

Rarity in Australian desert lizards

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Abstract Most species of Australian desert lizards are uncommon. Possible causes of rarity are examined, including body size as measured by snout–vent length (SVL), fecundity, number of sites occupied, habitat niche breadth, microhabitat niche breadth, dietary niche breadth, and average total niche overlap with other species. Rare species tend to be larger with lower fecundities than abundant species and they occur at fewer sites. Many, but not all, uncommon species are specialists, either in habitat, microhabitat, or diet. The niche breadth hypothesis, which states that abundant species should be generalists whereas specialized species should be rare, is tested, but rejected as a general explanation for rarity. Some uncommon species exhibit high overlap with other species suggesting that they may experience diffuse competition. However, no single cause of rarity can be identified, but rather each species has its own idiosyncratic reasons for being uncommon. Multivariate analyses show distinct ecological differences between abundant and uncommon species.

Key words: diffuse competition, fecundity, generalists *versus* specialists, niche breadth, niche overlap, relative abundance.

INTRODUCTION

Understanding rarity constitutes a major challenge confronting ecologists. Main (1982) asked ‘Are rare species precious or dross? And, are they vital to community function?’ Do rare species persist in more stable communities in spite of their rareness, or does the presence of rare species enhance the stability of ecosystems? Main (1982) suggested that one reason so many rare species exist may be that ecosystems have been ‘over-written many times after imperfect erasures’ (incomplete extinctions). Consequently, current ecosystems contain numerous relicts of their predecessors assembled under different ecological conditions. Main suggested that rare species could be vital to long-term ecosystem sustainability, providing ‘insurance’ for the delivery of ecosystem functions by alternative means in the event of drastic environmental changes. Main’s hypotheses could well be of great importance in these times of rapid climatic change.

Most species of Australian desert lizards are uncommon, making them difficult to study. Some are extremely rare to the point of vanishing rareness (Pianka 2011). Regardless of how rareness is defined, most ecologists concur that the majority of species are indeed uncommon (Gaston 1994; Kunin & Gaston 1997). Magurran and Henderson (2003) distinguished between relatively abundant ‘core species’ and uncommon ‘occasional species’. Chronic rarity

has proven to be exceedingly difficult to study, but, as mentioned above, rare species could well be very important to community function (Preston 1948, 1962; Main 1982; Morton & James 1988; Kunin & Gaston 1997; Thompson *et al.* 2003).

Several hypotheses, not all of which can be tested here, for the continued existence of rare species spring to mind:

- H 1. Body size-trophic level hypothesis.** Larger species are uncommon either because they are top predators (monitor lizards) or for other reasons.
- H 2. Fecundity hypothesis.** Some species could be uncommon because of their low fecundity.
- H 3. Geographic range hypothesis.** Rare species could have narrow geographic ranges, occurring at only a few sites (Rabinowitz *et al.* 1986).
- H 4. Niche breadth hypothesis.** Rare species are uncommon because they are specialized with narrow niche requirements. Resources such as habitats, microhabitats, or foods might be scarce or limited. These alternatives can be tested with data on niche breadths (below).
- H 5. Diffuse competition hypothesis.** Rare species could be uncommon because of diffuse competition from many other, more abundant, species (MacArthur 1969, 1970, 1972a,b).
- H 6. Physical tolerance hypothesis.** Rare species might have narrow tolerances to physical environments.
- H 7. Sink *versus* source population hypothesis.** Rare species might be uncommon only locally in ‘sink’ populations, but might be more abundant in nearby ‘source’ areas.

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H 8. Dispersal hypothesis. Rare species could be rare because they do not have dispersal powers necessary to find and invade suitable habitats. Are rare species merely accidentals, dispersing from one habitat to another?

H 9. Predation hypothesis. Predators could hold population densities of uncommon prey species at low levels.

Some related questions that can be asked about rare species include:

How can rare species find mates and continue to exist?

Is rarity an illusion because of cryptic behaviour making putative rare species difficult to find?

Merely being in an alien habitat is not necessarily a death sentence, as these habitats offer shelter and food – a migrant that succeeds in reaching its correct habitat could also reap the benefits of sweepstakes reproductive success. Which of these factor(s) is/are crucial determinants of commonness or rarity needs to be determined for each species.

METHODS

Field collections

In the past few decades, ecology has gradually changed with greater emphasis now being placed on conservation biology, rare species, and phylogenetically corrected analyses of evolution using modern comparative methods. Whereas data collected before 1979 were intended for studying niche partitioning and community structure, data collected since 1989 using pit traps were designed to study rare species, fire succession, long-term change, habitat and microhabitat requirements, adaptive radiations, and phylogenetic constraints. New data thus complement older data but are qualitatively different than those collected earlier.

On 11 separate research expeditions from 1966 to 2008, 41 months and 1256 days were spent in the field (Pianka 1969a,b, 1982, 1986, 1994, 1996; Pianka & Goodyear 2012). Extensive data were gathered at ten major study sites in the Great Victoria Desert of Western Australia (for exact locations, see Pianka 1986 and Pianka & Goodyear 2012). Lizards were collected by any means possible using a wide variety of different techniques including exhuming, grabbing, noosing, shooting, tracking, whomping (smashing a spinifex tussock with a shovel), locating lizards at night by eyeshine and/or body shine, and by pit trapping.

Early on (1966–1968, 1978–1979), lizards were hunted and captured during their normal daily course of activity, providing data on time of activity, microhabitat, ambient air temperature, and active body temperature. Data acquired up until 1979 were summarized with totals and means as appendices in Pianka (1986). These data suffered, however, from collector bias and do not provide very reliable estimates of relative abundance.

I changed my research protocol in 1989, since then all lizards have been pit trapped with drift fences between traps.

Trappability varies from species to species: slow moving species, especially agamids like bearded dragons and thorny devils, often walk around pits whereas most skinks run rapidly down drift fences and readily fall into pit traps. Fossorial *Lerista bipes* are exceptionally prone to fall into pit traps. Arboreal species are less likely to be trapped than terrestrial species. Nevertheless, pit trapping provides a standardized collecting method that allows relative abundances to be compared across space and time. This technique also allows informative estimates of point diversity, which can be exploited to infer habitat requirements.

To maximize sample sizes, I combine all data here and classify species into three broad natural abundance categories: common, rare, and species of intermediate abundance (see Fig. 1). A species was considered common if more than 500 individuals were captured over the course of my surveys, rare if 100 or fewer were caught, and intermediate if from 100 to 500 were collected.

Niche breadths were computed for each species based on proportional representation of each resource category using the inverse of Simpson's (1949) index of diversity, $1/\sum p_i^2$ where p_i is the proportion in a given category i . Standard multivariate statistical methods including principal component analysis (PCA) and discriminant function analysis were employed.

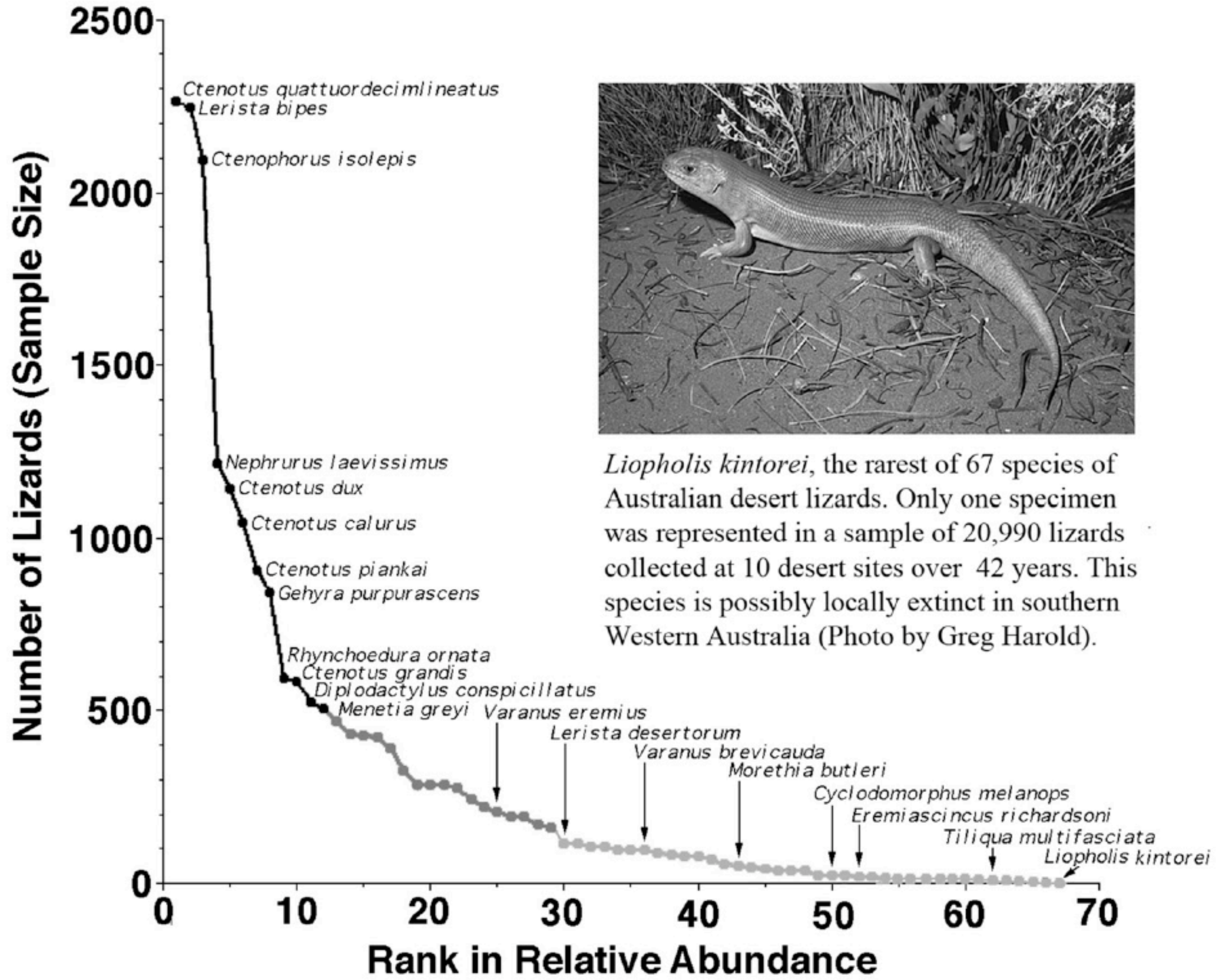
RESULTS

Over the last 42 years, I have witnessed metapopulation-like local extinctions and colonization in a few species. I have captured migrants of a number of species (*Ctenophorus fordi*, *Ctenophorus scutulatus*, *Ctenopus greeri*, *Ctenopus leae*, *Ctenopus leonhardii*, *Lophognathus longirostris*, *Nephruroides vertebralis*, and *Tiliqua occipitalis*) dispersing through habitats that they do not normally occupy. Until recently, inadequate sample sizes have prevented me from doing much with uncommon species, but I have now finally managed to acquire large enough samples to attempt to understand the ecologies of most of them – no one else has ever managed to collect such large samples of uncommon Australian desert lizards.

One species, the Great Desert Skink *Liopholis* (formerly *Egernia*) *kintorei* merits special comment. One juvenile specimen of this very rare nocturnal lizard was collected on my L-area in 1967. This represents the southernmost known locality for the species and its identity has been confirmed by experts. Despite considerable effort, no others were found either at the L-area or on any other study area. This singleton may have been among the last of its kind, now considered endangered in Western Australia and possibly on its way to local extinction (Pearson *et al.* 2001).

Dates, numbers of sites visited, numbers of species and total numbers of individuals collected on study sites over different time intervals are summarized in Table 1.

The total number of lizards of 67 species collected on 10 desert study sites are plotted against their rank



Liopholis kintorei, the rarest of 67 species of Australian desert lizards. Only one specimen was represented in a sample of 20,990 lizards collected at 10 desert sites over 42 years. This species is possibly locally extinct in southern Western Australia (Photo by Greg Harold).

Fig. 1. Total number of lizards of 67 species (20 990 individuals) collected on 10 desert study sites from 1966 to 2008 plotted against their rank in relative abundance. Abundant species are shown in black, rare species in light grey, and those of intermediate abundance in darker grey. These same shade codes are used in following graphs.

Table 1. Numbers of species and individuals captured at 10 study areas over different time intervals

| Sites | Year | No. of sites | No. species | No. individuals |
|------------------------|-----------|--------------|-------------|-----------------|
| A, D, E, G, L, M, N, Y | 1966–1968 | 8 | 15–39 | 2 845 |
| L, R | 1978–1979 | 2 | 32–42 | 3 002 |
| L, R | 1989–1991 | 2 | 34–43 | 4 436 |
| B, L, R | 1992 | 3 | 28–33 | 1 489 |
| B, R | 1995–1996 | 2 | 20–43 | 2 836 |
| B, R | 1998 | 2 | 36–37 | 2 143 |
| B, R | 2003 | 2 | 33–38 | 1 435 |
| B, R | 2008 | 2 | 38–40 | 1 136 |
| Totals | 1966–2008 | 10 | 15–55 | 19 322 |

in relative abundance in Figure 1. Species fall into three natural groups. On the leftmost ascending limb, the 12 most common species shown in black are named. The next group includes 17 species with intermediate abundances shown in grey. The rightmost

long tail includes 38 less common rare species (light grey), seven of which are identified by name. These same shade codes are used in following graphs. Of 67 Australian species studied, samples now exceed 30 for 48 species.

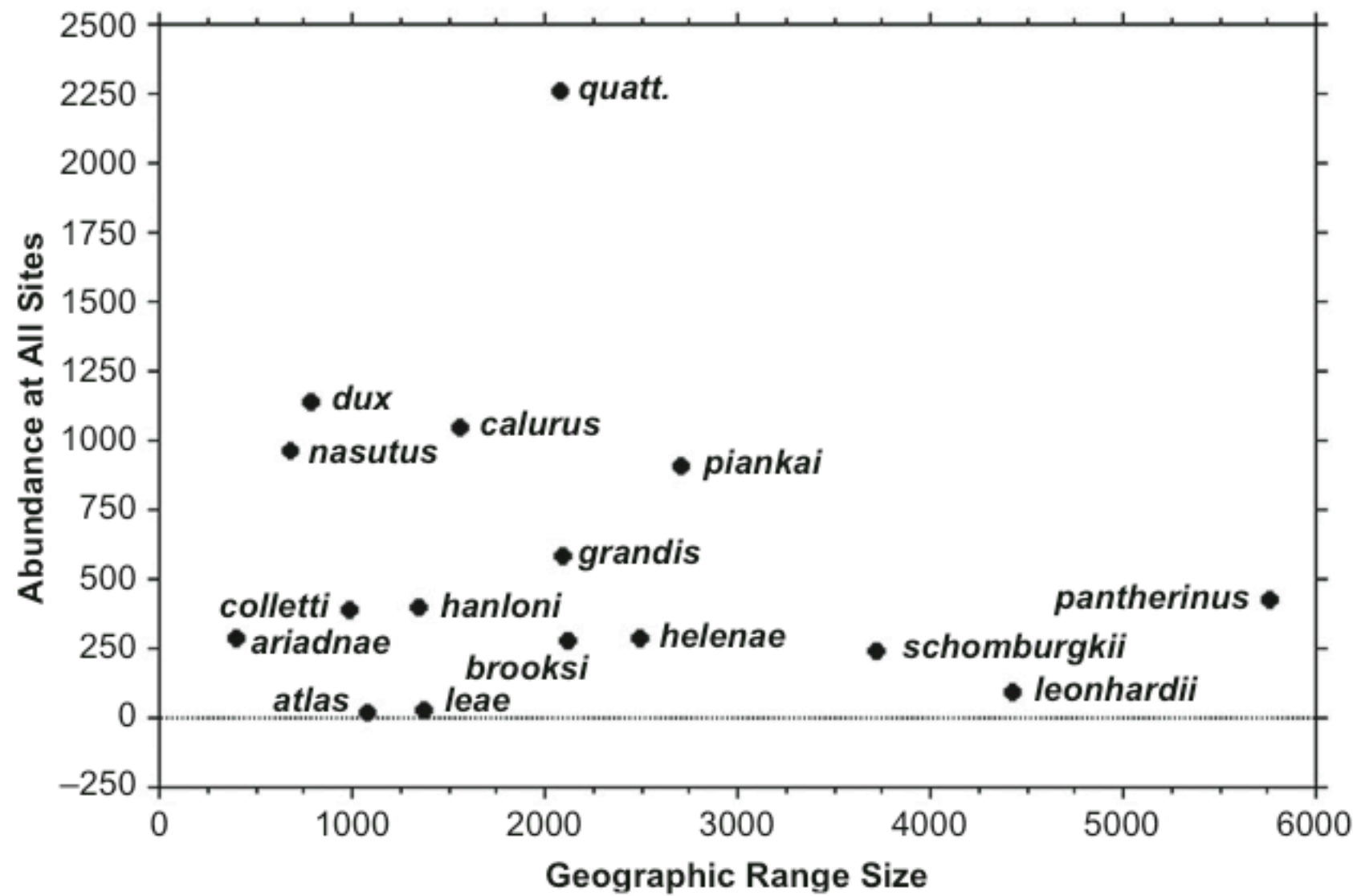


Fig. 2. Abundances of 15 species of *Ctenotus* skinks plotted against the size of their geographic ranges.

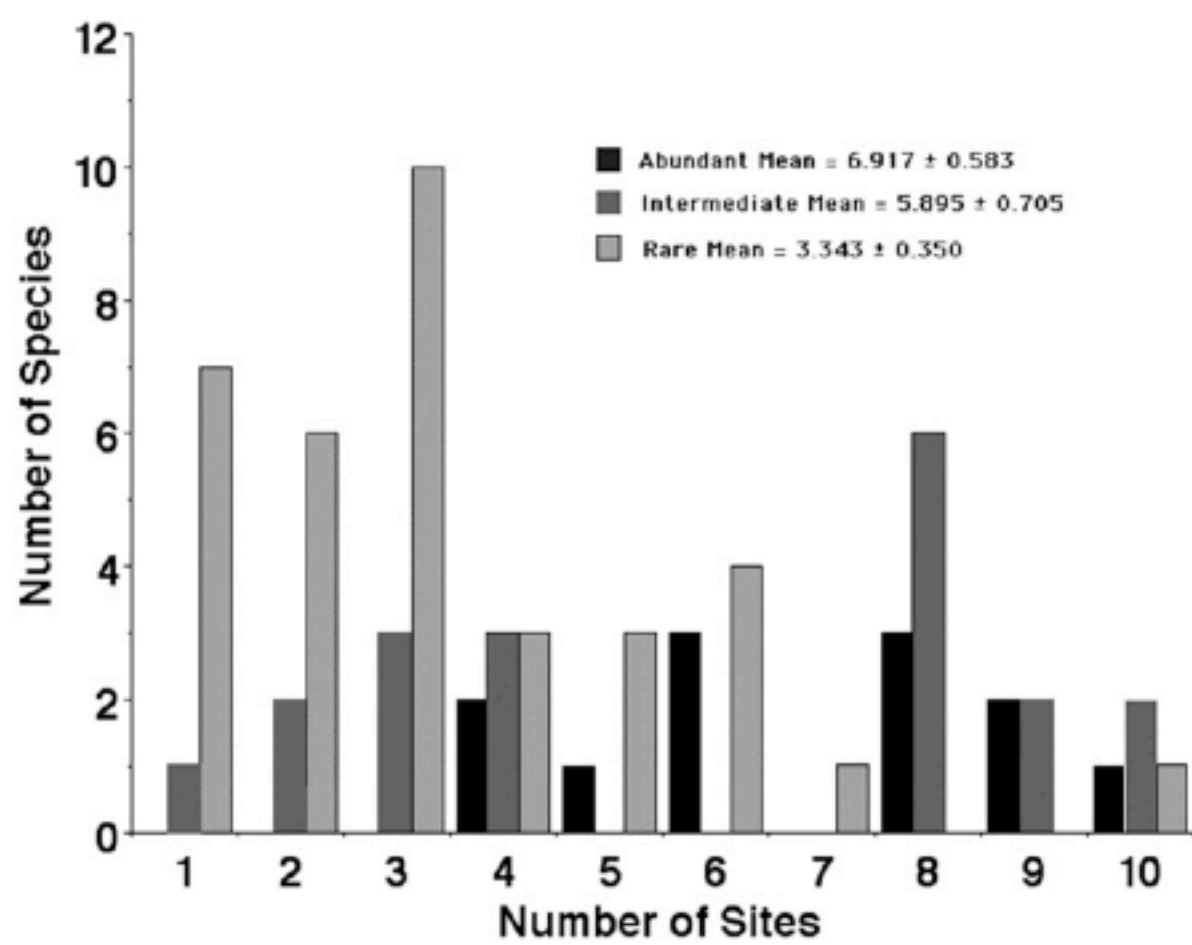


Fig. 3. Histograms showing the number of abundant species (black), species of intermediate abundance (grey), and rare species (light grey) found at 10 different study sites in the Great Victoria Desert.

Geographic ranges versus abundances

To test the geographic range hypothesis, abundances of *Ctenotus* skinks are plotted against the size of their ranges in Figure 2. Widespread species like *C. pantherinus* are not necessarily common, but species with narrower ranges such as *Ctenotus quattuordecimlineatus* can be much more abundant locally. Hence, the geographic range hypothesis H 3 (above) is not supported.

Rare species tend to be found on fewer sites, but one rare species is found on all 10 study areas (Fig. 3). Species of intermediate abundance are distributed bimodally, with some occurring at only a few sites but

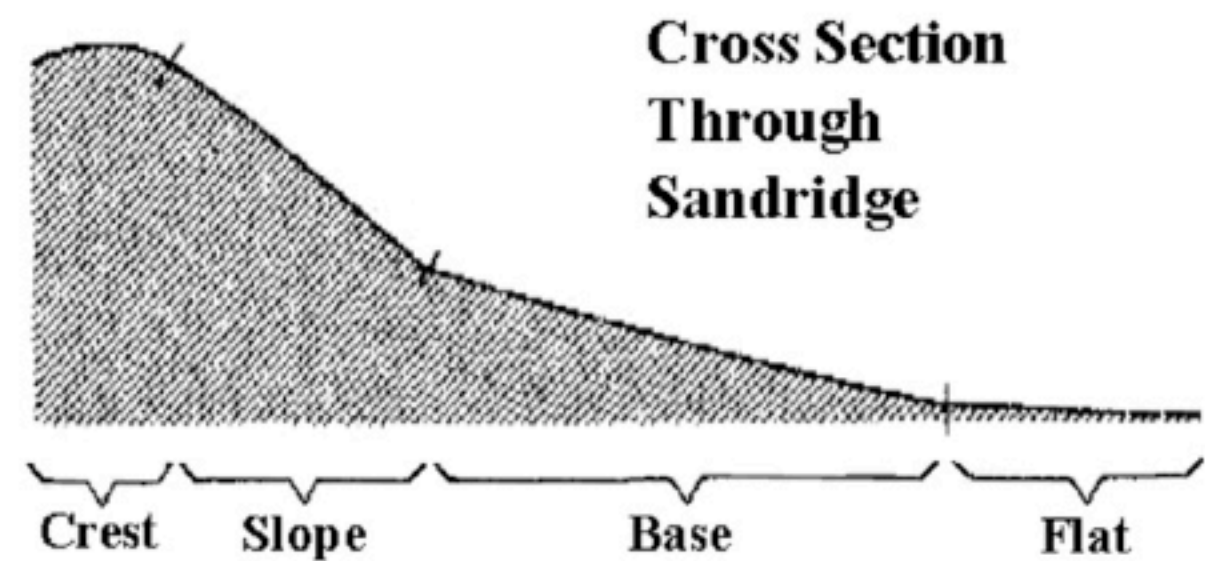


Fig. 4. Australian desert lizards occur at four different habitat types in sandridge deserts: crest, slope, base, and flat (shown in above figure). Some species are largely restricted to one of these habitats, but other species display more generalized habitat requirements.

others are present on most sites. Abundant species are also bimodally distributed and occur at a greater number of sites on average. These data also do not support the geographic range hypothesis H 3 (above).

Niche breadth hypothesis

Habitat niche breadths (Figs 4,5), which range from 1 to 4, were computed for each species based on proportional representation in each of the four habitats using the inverse of Simpson's index of diversity, $1/\sum p_i^2$ where p_i is the proportion of lizards found in habitat i .

Many rare species are habitat specialists, as are some intermediate and a few abundant species (Fig. 5). Habitat niche breadths are broadest in abundant species and those of intermediate abundance, although six rare species also have relatively broad habitat

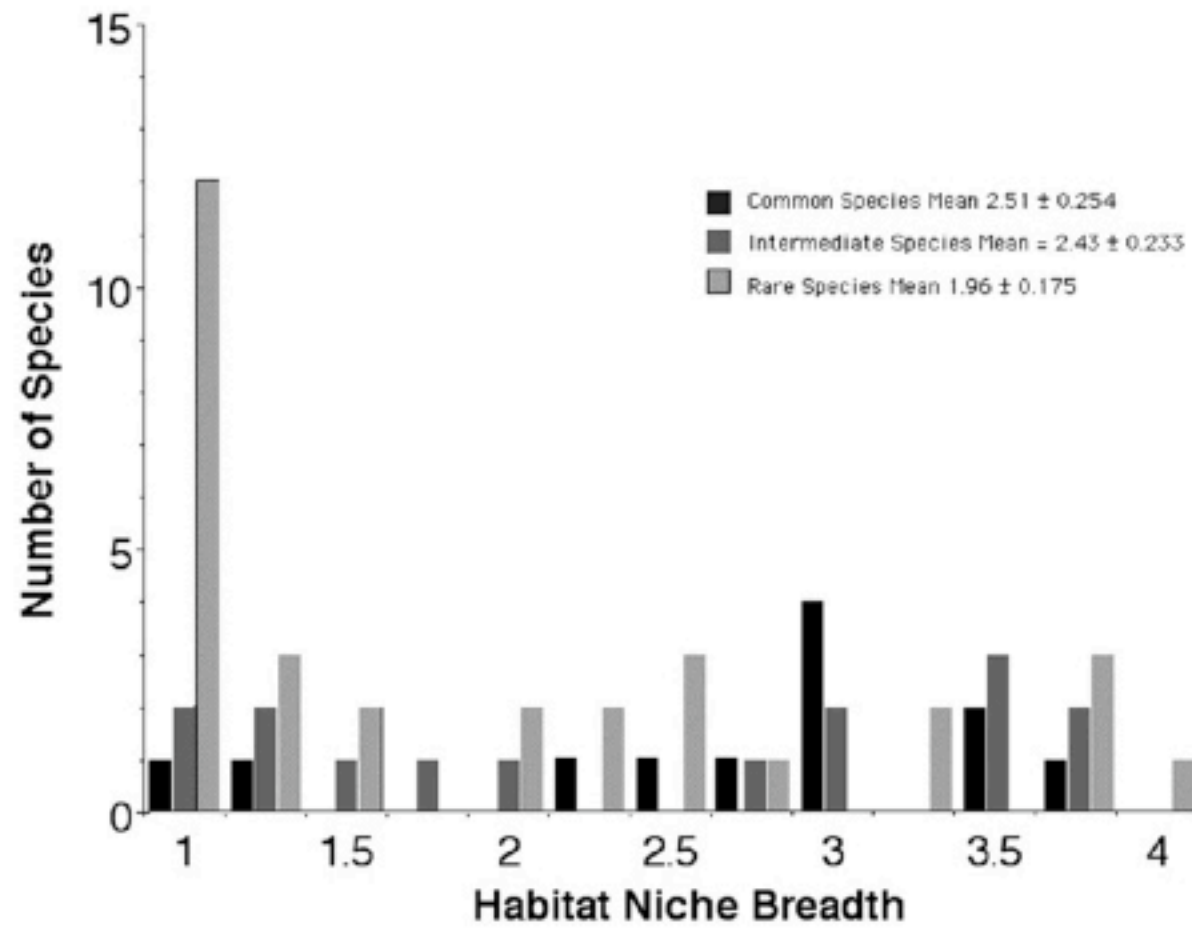


Fig. 5. Histograms of habitat niche breadths of abundant species (black), species of intermediate abundance (grey), and rare species (light grey).

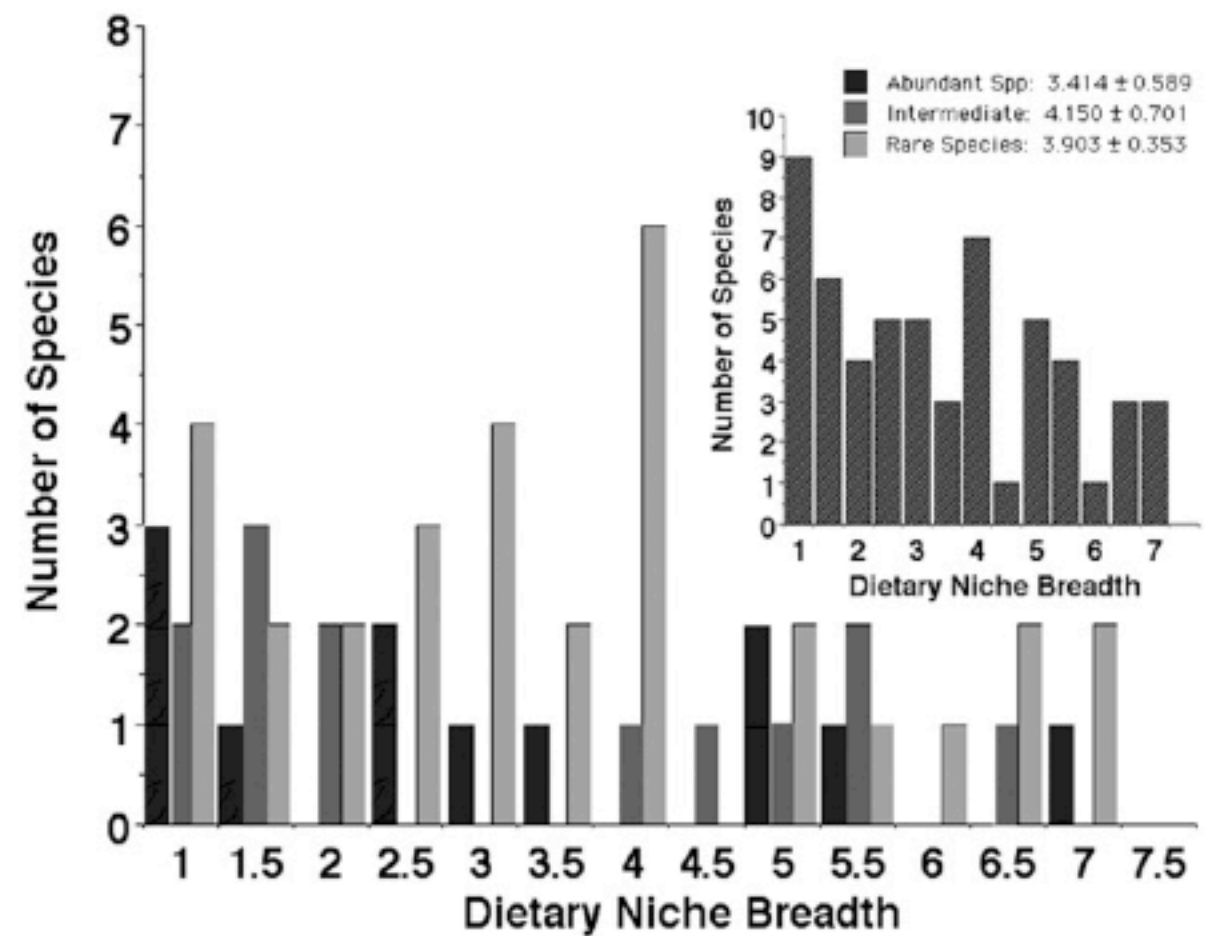


Fig. 7. Histograms of dietary niche breadths for abundant species (black), species of intermediate abundance (grey), and rare species (light grey). The frequency distribution for all species is shown in the inset.

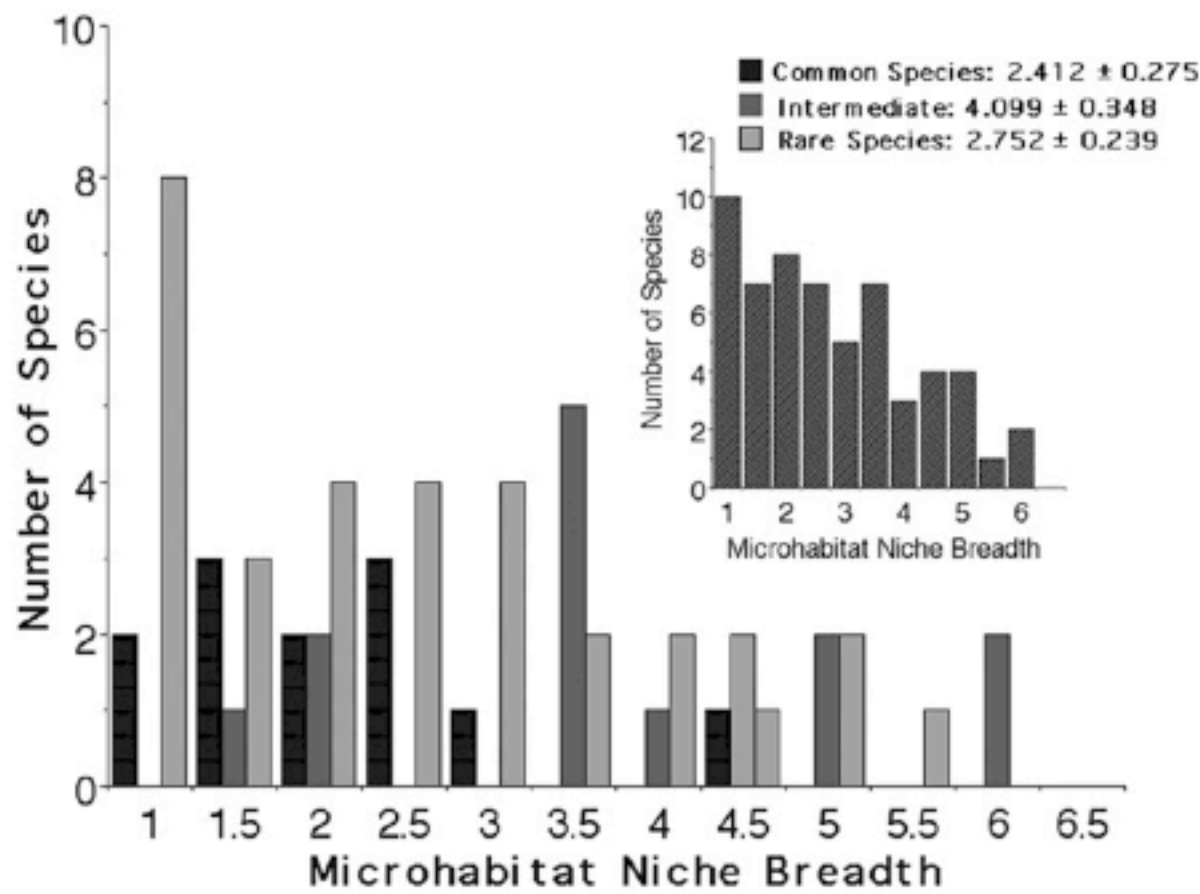


Fig. 6. Histograms of microhabitat niche breadths for abundant species (black), species of intermediate abundance (grey), and rare species (light grey). Inset shows the frequency distribution for all species.

niches. In all three abundance categories, species exhibit the full range of habitat niche breadths. The niche breadth hypothesis (H 4 above) is not strongly supported by these data on habitat niche breadths.

Each lizard was assigned to one of 15 different microhabitat resource categories. Microhabitat niche breadths were computed using the inverse of Simpson's index of diversity. Most abundant species and many rare species are microhabitat specialists, as are a few species of intermediate abundance (Fig. 6). Surprisingly, microhabitat niche breadths are actually narrowest in the most abundant species. Many species of intermediate abundance exhibit broad microhabitat niches. A few rare species are actually microhabitat generalists. Hence, again, the niche breadth hypothesis (H 4 above) seems to be refuted by these data on microhabitat niche breadths.

To estimate dietary niche breadth, 20 prey categories were recognized, corresponding mostly to arthropod orders plus categories for plant and vertebrate food items. Simpson's index was again used to estimate dietary niche breadths. Species in all three abundance categories exhibit a wide range of food niche breadths (Fig. 7). As with microhabitat niche breadths, dietary niche breadths on average are narrowest in abundant species and broadest in species of intermediate abundance. Abundant species and those of intermediate abundance have bimodal distributions, with some relatively specialized species and others with broader diets. Rare species are distributed more uniformly, with a complete range of food niche breadths. Hence, once again, the niche breadth hypothesis H 4 is not supported by these data on dietary niche breadths.

Microhabitat niche breadths are weakly positively correlated with dietary niche breadths in all three abundance categories, although a great deal of scatter exists (Fig. 8). In all three abundance categories, some species are both dietary and microhabitat specialists. Several species of intermediate abundance exhibit narrow diets but relatively broad microhabitat niche breadths, whereas others, including several rare species, have broad niches on both dimensions.

Diffuse competition: abundance versus dietary overlap

To attempt to test the diffuse competition hypothesis (H 5), the logarithm of abundance is plotted against the average total dietary overlap with all other species in Figure 9. The correlation goes against the prediction

with higher overlaps among more abundant species. However, many rare species do exhibit higher than average overlaps with other species.

Multivariate analyses

In Table 2, abundances and values of each of nine variates are listed for each of the 12 most abundant species, along with averages for all abundant species plus those for all species. Values that deviate above or below predicted values are highlighted in bold. As expected, all the abundant species are small and all but a couple are widespread, occurring on most sites. Also, as expected, most tend to have broad niches although some are specialists.

Table 3 gives abundances and values of each of nine variates for each of the 18 species of intermediate

abundance, along with averages for all intermediate species plus those for all species. Again, values that deviate from expected are highlighted in bold.

Table 4 lists abundances and values of each of nine variates for each of 33 rare species, along with averages for all species. Values that deviate as expected for rare species are highlighted in bold. Eight rare species are large. Most, but not all, are found at few sites. Eleven experience high dietary overlap, hence presumed diffuse competition. Many rare species have narrow niche breadths. Each and every rare species displays at least one value expected to be associated with rarity. Many exhibit several values as predicted.

Table 5 summarizes correlations and partial correlations among variates and with the logarithm of abundance. The three strongest correlations (shown in bold) are with the number of sites, dietary overlap, and habitat niche breadth. Results of stepwise multiple regression with the logarithm of abundance as the dependent variable are given below the table. These three variables reduce the variance in the logarithm of abundance by 59.8%.

The first two principal components of a PCA based on the same nine variates capture 46.3% of the variance (Fig. 10). Rare species tend to be separated from common species and those of intermediate abundance. Adding PC3 and PC4 (not shown) reduces residual variance by a further 26.9%, for a total of 73.2%.

A discriminant function analysis based on the same nine variables clearly separates the 12 abundant species from the less common species. Some overlap occurs between rare species and those of intermediate abundance (Fig. 11), but species in these two abundance categories display some separation.

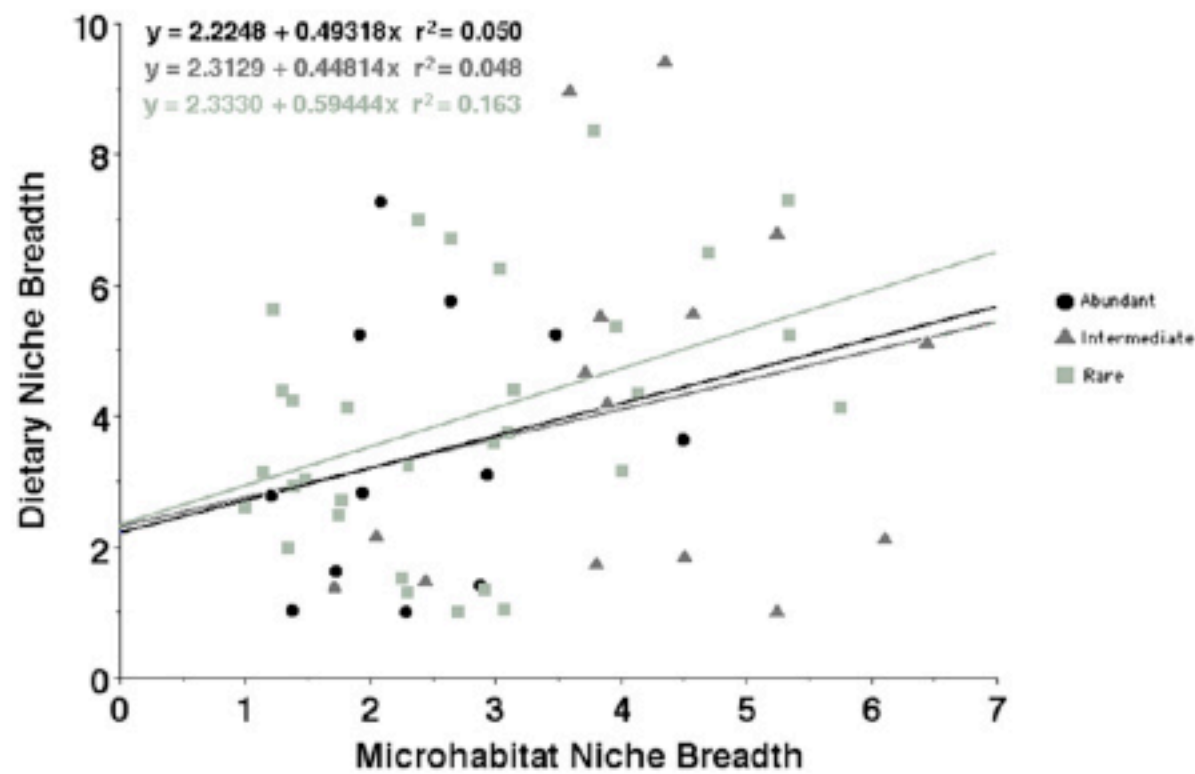


Fig. 8. Dietary niche breadths plotted against microhabitat niche breadths.

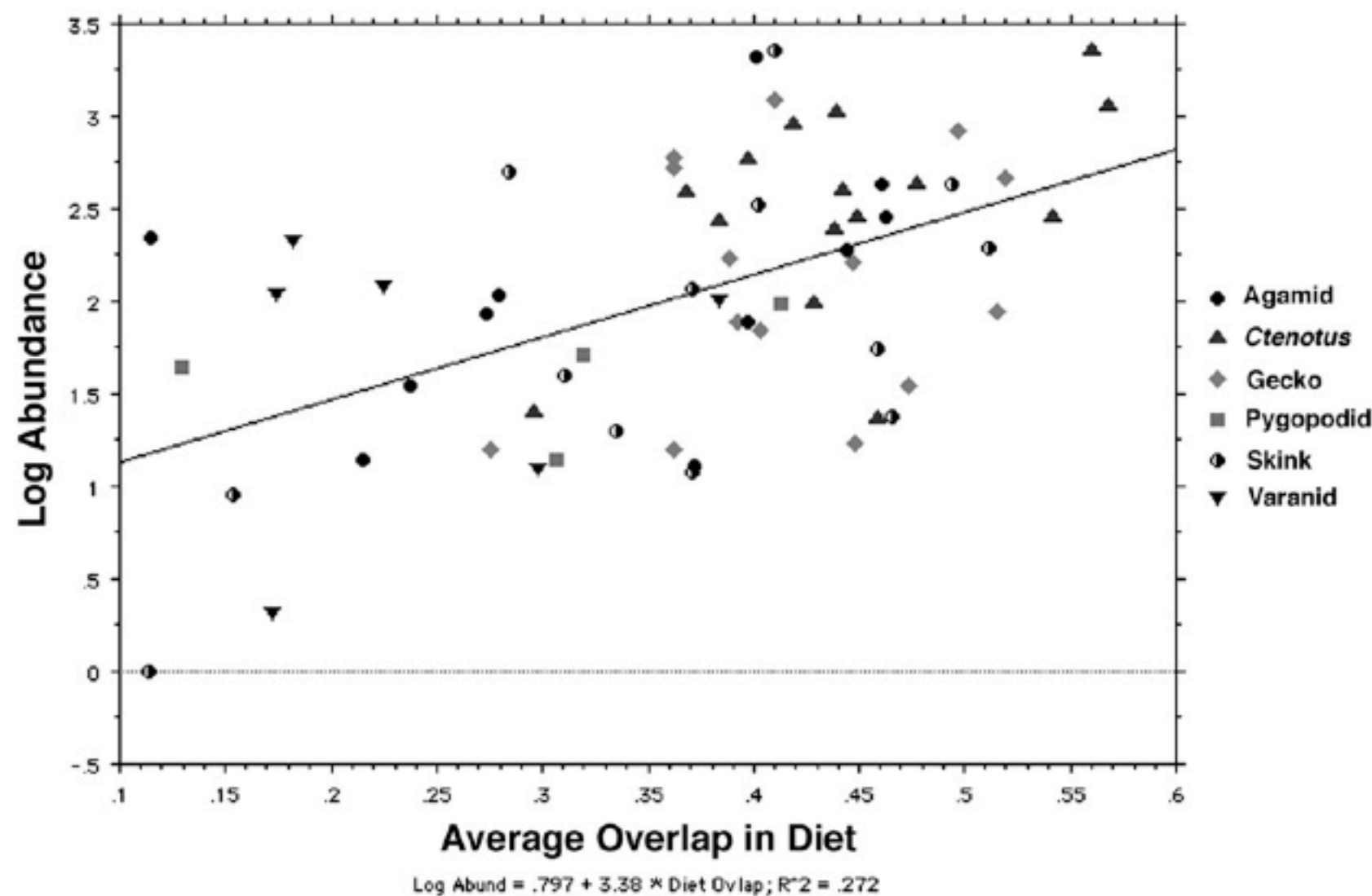


Fig. 9. Log Abundance plotted against average total dietary overlap with all other species.

Table 2. Values of each of nine variates listed for each of the 12 most abundant species, along with averages for all abundant species plus those for all species

| Abundant species | Log abundance | Snout–vent length | Number of sites | Average dietary overlap | Ave. microhabitat overlap | Average habitat overlap | Average fecundity | Habitat niche breadth | Microhabitat niche breadth | Dietary niche breadth |
|-------------------------------------|---------------|-------------------|-----------------|-------------------------|---------------------------|-------------------------|-------------------|-----------------------|----------------------------|-----------------------|
| <i>Ctenotus quatt.</i> | 3.355 | 54.17 | 6 | 0.560 | 0.468 | 0.725 | 3.6 | 3.57 | 1.93 | 2.85 |
| <i>Lerista bipes</i> | 3.352 | 47.62 | 5 | 0.410 | 0.045 | 0.496 | 2 | 2.82 | 1.22 | 2.79 |
| <i>Ctenophorus isolepis</i> | 3.322 | 50.25 | 9 | 0.401 | 0.399 | 0.723 | 3 | 2.28 | 2.93 | 3.11 |
| <i>Nephrurus laevissimus</i> | 3.084 | 67.68 | 3 | 0.410 | 0.492 | 0.482 | 1.96 | 2.51 | 2.08 | 7.29 |
| <i>Ctenotus dux</i> | 3.058 | 56.39 | 4 | 0.568 | 0.475 | 0.632 | 2.6 | 3.80 | 3.48 | 5.30 |
| <i>Ctenotus calurus</i> | 3.020 | 41.93 | 8 | 0.439 | 0.435 | 0.646 | 1.84 | 1.16 | 2.87 | 1.44 |
| <i>Ctenotus piankai</i> | 2.957 | 44.68 | 6 | 0.419 | 0.466 | 0.726 | 2.56 | 2.91 | 1.91 | 5.61 |
| <i>Gehyra variegata</i> | 2.925 | 54.12 | 9 | 0.497 | 0.182 | 0.780 | 1 | 2.50 | 2.64 | 5.76 |
| <i>Rhynchoedura ornata</i> | 2.775 | 49.73 | 10 | 0.362 | 0.316 | 0.776 | 1.97 | 2.88 | 1.38 | 1.03 |
| <i>Ctenotus grandis</i> | 2.767 | 65.60 | 8 | 0.397 | 0.450 | 0.636 | 4 | 1.07 | 1.72 | 1.61 |
| <i>Diplodactylus conspicillatus</i> | 2.721 | 58.87 | 8 | 0.362 | 0.387 | 0.574 | 2 | 2.72 | 2.28 | 1.01 |
| <i>Menetia greyi</i> | 2.703 | 25.84 | 6 | 0.284 | 0.417 | 0.633 | 1.54 | 2.92 | 4.50 | 3.64 |
| Average (Abundant) | 3.003 | 51.41 | 6.8 | 0.426 | 0.378 | 0.653 | 2.34 | 2.60 | 2.41 | 3.45 |
| Average (All species) | 2.055 | 78.00 | 4.9 | 0.372 | 0.366 | 0.627 | 3.12 | 2.21 | 2.91 | 4.16 |

DISCUSSION

While some species may be rare because of narrow niche requirements, other specialized species are abundant. No general explanation for rarity may exist, but rather each species appears to have its own idiosyncratic reasons for being uncommon. Many of the possible factors that could contribute to rarity remain to be evaluated, and the difficulty of studying uncommon species remains a formidable challenge to ecologists.

Returning to Main's question 'How important are rare species to the function and stability of communities?' Foregoing analyses are overly simplistic in that they assume abundances and niche breadths remain fixed in time, but of course, they must vary. These lizard populations can be viewed more realistically using a metaphor: their relative abundances are analogous to three-dimensional waves in as many dimensions as there are species: the vertical coordinate represents the abundances of each of the various species moving up and down and around in space and time. At any given time, some species are abundant while others may be scarce. These abundance surfaces are relatively placid for some species, but very rough for others. Some species like *Ctenophorus clayi* and *Ctenophorus nuchalis* boom and bust, exhibiting intermittent rarity, whereas others like *Cyclodomorphus*, *Eremiascincus*, and *Tiliqua*, are always uncommon (chronic rarity). Still other common species, like *Ctenophorus isolepis*, exhibit more stable populations.

These waves of relative abundance respond to fire and episodic precipitation events (see Pianka & Goodyear 2012) both of which drive changes in resource availabilities of prey and microhabitats through time and space. One of my long-term goals is to attempt to model this multidimensional spatial-temporal wave-like landscape.

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Table 3. Values of each of nine variates for each of the 18 species of intermediate abundance, along with averages for all intermediate species plus those for all species

| Species of intermediate abundance | Log abundance | Snout-vent length | Number of sites | Average dietary overlap | Ave. microhabitat overlap | Average habitat overlap | Average fecundity | Habitat niche breadth | Microhabitat niche breadth | Dietary niche breadth |
|-----------------------------------|---------------|-------------------|-----------------|-------------------------|---------------------------|-------------------------|-------------------|-----------------------|----------------------------|-----------------------|
| <i>Gehyra purpurascens</i> | 2.670 | 52.41 | 9 | 0.519 | 0.182 | 0.780 | 1 | 3.49 | 2.64 | 5.76 |
| <i>Ctenophorus nuchalis</i> | 2.634 | 73.99 | 10 | 0.460 | 0.415 | 0.762 | 4.1 | 3.22 | 5.24 | 6.84 |
| <i>Egernia striata</i> | 2.631 | 89.41 | 8 | 0.494 | 0.478 | 0.683 | 2.7 | 1.69 | 6.1 | 2.11 |
| <i>Ctenotus pantherinus</i> | 2.628 | 68.94 | 10 | 0.477 | 0.411 | 0.661 | 5.8 | 1.29 | 1.71 | 1.42 |
| <i>Ctenotus hanloni</i> | 2.598 | 59.66 | 3 | 0.442 | | 0.632 | 4 | 1.5 | 1.8 | 7.42 |
| <i>Ctenotus colletti</i> | 2.593 | 40.59 | 2 | 0.368 | 0.505 | 0.560 | 4 | 3.46 | 3.89 | 5.02 |
| <i>Egernia inornata</i> | 2.517 | 71.60 | 7 | 0.402 | 0.510 | 0.524 | 2.1 | 3.1 | 6.44 | 5.16 |
| <i>Ctenotus ariadnae</i> | 2.458 | 51.40 | 3 | 0.542 | 0.483 | 0.655 | 3.33 | 1.21 | 2.44 | 1.80 |
| <i>Ctenophorus clayi</i> | 2.456 | 43.90 | 3 | 0.462 | 0.469 | 0.709 | 1.9 | 3.74 | 3.71 | 4.70 |
| <i>Ctenotus helenae</i> | 2.455 | 75.83 | 8 | 0.449 | 0.416 | 0.726 | 4 | 2.1 | 2.05 | 2.19 |
| <i>Ctenotus brooksi</i> | 2.438 | 41.41 | 2 | 0.384 | 0.379 | 0.386 | 1.83 | 1.47 | 3.59 | 8.97 |
| <i>Ctenotus schomburgkii</i> | 2.384 | 42.52 | 7 | 0.438 | 0.502 | 0.715 | 2.3 | 1.95 | 4.51 | 1.85 |
| <i>Moloch horridus</i> | 2.346 | 87.90 | 8 | 0.115 | 0.480 | 0.597 | 6.8 | 3.37 | 5.24 | 1.02 |
| <i>Varanus eremius</i> | 2.312 | 131.60 | 9 | 0.182 | 0.501 | 0.772 | 3.68 | 2.68 | 3.8 | 1.76 |
| <i>Cryptoblepharus buchananii</i> | 2.286 | 39.69 | 3 | 0.512 | 0.147 | 0.627 | 2 | 1 | 4.36 | 9.43 |
| <i>Pogona minor</i> | 2.283 | 107.80 | 8 | 0.444 | 0.368 | 0.772 | 7.6 | 3.66 | 4.57 | 5.56 |
| <i>Diplodactylus ciliaris</i> | 2.228 | 73.56 | 4 | 0.389 | 0.273 | 0.535 | 2 | 2.89 | 3.84 | 5.55 |
| <i>Diplodactylus damaeus</i> | 2.207 | 51.89 | 4 | 0.447 | 0.390 | 0.512 | 2 | 2.49 | 1 | 2.62 |
| Average (Intermediate) | 2.451 | 66.89 | 6 | 0.418 | 0.406 | 0.645 | 3.39 | 2.46 | 3.72 | 4.40 |
| Average (All species) | 2.055 | 78.00 | 4.9 | 0.372 | 0.366 | 0.627 | 3.12 | 2.21 | 2.91 | 4.16 |

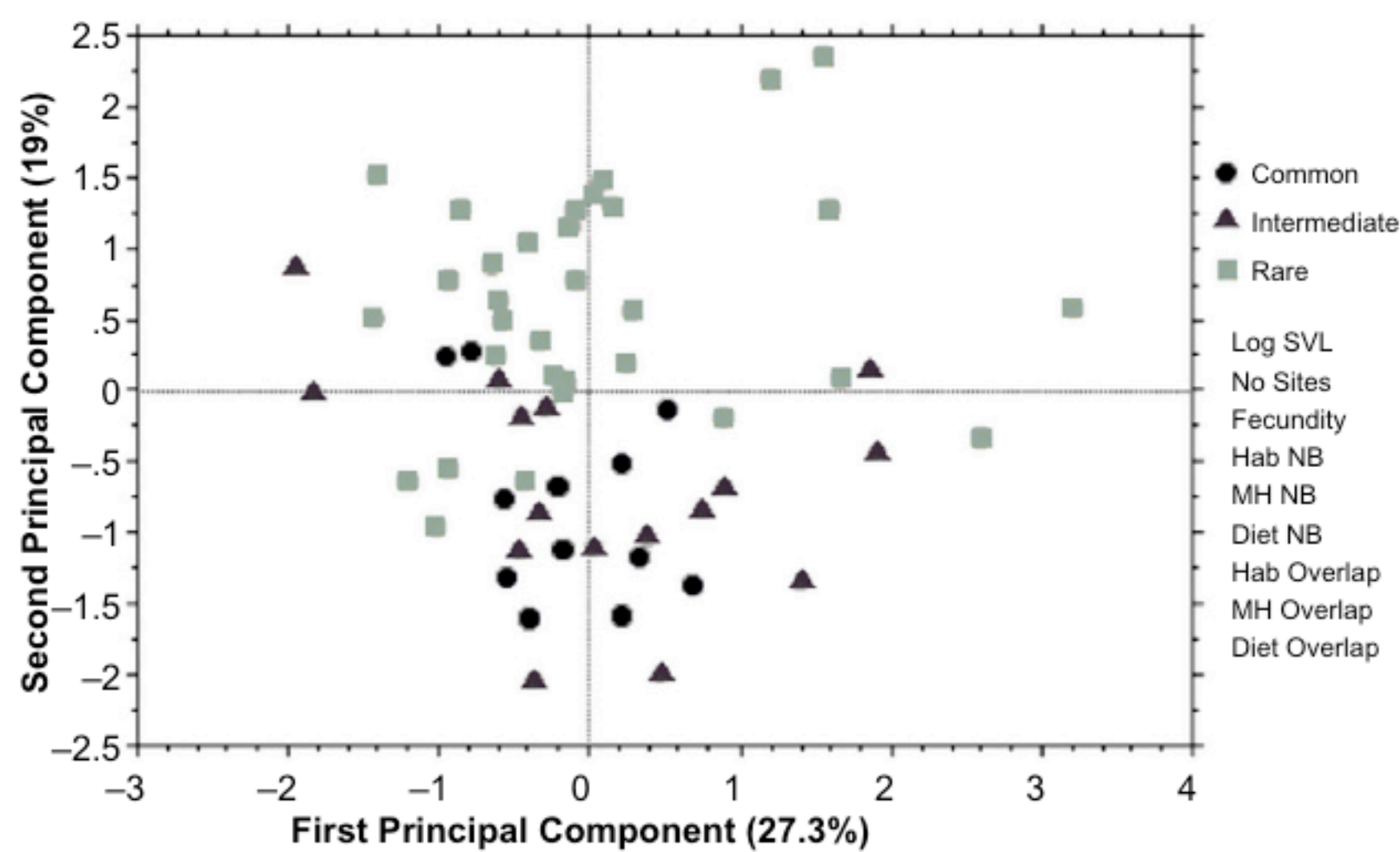


Fig. 10. The first two principal components of a principal component analysis based on the following nine variates: Log SVL, Number of Sites, Fecundity, Habitat Niche Breadth, Microhabitat Niche Breadth, Dietary Niche Breadth, Habitat Overlap, Microhabitat Overlap, and Dietary Overlap.

Table 4. Values of each of nine variates for each of 33 rare species, along with averages for all species

| Rare species | Log abundance | Snout-vent length | Number of sites | Average dietary overlap | Ave. microhabitat overlap | Average habitat overlap | Average fecundity | Habitat niche breadth | Microhabitat niche breadth | Dietary niche breadth |
|------------------------------------|---------------|-------------------|-----------------|-------------------------|---------------------------|-------------------------|-------------------|-----------------------|----------------------------|-----------------------|
| <i>Lerista desertorum</i> | 2.068 | 77.60 | 3 | 0.371 | 0.333 | 0.478 | 3 | 3.67 | 2.29 | 7.36 |
| <i>Varanus gouldii</i> | 2.064 | 247.58 | 10 | 0.225 | 0.337 | 0.739 | 6.2 | 3.67 | 1.75 | 2.49 |
| <i>Ctenophorus fordii</i> | 2.029 | 49.30 | 3* | 0.279 | 0.382 | 0.387 | 2.4 | 2.09 | 2.99 | 3.60 |
| <i>Varanus tristis</i> | 2.017 | 245.13 | 8 | 0.174 | 0.167 | 0.758 | 10.1 | 3.34 | 2.25 | 1.51 |
| <i>Delma butleri</i> | 1.991 | 67.90 | 5 | 0.413 | 0.411 | 0.676 | 2 | 1.37 | 1.14 | 4.26 |
| <i>Ctenotus leonhardii</i> | 1.987 | 89.30 | 4* | 0.428 | 0.496 | 0.635 | 5.6 | 1.22 | 5.34 | 5.24 |
| <i>Varanus brevicauda</i> | 1.987 | 66.50 | 5 | 0.384 | 0.482 | 0.651 | 2.42 | 1.22 | 1.5 | 5.37 |
| <i>Diplodactylus elderi</i> | 1.944 | 43.75 | 6 | 0.515 | 0.413 | 0.515 | 2 | 2.28 | 1.3 | 4.39 |
| <i>Lophognathus longirostris</i> | 1.929 | 65.86 | 4* | 0.274 | 0.302 | 0.558 | 3.9 | 2.67 | 5.33 | 7.30 |
| <i>Nephrurus levis</i> | 1.892 | 78.64 | 3 | 0.392 | 0.461 | 0.627 | 2 | 1 | 2.64 | 6.73 |
| <i>Ctenophorus scutulatus</i> | 1.886 | 73.90 | 4* | 0.398 | 0.367 | 0.631 | 6.8 | 1.02 | 3.96 | 5.37 |
| <i>Diplodactylus strophurus</i> | 1.845 | 64.32 | 5 | 0.403 | 0.285 | 0.668 | 2 | 3.28 | 2.38 | 7.01 |
| <i>Morethia butleri</i> | 1.748 | 42.70 | 6 | 0.459 | 0.186 | 0.501 | 2 | 3.36 | 3.1 | 6.70 |
| <i>Pygopus nigriceps</i> | 1.708 | 160.00 | 6 | 0.319 | 0.410 | 0.673 | 2 | 3.36 | 1.47 | 3.94 |
| <i>Lialis burtonis</i> | 1.643 | 156.00 | 7 | 0.130 | 0.511 | 0.658 | 2 | 3.67 | 2.69 | 1.00 |
| <i>Lerista muelleri</i> | 1.602 | 39.38 | 3 | 0.311 | 0.060 | 0.645 | 1.9 | 1.5 | 1.22 | 5.63 |
| <i>Diporiphora winneckeii</i> | 1.544 | 45.40 | 2 | 0.237 | 0.301 | 0.377 | 2 | 1.38 | 4.7 | 6.52 |
| <i>Heteronotia binoei</i> | 1.544 | 44.14 | 8 | 0.473 | 0.389 | 0.647 | 2 | 1.19 | 3.78 | 8.37 |
| <i>Ctenotus leae</i> | 1.398 | 52.95 | 3* | 0.296 | 0.438 | 0.435 | 3 | 1.95 | 4.14 | 4.34 |
| <i>Cyclodomorphus melanops</i> | 1.380 | 85.10 | 3 | 0.465 | 0.416 | 0.635 | 3 | 2.33 | 1.38 | 4.98 |
| <i>Ctenotus atlas</i> | 1.362 | 62.11 | 1 | 0.459 | 0.413 | 0.645 | 1.5 | 1 | 1.77 | 2.71 |
| <i>Eremiascincus richardsoni</i> | 1.301 | 71.60 | 2 | 0.335 | 0.167 | 0.639 | 5 | 2.41 | 1.81 | 6.65 |
| <i>Diplodactylus stenodactylus</i> | 1.230 | 51.00 | 3 | 0.448 | 0.252 | 0.441 | 2 | 2 | 3.03 | 6.26 |
| <i>Diplodactylus pulcher</i> | 1.204 | 54.30 | 1 | 0.362 | 0.301 | 0.627 | 1.8 | 1 | 3.06 | 1.04 |
| <i>Nephrurus vertebralis</i> | 1.204 | 79.83 | 3* | 0.275 | 0.319 | 0.627 | 2 | 1 | 1.37 | 4.25 |
| <i>Ctenophorus reticulatus</i> | 1.146 | 72.30 | 1 | 0.215 | 0.489 | 0.627 | 4 | 1 | 5.75 | 4.14 |
| <i>Delma nasuta</i> | 1.146 | 86.90 | 2 | 0.307 | | 0.638 | 2 | 2.06 | 1.2 | 1.86 |
| <i>Caimanops amphiboluroides</i> | 1.114 | 71.15 | 1 | 0.372 | 0.265 | 0.627 | 3 | 1 | 2.29 | 1.31 |
| <i>Egernia depressa</i> | 1.079 | 111.10 | 1 | 0.371 | 0.157 | 0.645 | 2 | 1 | 2.91 | 1.35 |
| <i>Varanus caudolineatus</i> | 1.079 | 87.80 | 1 | 0.298 | 0.291 | 0.627 | 4.3 | 1 | 3.14 | 4.42 |
| <i>Tiliqua multifasciata</i> | 0.954 | 211.00 | 3 | 0.153 | 0.366 | 0.738 | 3 | 2.05 | 2.57 | 1.86 |
| <i>Varanus gilleni</i> | 0.301 | 186.00 | 1* | 0.172 | 0.283 | 0.627 | 4.3 | 1.5 | 1.34 | 2.00 |
| <i>Egernia kintorei</i> | 0.000 | 152.00 | 1 | 0.113 | 0.446 | 0.627 | 6 | 1 | 2 | 1.44 |
| Average (all species) | 2.055 | 78.00 | 4.9 | 0.372 | 0.366 | 0.627 | 3.12 | 2.21 | 2.91 | 4.16 |

Stars (asterisks) in Table 4 indicate species that are transients (dispersers) not residents on some sites, so numbers are over estimates.

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Table 5. Correlations and partial correlations among variates and with the logarithm of abundance among variates

| Correlation coefficients (above diagonal), partial correlations (below diagonal) | | | | | | | | | | |
|--|--------------|--------|--------------|-----------|--------------|--------|---------|-----------|----------|--------------|
| | Log Abund | LogSVL | No Sites | Fecundity | Hab NB | MH NB | Diet NB | Hab Ovlap | MH Ovlap | Diet Ovlap |
| Log Abund | | -0.430 | 0.611 | -0.132 | 0.441 | 0.096 | 0.047 | 0.154 | 0.189 | 0.515 |
| LogSVL | -0.418 | | 0.057 | 0.557 | 0.092 | -0.119 | -0.354 | 0.332 | 0.036 | -0.567 |
| No. Sites | 0.525 | 0.126 | | 0.153 | 0.431 | 0.055 | -0.195 | 0.509 | 0.136 | 0.168 |
| Fecundity | 0.112 | 0.429 | 0.025 | | 0.084 | 0.131 | -0.216 | 0.254 | 0.064 | -0.354 |
| Hab. NB | 0.413 | 0.264 | 0.130 | -0.070 | | 0.056 | 0.078 | 0.148 | 0.034 | 0.016 |
| MH NB | -0.005 | -0.196 | 0.088 | 0.223 | -0.017 | | 0.236 | -0.103 | 0.271 | -0.043 |
| Diet NB | -0.134 | -0.083 | -0.095 | -0.014 | 0.243 | 0.317 | | -0.316 | -0.193 | 0.319 |
| Hab Ovlap | -0.090 | 0.266 | 0.406 | 0.058 | -0.032 | -0.016 | -0.197 | | 0.055 | 0.068 |
| MH Ovlap | 0.184 | 0.143 | -0.056 | -0.057 | -0.063 | 0.334 | -0.243 | -0.044 | | 0.007 |
| Diet Ovlap | 0.347 | -0.278 | -0.065 | -0.094 | -0.190 | -0.194 | 0.341 | 0.291 | 0.054 | |

Stepwise multiple regression, with Log Abundance as the Dependent Variable: 1st: Number of Sites, r squared = 0.362; 2nd: Dietary Overlap, r squared = 0.532; 3rd: Habitat Niche Breadth, r squared = 0.598. The strongest correlations are with number of sites, habitat niche breadth, and dietary overlap. Results of stepwise multiple regression with the logarithm of abundance as the dependent variable are given below the table.

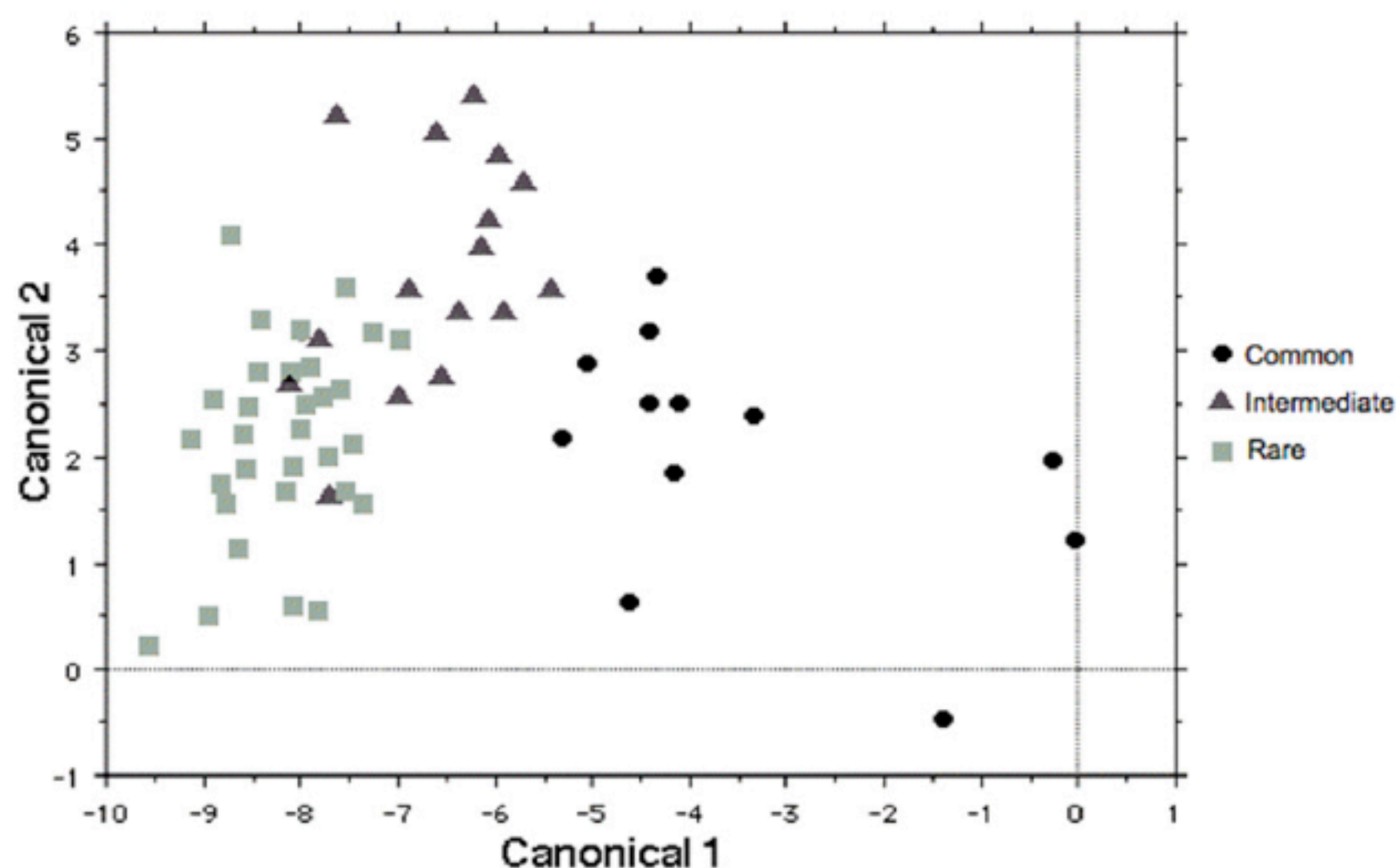


Fig. 11. Discriminant function analysis based on the same nine variables clearly separates the 12 abundant species from the less common species.

in Kalgoorlie, and the Western Australian Department of Environment and Conservation.

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