primarily in dune streets, geckos do differ significantly (G-test, $P < .001$) in microgeographic distributions. However, *Colopus* and *P. rugosus* (both extremely rare geckos before our study), which themselves do not differ significantly (STP-test, $P > .9$), are primarily associated with dune slopes (they occasionally occur in flats, too). [The association of *P. rugosus* with sandridge slopes may reflect the frequent occurrence of this species on sprawling *Acacia* shrubs (especially *A. mellifera* but also *A. haemotoxylon*, see below) that are most common on dune slopes (Leistner, 1967).] Similar differences in microgeographic distributions occur in Kalahari subterranean lizards (Huey and Pianka, 1974) and in Australian lizards (Pianka, 1969, 1972, 1978).

*Habitat associations of ground-dwelling geckos on sandplain sites.*—The three ground-dwelling gecko species differ significantly in habitat associations at sandplain sites (G-test, $P < .001$; Table 3). *Chondrodactylus* and *Ptenopus*, which themselves are very similar (STP-test, $P > .5$), are primarily associated with scrub, forest edge, and *Rhigozum* habitats. In contrast, *Colopus* is chiefly a forest species. *Colopus* is very rare at sandplain localities without well-developed forest habitats [areas D, R and G (Fig. 1)].

*Microhabitat utilization.*—Table 4 summarizes microhabitat locations of active geckos when first sighted. Arboreal and ground-dwelling

TABLE 4. MICROHABITATS OF GECKOS WHEN FIRST SIGHTED (PERCENTAGES). Sample sizes and microhabitat niche breadths are also given.

| | | | | | *Pachydactylus* | | | |
|---|---|---|---|---|---|---|---|---|
| | | *Colopus* | *Chondrodactylus* | *Ptenopus* | *capensis* | *rugosus* | *bibroni* | *Lygodactylus* |
| Terrestrial | Open | 43.4 | 35.7 | 64.8 | 9.2 | 4.5 | 3.3 | 0.0 |
| on ground near | Grass | 17.2 | 16.5 | 7.3 | 6.2 | 4.5 | 0.0 | 0.0 |
| | Bush | 27.9 | 41.0 | 23.9 | 27.7 | 9.1 | 3.3 | 0.0 |
| | Tree | 11.5 | 5.5 | 3.1 | 12.3 | 4.5 | 2.2 | 0.0 |
| | Other | 0.0 | 0.5 | 0.9 | 3.1 | 0.0 | 1.1 | 0.0 |
| Arboreal | Low* | 0.0 | 0.4 | 0.0 | 29.2 | 34.1 | 41.8 | 34.2 |
| | High* | 0.0 | 0.4 | 0.0 | 12.3 | 43.2 | 48.4 | 65.8 |
| | N | 122 | 417 | 423 | 65 | 22 | 91 | 19 |
| Microhabitat niche breadth | | .461 | .439 | .296 | .694 | .450 | .347 | .260 |

* Low is 30 cm and less above ground surface, High is above 30 cm.

species overlap little in microhabitat. *Colopus* and *Ptenopus* have nearly identical microhabitat associations, but they differ in habitats used. Climbing species differ substantially in their associations with different species of plants or logs or both (Table 5). *Pachydactylus capensis* has the broadest microhabitat niche breadth using Simpson's (1949) index of diversity, $1/\Sigma p_i^2$, where $p_i$ represents the proportion of the ith resource category used (Table 4, bottom line).

*Body size.*—Statistics on mean snout–vent lengths (SVL, in mm), head length (mm), weight (g), and on hind leg length as a percentage of SVL are presented in Table 6. The diurnal *Lygodactylus* is diminutive ($\bar{x} = .9$ g). Remaining species, except for the larger *P. bibroni* (mean weight 8.9 g) and especially *Chondrodactylus* ($\bar{x} = 15.7$ g), are all small geckos (2.2–4.3 g).

TABLE 5. PLANT ASSOCIATIONS OF ARBOREAL GECKOS (PERCENTAGES.) At some other localities, *P. bibroni* are frequently associated with *Acacia* trees.

| | Gecko species | | | |
|---|---|---|---|---|
| Plant type | *P. capensis* | *P. rugosus* | *P. bibroni* | *Lygodactylus* |
| *Acacia* tree | 22.7 | 7.1 | 6.1 | 6.7 |
| Shrubby *Acacia* | 18.2 | 57.1 | 0.0 | 0.0 |
| Log | 45.5 | 0.0 | 38.8 | 0.0 |
| "*Parkinsonia*" | 0.0 | 0.0 | 4.1 | 60.0 |
| *Boscia* | 4.5 | 21.4 | 46.9 | 33.3 |
| Misc. | 9.1 | 14.3 | 4.1 | 0.0 |
| N | 22 | 14 | 49 | 15 |

*Diets.*—Kalahari geckos consume a variety of arthropods (Table 7). Major foods of *Lygodactylus* and *P. rugosus* are, respectively, ants and adult moths. The dominant food of the two large geckos (*Chondrodactylus* and *P. bibroni*) is the large termite *Hodotermes mossambicus*. *Pachydactylus capensis* has a generalized diet compared with other species. *Colopus* and *Ptenopus*, both termite specialists, eat substantial numbers of an unidentified species of termite that is taken only infrequently by other species. Thus, diets differ between most pairs of species, except for *Chondrodactylus* × *P. bibroni* and *Colopus* × *Ptenopus* (note that both of these pairs are clearly segregated in their use of space—see above).

The largest two species, *Chondrodactylus* and *P. bibroni*, eat substantially larger prey than smaller species; the smallest species, the diurnal *Lygodactylus*, consumes exceedingly small prey (Table 8). Average prey size is not, however, significantly correlated with gecko size (either SVL or weight; $r_s = .49$, $P > .05$). Average size of the ten largest prey items is correlated with gecko size ($r_s = .75$, $P < .05$), as it is in many other lizards (e.g., Pianka, 1969; Pianka and Pianka, 1976).

Brain (1962) suggested that *Chondrodactylus* might be a major predator of *Ptenopus* in the southern Kalahari. Haacke (1976b) found no vertebrate remains in "more than 25 specimens."

TABLE 6. MEAN SIZES (± s.e.) OF SNOUT-TO-VENT LENGTH (SVL), WEIGHT, HEAD LENGTH AND HIND LEG LENGTH AS PERCENTAGE OF SVL FOR KALAHARI GECKOS.

| | *Colopus* | *Chondrodactylus* | *Ptenopus* | *P. capensis* | *P. rugosus* | *P. bibroni* | *Lygodactylus* |
|---|---|---|---|---|---|---|---|
| SVL (mm) | 48.0 ± 0.66 | 75.5 ± 0.79 | 42.9 ± 0.32 | 51.5 ± 1.00 | 52.0 ± 1.11 | 65.1 ± 1.14 | 30.9 ± 1.11 |
| (N) | (87) | (442) | (485) | (107) | (29) | (174) | (28) |
| Weight (g) | 2.6 ± 0.16 | 15.7 ± 0.49 | 2.2 ± 0.05 | 3.9 ± 0.23 | 4.3 ± 0.37 | 8.9 ± 0.51 | 0.9 ± 0.11 |
| (N) | (107) | (340) | (469) | (92) | (19) | (127) | (21) |
| Head length (mm) | 10.7 ± 0.15 | 17.9 ± 0.17 | 9.2 ± 0.06 | 12.0 ± 0.21 | 12.9 ± 0.24 | 16.2 ± 0.25 | 7.6 ± 0.22 |
| (N) | (87) | (442) | (487) | (107) | (29) | (174) | (28) |
| Hind leg % of SVL | 44.9 | 44.2 | 48.8 | 39.7 | 45.0 | 41.0 | 41.9 |

Eleven of the 304 stomachs examined in the present study contained vertebrate material: this includes four *Ptenopus* (one corpse covered with ants was evidentally carrion when eaten), two *Colopus*, remains of two unidentifiable geckos, two lizard tails, and two unidentified bones.

*Thermal biology.*—Statistics on body ($T_b$) and air ($T_a$) temperatures and time of activity of Kalahari geckos are presented in Table 9. Mean body ($\bar{T}_b$) and mean air ($\bar{T}_a$) temperatures are positively correlated between species of nocturnal geckos ($r_s = .87$, $P < .05$), and $T_b$ and $T_a$ are also strongly correlated within species (all $P < .001$). Not surprisingly, $T_b$ varies seasonally in *Chondrodactylus angulifer*, the species for which we have most complete data (Fig. 2). Pianka and Pianka (1976) presented similar data on Australian desert geckos.

Mean time of activity is similar among noc-

TABLE 7. STOMACH CONTENTS, PERCENTAGE COMPOSITION BY VOLUME. Food niche breadth and number of stomachs are also given.

| | Gecko species | | | | | | |
|---|---|---|---|---|---|---|---|
| Prey categories | *Colopus* | *Chondrodactylus* | *Ptenopus* | *P. capensis* | *P. rugosus* | *P. bibroni* | *Lygodactylus* |
| Spiders | 5.5 | 1.9 | 2.5 | 3.5 | 3.5 | 1.6 | 11.4 |
| Scorpions | 0.2 | 10.5 | 0.0 | 3.4 | 0.0 | 1.0 | 0.0 |
| Formicidae | 3.5 | 0.5 | 12.6 | 2.6 | 0.6 | 3.7 | *29.3* |
| Grasshoppers & Crickets | 7.1 | 12.4 | 2.1 | 8.8 | 4.1 | 4.4 | 9.0 |
| Blattidae | 0.9 | 0.4 | 0.3 | 0.9 | 14.9 | 1.4 | 0.0 |
| Coleoptera | 0.0 | 10.9 | 7.2 | 10.2 | 12.0 | 16.9 | 6.5 |
| Hemiptera | 0.1 | 0.0 | 0.8 | 1.8 | 5.2 | 0.3 | 8.3 |
| Lepidoptera | | | | | | | |
| Adults | 0.0 | 0.0 | 0.2 | 5.3 | *22.6* | 2.2 | 0.0 |
| Larvae | 2.6 | 0.0 | 0.0 | 2.8 | 1.2 | 7.4 | 0.6 |
| Isoptera | | | | | | | |
| *Hodotermes mossambicus* | 7.2 | *26.8* | 15.9 | *10.8* | 8.2 | *36.2* | 0.0 |
| *Trinervitermes* sp. | 1.8 | 8.2 | 5.7 | 6.0 | 0.0 | 11.0 | 3.0 |
| Termite sp. "O" | *36.0* | 1.4 | *27.3* | 4.5 | 0.0 | 0.0 | 0.0 |
| Termite sp. "P" | 12.1 | 4.3 | 7.2 | 5.6 | 0.0 | 1.2 | 0.0 |
| Misc. termites | 6.5 | 5.0 | 6.1 | 5.1 | 0.0 | 2.9 | 7.2 |
| Misc. Arthropods | 12.4 | 3.6 | 6.5 | 14.8 | 11.6 | 4.3 | 7.2 |
| Vertebrates* | 2.1 | 8.9 | 0.2 | 6.1 | 4.4 | 2.0 | 3.0 |
| Unidentified | 5.1 | 4.8 | 5.1 | 7.7 | 11.8 | 3.5 | 9.3 |
| Food Niche Breadth | 0.16 | 0.20 | 0.19 | 0.43 | 0.22 | 0.14 | 0.19 |
| No. Stomachs | 79 | 304 | 331 | 43 | 17 | 114 | 20 |

* Includes sloughed skins.

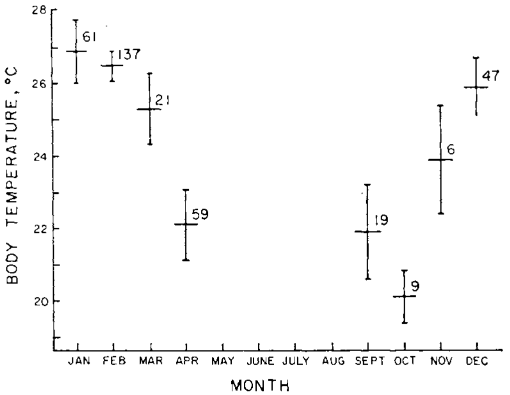

Fig. 2. Body temperatures of active *Chondrodactylus angulifer* vary seasonally. Horizontal bars represent means, vertical lines plot two standard errors on each side of the mean, while numbers indicate sample sizes.

turnal species (Table 9). However, these geckos do alter activity on a seasonal basis: all brumate during winter months. Moreover, geckos seemingly are active until later at night during warm summer months. *Chondrodactylus*, for example, is active significantly later (t-test modified for unequal variances, $P < .05$) between December and March (2.4 ± .06 hrs past sunset, $N = 315$) than during cooler months (2.2 ± .07 hrs, $N = 106$); similarly, variance in time of activity is significantly greater (F-test, $P < .001$) during warm months (all these trends may simply be artifacts of our own sampling bias). Both brumation and regulation of activity time should reduce the variance in body temperatures experienced by active geckos.

Nocturnal lizards differ strikingly in thermal biology from diurnal lizards in the Kalahari (for data and discussion of thermoregulation of diurnal species, see Huey and Pianka, 1977). First, $\overline{T}_b$ of diurnal species ($\bar{x} = 36.4 \pm .54$ C, $N = 12$) is much higher than that of nocturnal species ($\bar{x} = 26.1 \pm .51$ C). Second, $\overline{T}_b$'s are above $\overline{T}_a$'s in diurnal species (+6.8 ± .42 C) but not in nocturnal ones (–0.3 ± .4 C). Third, $T_b$ is more strongly correlated with $T_a$ in nocturnal species (mean parametric correlation coefficients 0.87 ± .045 vs. 0.51 ± .037). Fourth, slopes of $T_b \cdot T_a$ regressions are much steeper in nocturnal species (.87 ± .049 vs. .30 ± .028, see Huey and Slatkin, 1976). Fifth, standard deviations of $T_b$ are significantly larger ($P < .001$) in nocturnal species (3.6 ± .14 vs. 2.4 ± .14 C, see Pianka and Pianka, 1976, for similar results with Australian geckos). Sixth, the maximum difference between $T_b$'s is much greater among diurnal species (6.7 vs. 2.6 C).

These data reinforce and extend earlier observations on marked differences in thermal biology between diurnal and nocturnal lizards (Brattstrom, 1965; Bustard, 1967; Cowles and Bogert, 1944; Huey and Slatkin, 1976; Licht et al., 1966; Parker and Pianka, 1974; Pianka and Pianka, 1976), especially in emphasizing that the nocturnal thermal environment is more homogeneous and offers fewer opportunities for thermoregulation (except for regulation of time of

TABLE 8. PREY SIZE DISTRIBUTIONS (PERCENTAGE OF PREY IN VARIOUS SIZE CATEGORIES).

| | Gecko species | | | | | | |
|---|---|---|---|---|---|---|---|
| Prey size (microliters) | *Colopus* | *Chondrodactylus* | *Ptenopus* | *P. capensis* | *P. rugosus* | *P. bibroni* | *Lygodactylus* |
| <.005 | 19.2 | 0.6 | 34.2 | 17.2 | 18.8 | 2.1 | 62.0 |
| .006–.014 | 12.7 | 28.5 | 19.1 | 22.3 | 6.3 | 24.1 | 21.5 |
| .015–.024 | 28.9 | 51.0 | 27.9 | 30.2 | 37.5 | 60.5 | 11.4 |
| .025–.034 | 12.0 | 10.5 | 6.3 | 10.8 | 31.3 | 5.0 | 2.5 |
| .035–.054 | 8.1 | 3.6 | 3.0 | 9.5 | 4.7 | 3.9 | 2.6 |
| .055–.064 | 6.2 | 1.2 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| .065–.074 | 4.9 | 0.6 | 0.9 | 0.0 | 0.0 | 0.3 | 0.0 |
| .075–.094 | 4.6 | 1.3 | 4.3 | 3.0 | 1.6 | 0.3 | 0.0 |
| .095–.174 | 3.3 | 1.2 | 3.7 | 3.9 | 0.0 | 2.1 | 0.0 |
| >.175 | 0.3 | 1.5 | 0.2 | 1.7 | 0.0 | 1.5 | 0.0 |
| Mean prey size | 0.030 | 0.029 | 0.020 | 0.027 | 0.020 | 0.026 | 0.007 |
| Mean size of ten largest prey | 0.145 | 1.320 | 0.155 | 0.167 | 0.041 | 0.410 | 0.024 |
| No. prey items | 308 | 4821 | 1935 | 232 | 64 | 1487 | 79 |

TABLE 9. BODY AND AIR TEMPERATURE AND TIME OF ACTIVITY (HRS) OF KALAHARI GECKOS. r = product-moment correlation coefficient between BT and AT. Slope is for regression of BT on AT.

| | Air temp. | | Body temp. | | | | |
|---|---|---|---|---|---|---|---|
| Species | $\bar{x} \pm$ s.e. | N | $\bar{x} \pm$ s.e. | N | r | Slope | Time |
| *Colopus* | 25.9 ± .34 | 87 | 25.3 ± .44 | 58 | .91 | .91 | 21.1 ± .14 |
| *Chondrodactylus* | 26.1 ± .17 | 375 | 25.4 ± .19 | 349 | .90 | .96 | 21.1 ± .05 |
| *Ptenopus* | 26.1 ± .22 | 246 | 27.6 ± .32 | 148 | .83 | .80 | 20.9 ± .07 |
| *Pachydactylus capensis* | 25.2 ± .52 | 54 | 25.3 ± .55 | 44 | .89 | .83 | 20.7 ± .12 |
| *P. rugosus* | 25.6 ± 1.05 | 17 | 25.3 ± 1.23 | 11 | .99 | 1.03 | 21.5 ± .25 |
| *P. bibroni* | 26.1 ± .38 | 69 | 27.9 ± .42 | 58 | .67 | .71 | 21.1 ± .11 |
| *Lygodactylus* | 26.9 ± 1.11 | 14 | 36.0 | 1 | — | — | 12.6 ± .46 |

activity) and that geckos thermoregulate less precisely and more passively than diurnal species of lizards. Unfortunately, little is known (Brattstrom, 1952; Bustard, 1967; Dial, 1977; Huey, 1969) of the behavior of nocturnal geckos during the day or of diurnal lizards at night (during the course of this study, we did observe a *P. bibroni* basking in full sunlight early in the morning—this animal had a $T_b$ of 32.8 C). A complete comparison of the thermoregulatory behavior of diurnal and nocturnal lizards with an integration of possible physiological differences must therefore await further study.

*Reproduction.*—Information on reproduction among females of the six nocturnal species is summarized in Table 10 (no gravid female *Lygodactylus* were collected). Estimates of clutch size are based on counts of both enlarged ovarian eggs and shelled oviducal eggs. One species, *Ptenopus*, probably lays only a single egg at a time (see Haacke, 1975), whereas the other species usually produce two eggs (a few *Chondrodactylus* and *P. capensis* contained only one egg, however—perhaps these had already deposited one egg of their clutch as Parker (1972) suggested for *Coleonyx variegatus*).

In most species eggs evidently yolk from late August or early September through late January or February. Table 10 lists the dates of collection of females with eggs in their oviducts. The rather long egg-laying season of *Chondrodactylus* probably reflects the production of at least two clutches: 15 females contained both oviducal eggs and enlarged yolked ovarian eggs simultaneously, presumed evidence of multiple clutches. (These were collected on 21 and 26 Sept., 7 and 10 Oct., 11 and 13 Dec., 3, 4, 6 and 28 Jan.—another female collected on 8 February had obviously just laid eggs as judged from greatly enlarged oviducts and yet contained a pair of very large 11 mm diameter yolked ovarian follicles.)

*Tail break frequencies.*—Arboreal gecko species may have a higher incidence of broken tails than terrestrial species (Werner, 1968; Pianka and Pianka, 1976). This trend also seems to hold among nocturnal Kalahari geckos (Table 11). Two possible interpretations are 1) that climbing species are exposed to more intense predation than ground-dwelling species, and/or 2) that ground dwellers do not escape predators by tail loss as effectively as arboreal species (i.e., more animals actually die and are consumed in their entirety, leaving fewer with broken regenerated tails). Schoener (pers. comm.) discusses problems of inferring predation rate from tail loss data.

TABLE 10. STATISTICS AND INFORMATION ON SOME ASPECTS OF REPRODUCTION OF FEMALE GECKOS.

| | | | Clutch volume/Body weight | | | Egg volume (cc) | | |
|---|---|---|---|---|---|---|---|---|
| Species | Mean clutch size | N | $\bar{x}$ | s.e. | N | $\bar{x}$ | N | Ovigerous females |
| *Colopus* | 2.0 | 18 | 8.2 | 1.33 | 2 | 0.14 | 3 | 22 Jan. |
| *Chondrodactylus* | 1.92 | 92 | 12.2 | 0.74 | 22 | 1.10 | 41 | 21 Sept.–8 Feb. |
| *Ptenopus* | 1.0 | 20 | 8.8 | — | 1 | 0.28 | 1 | 7 Oct. |
| *P. capensis* | 1.93 | 15 | 11.1 | 1.44 | 3 | 0.28 | 6 | 4 Dec.–7 Jan. |
| *P. rugosus* | 2.0 | 3 | — | — | — | — | — | None |
| *P. bibroni* | 2.0 | 16 | 10.6 | 0.65 | 8 | 0.59 | 14 | 1 Dec.–8 Feb. |

Table 11. Percentages of Broken Tails and Sample Sizes of Kalahari Geckos.

| Species | % Broken tails | Sample size |
|---|---|---|
| *Colopus wahlbergi* | 27.7 | 119 |
| *Chondrodactylus angulifer* | 24.1 | 427 |
| *Ptenopus garrulus* | 21.1 | 399 |
| *Pachydactylus capensis* | 52.8 | 89 |
| *Pachydactylus rugosus* | 65.2 | 23 |
| *Pachydactylus bibroni* | 50.0 | 140 |
| *Lygodactylus sapensis* | 40.9 | 22 |

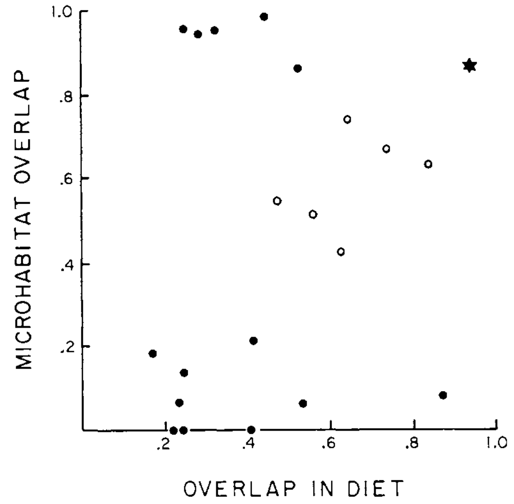

Fig. 3. Overlap in microhabitat plotted against dietary overlap for all interspecific pairs of Kalahari geckos. Open circles indicate pairs involving the microhabitat and dietary generalist *Pachydactylus capensis*. The star is *Ptenopus* × *Colopus*, which are separated in habitat associations (see text).

*Differences in resource utilization.*—Using the symmetric overlap index of Pianka (1973), microhabitat overlap was computed among all possible pairs of species from the data presented in Table 4 (Table 12—below diagonal). With the exception of overlap pairs involving the microhabitat generalist *P. capensis*, overlap in microhabitat is distinctly all-or-none, with very high overlap both among the ground-dwelling triad (*Colopus*, *Ptenopus* and *Chondrodactylus*) and among various pairs of climbing species (*P. capensis*, *P. rugosus*, *P. bibroni* and the diurnal *Lygodactylus*). Overlap in microhabitat is very low however among all arboreal × ground-dwelling pairs (Table 12, Fig. 3).

Dietary overlap, computed from data presented in Table 7, is more continuous, varying from .17 to .87 among the 21 pairs of species (Table 12, Fig. 3). Overlaps with the microhabitat and dietary generalist *P. capensis* are moderate (open circles in Fig. 3); moreover, average or total overlap is greatest for this species on both niche dimensions (Table 12, margins). Only *Colopus* × *Ptenopus* exhibit very high overlap in both diet and microhabitat; however, recall that *Colopus* is found primarily on sandridge slopes and crests whereas *Ptenopus* occurs in the interdunal flats (Table 2) and that *Colopus* and *Ptenopus* also differ in habitat associations (Table 3) at sandplain sites.

All possible pairs of species therefore differ in their use of resources. Whether or not this apparent resource partitioning is a consequence of interspecific competition cannot, however, be inferred from these data (Pianka, 1976 discusses the problems involved in studying competition). A comparison with Australian geckos (below) does suggest a possible impact of competition on the structure of both communities.

Table 12. Above Diagonal = Overlap in Diet. Below Diagonal = Microharitat Overlap.

| | *Colopus* | *Chondrodactyus* | *Ptenopus* | *P. capensis* | *P. rugosus* | *P. bibroni* | *Lygodactylus* | Diet overlap mean |
|---|---|---|---|---|---|---|---|---|
| *Colopus* | — | .325 | .874 | .515 | .173 | .233 | .221 | .390 |
| *Chondrodactylus* | .958 | — | .525 | .842 | .416 | .877 | .248 | .539 |
| *Ptenopus* | .942 | .865 | — | .624 | .250 | .542 | .405 | .537 |
| *P. capensis* | .563 | .638 | .427 | — | .645 | .738 | .473 | .640 |
| *P. rugosus* | .186 | .206 | .143 | .746 | — | .445 | .285 | .369 |
| *P. bibroni* | .073 | .081 | .067 | .677 | .988 | — | .254 | .515 |
| *Lygodactylus* | .000 | .008 | .000 | .551 | .947 | .959 | — | .314 |
| Mean overlap in microhabitat | .454 | .459 | .407 | .600 | .536 | .474 | .411 | |

TABLE 13. PERCENTAGES, BY VOLUME, OF VARIOUS PREY TAXA EATEN BY THE GECKO FAUNAS OF TWO DESERT SYSTEMS.

| Prey taxon | Kalahari | Australia |
|---|---|---|
| Centipedes | 0.00 | 2.47 |
| Spiders | 2.15 | 13.20 |
| Scorpions | 6.65 | 2.56 |
| Ants | 3.03 | 0.37 |
| Other Hymenoptera | 0.07 | 0.31 |
| Grasshoppers | 9.06 | 14.85 |
| Roaches | 0.64 | 7.04 |
| Mantids | 0.14 | 1.19 |
| Beetles | 10.58 | 15.91 |
| Termites | 48.18 | 21.17 |
| Hemiptera | 0.30 | 3.07 |
| Diptera | 0.03 | 0.28 |
| Lepidoptera | 0.84 | 1.89 |
| Eggs of insects | 0.02 | 0.00 |
| Pupae | 2.03 | 0.31 |
| Larvae | 2.03 | 7.00 |
| Miscellaneous arthropods | 7.38 | 3.78 |
| Vertebrates | 6.01 | 4.26 |
| Plant material | 0.86 | 0.36 |

## COMPARISONS WITH AUSTRALIAN DESERT GECKOS

Some instructive comparisons can be made between the Kalahari geckos and those of the climatologically and physiognomically nearly identical Australian desert, whose independently-evolved gecko fauna was examined by Pianka and Pianka (1976). From 5 to 9 species of geckos (mean 6.6) plus 2 species of nocturnal skinks (genus *Egernia*) are sympatric in Australia as compared with 4 to 7 gecko species in the Kalahari (mean 5.3), one of which is diurnal. Overlap between all pairs of Kalahari gecko species except *Colopus* × *Ptenopus* (star in Fig. 3) are either included within or very close to the subjective envelope curve drawn for the Australian geckos (Fig. 5 of this paper or Fig. 8 of Pianka and Pianka, 1976), so that overall overlap among Kalahari geckos appears to be no greater than it is among Australian geckos (but see also below).

To facilitate comparison of the two faunas, niche breadths and overlaps were computed using the same prey and microhabitat categories for each desert lizard system (these values differ somewhat from those presented in the above analysis—for instance, all termites are lumped into a single prey category). Thus calculated, niche breadths (diet or microhabitat) are similar on both continents (Median test using Fisher's exact probability method, P's > .30): food niche breadth in the Kalahari ranges from .13 to .46 among species (mean .27) compared with .05 to .57 in Australia (mean .27), whereas microhabitat niche breadths vary from .14 to .32 (mean .20) in the Kalahari and from .09 to .27 (mean .16) in Australia.

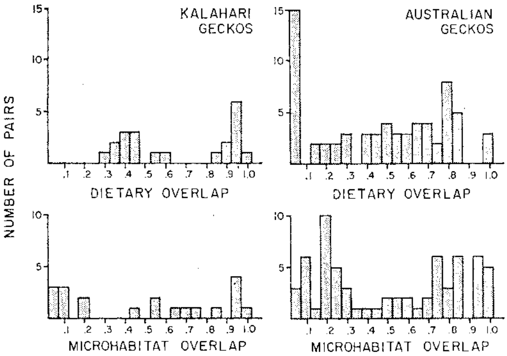

Fig. 4. Frequency distributions of overlap values on two niche dimensions in two independently-evolved gecko faunas. Distributions of dietary overlap differ significantly but those for microhabitat do not.

The overall diversity of microhabitats actually used by all species of geckos combined is similar on both continents (.24 in the Kalahari versus .25 in Australia). However, the Australian geckos together consume a substantially greater diversity of foods (.42) than do Kalahari geckos (.20), largely due to the prevalence of termites in the Kalahari diet (Table 13). Distributions of niche overlap values also differ (Mann-Whitney z statistic = –2.604, P = .004) between the two continents (Fig. 4), with greater dietary overlap in the Kalahari (mean .67) than in Australia (mean .46). However, the distributions of overlap in microhabitat do not differ significantly (z = .823, P = .206), so the above difference in dietary overlap is not simply an artifact of the larger number of species in Australia (see Inger and Colwell, 1977). The lower dietary overlap among Australian geckos could of course be a direct consequence of the greater diversity of foods eaten. Alternatively, one could argue that the greater number of nocturnal species in Australia results in more intense interspecific competition and that this enhanced diffuse competition itself reduces maximal tolerable overlap forcing greater niche segregation and hence consumption of a wider variety of foods. Because we have no data on the actual availabilities of various food types on the two con-

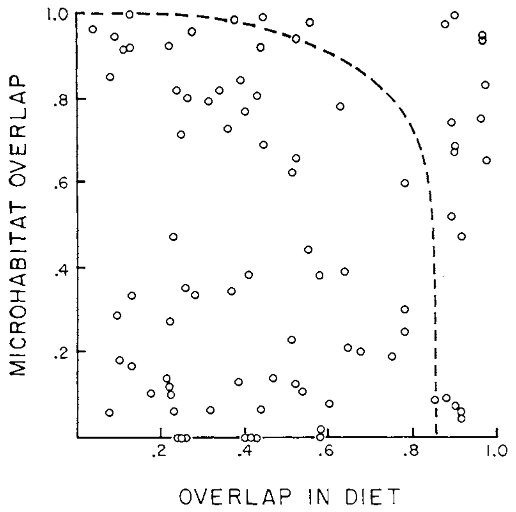

Fig. 5. Plot of microhabitat overlap versus overlap in diet for 84 intercontinental pairs of species. Each point thus represents the overlap between a Kalahari gecko and an Australian species on the two niche dimensions. Significantly more intercontinental pairs lie above the dashed envelope curve than intracontinental pairs.

tinents, we cannot distinguish between these two alternatives. In any case, however, greater gecko diversity in Australia is not associated with a greater degree of resource sharing on that continent (see also MacArthur, 1972; Pianka, 1973, 1974, 1975) nor with narrower niche breadths of component species. Rather, the major factor associated with the higher diversity of Australian geckos is their consumption of a greater variety of prey (i.e., the overall size of the food niche space used by geckos is greater in Australia than in the Kalahari).

*Morphological versus ecological convergence and niche segregation.*—On the basis of morphological similarities, Pianka (1975) suggested the following pairs as crude ecological equivalents: *Chondrodactylus* × *Nephrurus, Colopus* × *Diplodactylus stenodactylus, Pachydactylus rugosus* × *Diplodactylus strophurus,* and *Pachydactylus capensis* × *Heteronotia binoei.* In an attempt to identify ecological equivalents objectively, we used the same data set to perform an *intercontinental* niche analysis. Resource matrices for the two continents were merged and overlap in diet and microhabitat computed for all possible pairs of Kalahari × Australian gecko species (Fig. 5). This analysis did not substantiate Pianka's (1975) ecological equivalents: morphologically similar pairs differ in their use of resources. Pairs with extensive overlap in both diet and microhabitat are *P. bibroni* × *Gehyra, Colopus* × *D. conspicillatus, Colopus* × *Rhynchoedura, Ptenopus* × *D. conspicillatus, Ptenopus* × *Rhynchoedura,* as well as several other pairs with slightly lower overlap in microhabitat. Many species have no obvious ecological counterparts on the other continent: these include *P. capensis, P. rugosus,* and *Lygodactylus* in the Kalahari, and in Australia, the three species of *Nephrurus,* three arboreal species of *Diplodactylus, D. stenodactylus,* and *Heteronotia.*

In 18 of the 84 intercontinental pairs, overlap values lie above the envelope curve (Fig. 5): this fraction is significantly greater between continents than within (chi-square test, corrected for continuity, $P < .05$). Hence more intercontinental pairs have very high overlap along both niche dimensions than do intracontinental pairs, suggesting that niche segregation has in fact taken place within continents.

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