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Spatial and Temporal Variation in Diets of Sympatric Lizards (Genus *Ctenotus*) in the Great Victoria Desert, Western Australia

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ABSTRACT.—Studies of species coexistence within communities and food webs depend on knowing how species use varying resources. Diet has been asserted as a partitioned resource and an important proxy for measuring ecological similarity between species. Diet, like any aspect of an organism's ecology, varies over space and time, which may diminish the generality of conclusions made about how species interact. Few studies have examined diet variation across two or more dimensions, but here we evaluate diet variation over space and time for four lizard species within the genus *Ctenotus* (Scincidae). Samples were collected at three field sites in the Great Victoria Desert of Western Australia over the course of 16 years. Diet varies widely over both space and time. However, changes in diet over time overwhelm variation over space at the scale of our study. Despite diet variation within species, distinct differences exist between species in fundamental and realized dietary niche space. Limited overlap between species in dietary niche space implies fundamental ecological differences between species that may not be overturned by environmental variation.

Variation in species' use of dietary resources, both geographically and through time, adds to the complexities of community structure and species interactions. Consider even the most detailed food web that shows links between consumers and resources with proportions of interactions between links. Diet variation implies that moving that same food web model to a different location or tracking it through time results in, at least, changing the proportions of interactions between links and possibly deleting or adding links between species. A greater understanding of degree of diet variation observed in natural populations will enhance knowledge of the lability of food webs. Changes in food web dynamics are crucial to any consideration of stability and complexity as emergent properties of communities.

Variation of any population attribute can be studied within and among populations at different locations or over time. Studies of amphibians and reptiles have contributed a large proportion of what is known about diet variation. In a review of published studies on resource partitioning in amphibians, squamates, and turtles, Toft (1985) found food to be a partitioned resource in 36% ($N = 16$) of lizard studies and important to some degree in 94% ($N = 45$) of all studies. Only snakes partition food resources more finely than lizards. Habitat is the most partitioned resource in 53% ($N = 24$) of lizard studies. Here, we examine variation in use of dietary resources and consider how changes in diet impact generalities inferred about species resource use from isolated samples. Diet in amphibians, squamates, and fishes is relatively easier to obtain and more reliable than dietary data from other vertebrates. Ectotherms consume prey whole, or mostly whole, and lower energy requirements mean consumed prey items remain stored in stomachs for a longer time as compared to endotherms. We restrict our review of past diet studies to turtles, squamates, and amphibians but cite notable studies on other vertebrate groups.

In a spatial context, diet variation has been studied in lizards (How et al., 1986; Klawinski et al., 1994; Vitt and Colli, 1994; Vitt et al., 1998; Mesquita and Colli, 2003), snakes (Beaupre, 1995; de Queiroz et al., 2001; Bowen, 2004; Fillipi et al., 2005; Luiselli et al., 2007; Tuttle and Gregory, 2009; Weatherhead et al., 2009), a salamander (Zerba and Collins, 1992), and frogs (Siqueira et al., 2006; Bonansea and Vaira, 2007; Mahan and Johnson, 2007; Leavitt and Fitzgerald, 2009). Studies of diet change through time have been conducted for lizards (Christian et al., 1984; James, 1991; Hibbitts et al., 2005; Pianka and Goodyear, in press), snakes (Kephart and Arnold, 1982; Garcia and Drummond, 1988), a frog (Valderrama-Vernaza et

al., 2009); and the Loggerhead Sea Turtle, *Caretta caretta* (Seney and Musick, 2007). In some studies, diet variation over space and time was recorded concurrently in lizards (Pianka, 1970; Parker and Pianka, 1975; Vitt et al., 1981; Rodríguez et al., 2008) and angulate tortoises (Joshua et al., 2010).

Most studies consider either spatial or temporal dimensions in a single analysis. Population variation observed over two or more dimensions will add extensively to total variation observed between samples. The herpetological literature is lacking in such multidimensional analyses of diet variation. However, studies on fish in Venezuela (Winemiller, 1990) and France (Ferraton et al., 2007) are the most integrative investigations of diet variation over multiple dimensions and may set the groundwork for future herpetological studies on this subject. Winemiller (1990) demonstrated dynamic connectivity in freshwater fish food webs in Venezuela by studying fish diets during three intra-annual seasons. Winemiller (1990) found that food webs varied in content and connectivity between dry and wet seasons as well as among study sites. Ferraton et al. (2007) found great dietary shifts over a year at seven sampling locations in the fish, *Merluccius merluccius*, in the Gulf of Lions of southern France. They conclude that factors contributing most to diet variation are depth, year, and location along the shore (in decreasing order of importance). Fish forage over a more three-dimensional space compared to terrestrial amphibians, squamates, and mammals; thus, unsurprisingly, differences in water depth exhibit the strongest variation in diet between samples. Using stable isotopes, Ferraton et al. (2007) conclude that diet change over one year contributed more variation in their system than spatial variation between four collecting zones (farthest separated by about 200 km). Ability to rank importance of dimensions that contribute to diet variation is necessary for community stability studies as well as management efforts to conserve maximum biodiversity. Unfortunately, such all-inclusive studies are rare and most, as identified in the herpetological literature, focus on a single dimension at a time.

We present data on variation of diet in four congeneric Australian desert scincid lizards over space between three collecting locations and through time from five censuses over a 16-year span. We chose these species because of relatively large sample sizes at each location. Additionally, we chose to restrict our study to species within the genus *Ctenotus* to reduce phylogenetic dependencies of data when comparing species.

MATERIALS AND METHODS

Study Sites.—Lizards were collected at three separate sites within the Great Victoria Desert of Western Australia, all

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within 100 km of one another. Sites were chosen based on each having specific habitat differences to evaluate roles of vegetation cover and sand ridges on lizard species diversity. The R-area ("Redsands") is named for its red sand ridges. Vegetation is mostly spinifex grass (*Triodia basedowi*) with few *Eremophila*, *Grevillea*, and *Thyryptomene* bushes and marble gum (*Eucalyptus gongylocarpa*) and mulga (*Acacia aneura*) trees interspersed. Approximately 4 km south of the R-area is the B-area, named for being the site of a large experimental burn. No sand ridges or trees occur at the B-area. The B-area was chosen to represent a homogenous landscape to compare to the heterogeneous topography and vegetation found at the R-area. It was first sampled in 1992 before it was burned and mature spinifex was present. The area was burned experimentally in 1995. The L-area (40 km east of Laverton) is about 100 km west of the B- and R-areas. The L-area is a flat sandplain with many of the same habitat features as Redsands except it lacks sandridges. Further descriptions of two sites, the L- and R-areas, can be found in Pianka (1986:chapter 1).

Trapping.—All *Ctenotus* skinks were captured using pit traps. Linear series of traps spaced approximately 10 m apart were laid with associated drift fences. The number of traps varied at the three sites: B-area ($N = 75$), L-area (75 initially, later increased to 100), and R-area (77, later increased to 100). Traps were checked twice daily nearly every day for 70–100 days each over five austral spring seasons. Censuses were conducted between August and no later than February in 1992, 1995–96, 1998, 2003, and 2008. Traps were closed during any layover in collecting. All squamates caught in traps were sacrificed, preserved, cataloged by the Western Australia Museum and later shipped to the University of Texas at Austin for laboratory analyses.

Diet Analysis.—Most or all individuals of the four *Ctenotus* species from different areas and times were dissected, and stomach contents were analyzed. Items within stomachs were sorted among 23 categories; including common orders of arthropods, vegetation, vertebrates, unidentified objects, and inadvertently consumed pieces of wood and rocks. Items were counted and volumes estimated to the nearest cubic millimeter for each category. Volumes were estimated by placing a 1-mL thick layer of material over square-millimeter grid paper and approximating total volume. Each lizard's counted stomach contents were kept individually and stored in ethanol. Dietary niche breadths were estimated using Simpson's index of diversity ($D = 1/\sum p_i^2$) where p_i is the proportion by volume of food items in stomachs based on 23 prey categories.

Principal components analyses (PCA) were performed to extract the most important components of dietary niche space. For each species, a table with seven rows (each sample of lizards) and 23 columns (each diet category with volumetric stomach contents computed as relative proportions) were input and computed to return PCA scores and Euclidean distances between samples for construction of dendrograms. Each PCA returned seven component scores, one for each row or item examined. Scores for the first two principal components representing the greatest proportion of variance are shown graphically.

RESULTS

Stomach contents were sorted into 23 discrete categories. Items in some categories were not consumed or consumed very irregularly by certain species. Figure 1 displays percent abundances of the seven overall most common dietary resources used by each of these four species. Three key aspects of diet variation stand out in these graphs. First, variation is great across species. The most common resources consumed by one species may be hardly used by another. For example, *Ctenotus calurus* and *Ctenotus pantherinus* consume more

Isoptera (termites) compared to *Ctenotus piankai*, which eats Hemiptera (bugs), and *Ctenotus quattuordecimlineatus* consume more Hemiptera, Orthoptera, and Araneae (spiders). Second, diets of all species vary across sites. Shaded bars in the left column of Figure 1 show diets from the three study sites. For *C. calurus* and *C. piankai*, diet is relatively consistent across sites compared to diets of the other two species. Third, diets vary through time. Figures in the right column show diets for lizards captured on the B-area during each of the five censuses. Diet in every species varies between sampling intervals.

Relative contributions to diet variation by space and time dimensions are depicted in Figure 2. Results from a PCA and a cluster dendrogram based on Euclidean distances are shown for each species. Cluster analyses include data from all 23 diet categories. In only one case, *C. piankai*, data from across sites from the same year cluster together entirely (inside solid square on dendrogram). A cluster of all 1992 samples is nearly met for *C. calurus* and *C. quattuordecimlineatus*, but samples from the other times break up the 1992 across sites cluster (squares with dashed lines).

Another way of depicting diets is shown in Figure 3, where samples of all species were combined in a single PCA to show positions of species in dietary niche space through both time and space. The first two components reduce variation by 60% (PC3 contributes a further 13%, not shown). Positions of each of the five prey categories that most reduce variation in diet are shown in bold type. PC1 loads primarily on a Hemiptera–Isoptera axis, whereas PC2 loads on a Hemiptera–Orthoptera–Araneae axis. *Ctenotus piankai* and *C. quattuordecimlineatus* cluster on the left and *C. calurus* on the right. *Ctenotus pantherinus* is intermediate. Samples for each species cluster together within relatively small areas of total niche space, demonstrating dietary consistency. Two pairs of species exhibit some overlap: *C. piankai* and *C. quattuordecimlineatus* overlap more with each other than they overlap with the other two species, as do *C. calurus* and *C. pantherinus*.

DISCUSSION

Analysis of food web structure and species connectivity within a community is incomplete without considering variation in species interactions. Estimated realized dietary niche of each of these lizard species varies over space and time. Variation in how species interact may be important in determining how food webs bend and flex without breaking down completely and how communities show resiliency in the face of major environmental changes. Realized dietary niche may change at any particular site or year, as represented by individual points in Figure 3, but each species consumes prey resources within the bounds of its own fundamental niche space. *Ctenotus calurus* and *C. pantherinus* subsist mainly on termites and larvae; *C. pianka* eats mostly true bugs; and *C. quattuordecimlineatus* consumes more conspicuous items such as spiders and grasshoppers. The limited amount of overlap between species in dietary niche space implies fundamental ecological differences between species that may not be overturned by short-term environmental variation. Each species appears to be tied to one or two food types that comprise the bulk of their diets.

Wildfires in the arid Australian interior are large and cause major changes in vegetation composition (Haydon et al., 2000; Whelan, 1995). Several authors have recorded subsequent changes in lizard species compositions following fires in arid (Fyfe, 1980; Masters, 1996) and tropical (Braithwaite, 1987) regions of Australia. The relative importance of diet and prey resource availability compared to other factors such as vegetation cover in determining recovery of vertebrate abundances is yet to be determined. Difficulties involved in simulating natural fires limit replication, and hence, data

Compare Locations

Compare Time

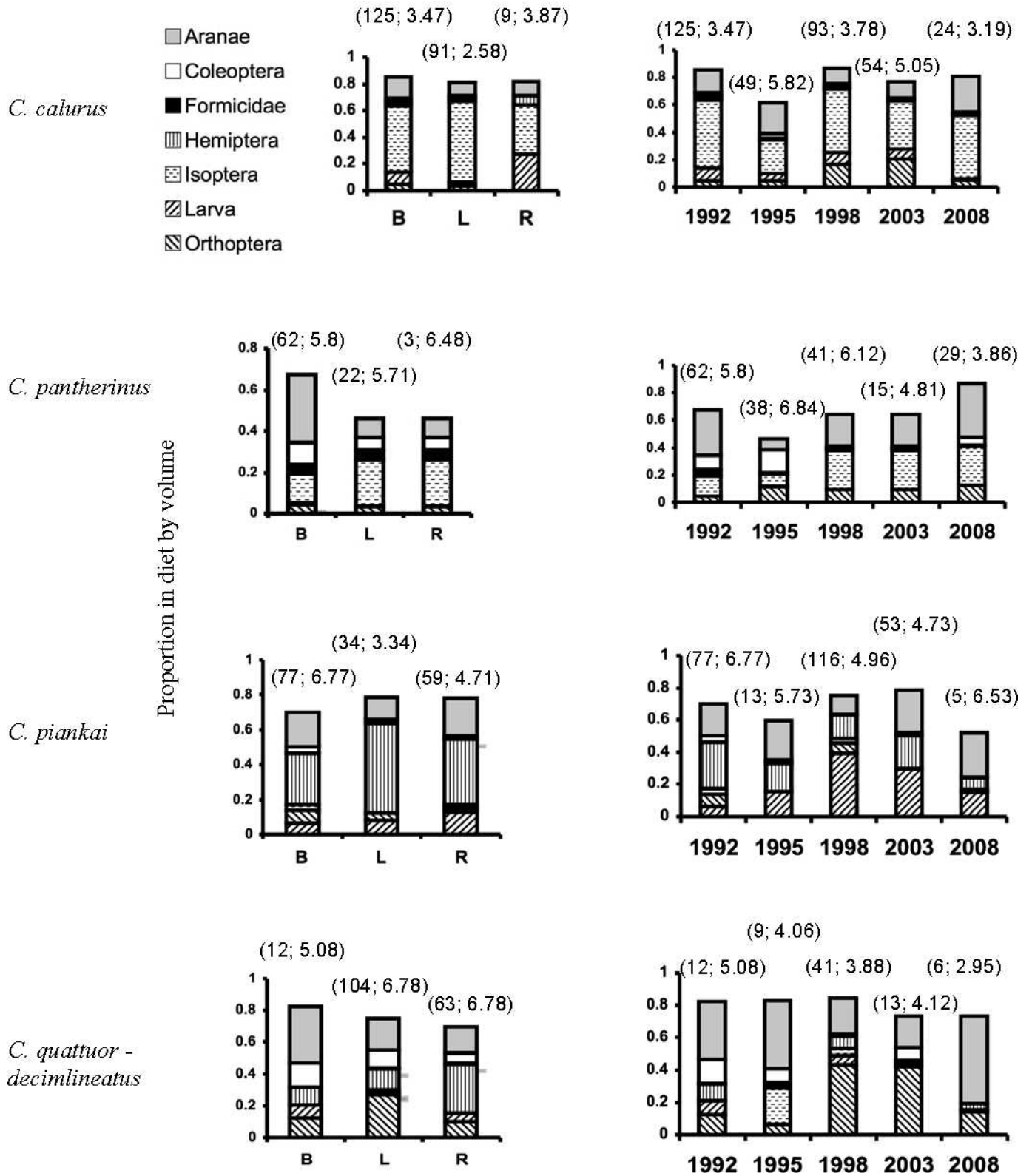


FIG. 1. Dietary composition of the seven most commonly eaten insect types by four species of *Ctenotus* skinks comparing diet at three study sites in 1992 and at the B-area study site during five censuses over a 16-year span. Sample sizes and dietary niche breadths based on Simpson's diversity index (*D*) are given above each bar.

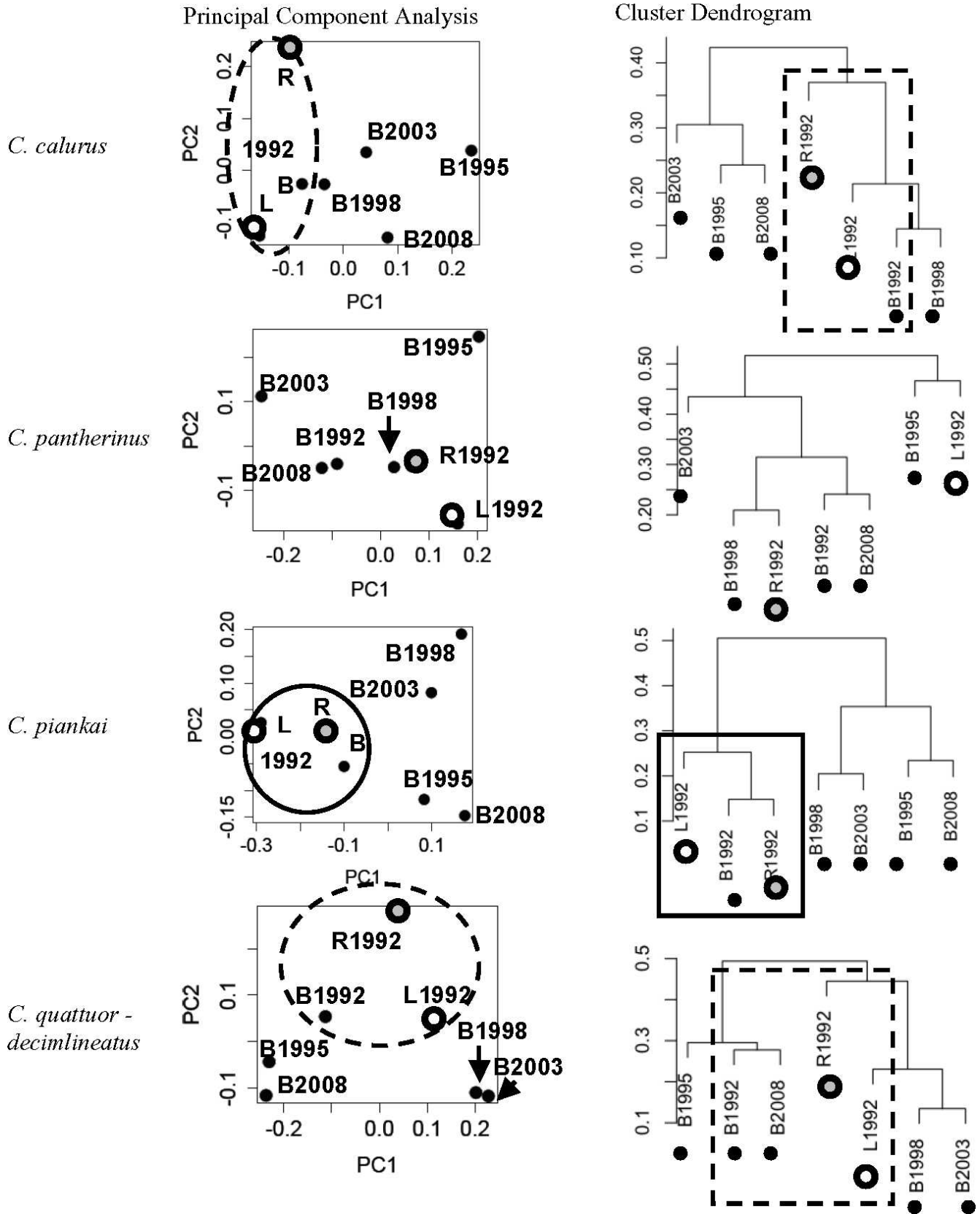


FIG. 2. Principal components plots and associated cluster dendrograms showing graphically the similarities in diets for each species across spatial and temporal dimensions. Solid circles or squares indicate where samples from the same time (1992) cluster together. B-area samples shown with small solid circles, those for the L and R sites with larger open circles. All 23 diet categories were used to make these plots.

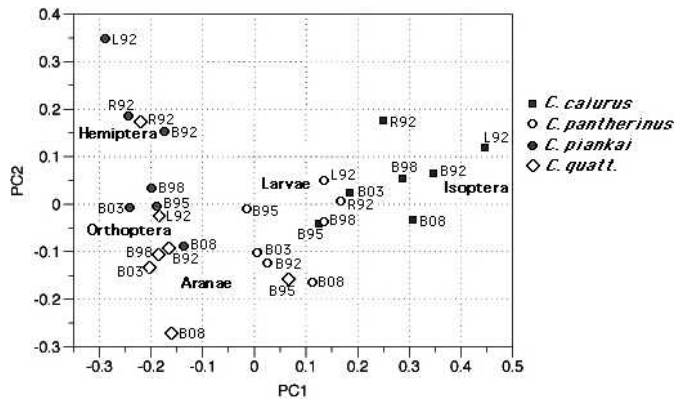


FIG. 3. Principal components plot showing dietary niche space with all samples of four species combined. All 23 diet categories were used to make this plot. The first two components reduce variation by 60%. PC1 loads primarily on a Hemiptera-Isoptera axis, and PC2 loads on Hemiptera-Orthoptera-Araneae axis. Because they eat Hemiptera, *Ctenotus piankai* are primarily in the upper left, whereas termite eating *Ctenotus calurus* are on the right. *Ctenotus pantherinus* is intermediate. Samples for each species cluster together within relatively small areas of total niche space, an indication of dietary consistency and niche conservatism. Note some overlap between two pairs of species: *C. piankai* with *Ctenotus quattuordecimlineatus* and *C. calurus* with *C. pantherinus*.

required for robust statistical analyses are lacking. Data presented here provide an indication of the amount of variation observed in diets of lizards that occur in habitats that vary in vegetation recovery stages. In three of these four species, diet appears to be more conserved over the spatial scale of this study than it is over time.

Variation is the rule at all scales in the biological hierarchy. One must pick away at many potentially contingent factors to unmask the main structural components that drive ecosystem processes. We encourage more studies involving inter-specific ecological comparisons to consider variation in multiple dimensions by pulling apart diverse samples rather than lumping together all samples for a particular species. Here, basic natural history observations revealed a broad ecological concept of a dynamic realized niche meandering within the bounds of a more rigid fundamental niche space.

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APPENDIX 1

All lizards were collected by ERP. All specimens collected in 2003 and 2008 are deposited in the Western Australian Museum (WAM). Specimens with only ERP catalog numbers have not been cataloged by WAM but are currently in ERP's possession—negotiations are proceeding to arrange to deposit these in the Texas Natural History Museum in Austin, Texas. The following catalog numbers are given separately for each species.

Ctenotus calurus: (WAM: R155991–R155999, R156001–R156016, R156017–R156042, R156044–R156047, R169447–R169458, R169460–R169471); (ERP: B2041, B2088, B2119, B2197, B2201, B2211–B2212, B2245, B2250, B2284, B2306, B2313, B2314, B2371, B2376, B26521–B26523, B26525, B26528–B26529, B26531, B26534–B26535, B26538–B26539, B26557–B26559, B26562–B26564, B26568, B26570–B26572, B26575, B26586, B26596, B26601, B26621–B26622, B26626, B26633, B26645, B26658–B26659, B26663–B26664, B26667–B26674, B26696, B26698, B26708, B26717, B26739, B26743, B26780–B26787, B26794, B26804, B26808–B26809, B26816, B26820, B26833, B26845, B26847, B26850, B26855, B26899, B26901, B26903, B26922, B26924, B26928, B26979, B26981, B26989, B27020, B27022, B27026, B27215, B27221–B27223, B27276, B27279, B27283, B27286, B27312, B27316, B27349, B27353, B27354, B27451, B27452, B27499, B27502, B27505, B27507–B27508, B27560, B27602, B27604, B27624, B27628, B27633–B27634, B27894, B27903, B27905, B27917, B27926, B27930, B27959, B27960, B28021, B28059, B28101, B28194, B28220, B28222, B28225, B28270, B28298, B28323–B28325, B28502–B28503, B28516, B28518, B28731, B28750–B28751, B28755, B28758–B28760, B28764, B28773, B28774, B28779, B28781, B28788–B28790, B28799, B28803, B28824–B28825, B28828, B28836–B28837, B28843, B28845, B28848, B28903, B28908, B28951, B28957–B29158, B29227, B29270, B29283, B30286, B30289, B30334, B30337–B30338, B30340–B30341, B30358, B30396, B30478, B30718, B30752, B30797, B30844, B30853, B30866, B31391, B31395, B31397, B31400, B31429, B31448, B31454, B31456, B31472–B31473,

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Ctenotus pantherinus: (WAM: R155733–R155747, R169681–R169689, R169691–R169694, R169696–R169699, R169701–R169702, R169704–R169707, R169710–R169712, R169714–R169716); (ERP: B2079, B2167, B2375, B2383, B2385, B2401, B2404, B2407, B2429, B2487, B2491, B2495, B26530, B26536, B26540–B26541, B26543, B26545, B26561, B26565, B26569, B26573, B26582, B26589, B26599, B26617, B26624, B26629, B26632, B26648, B26656, B26660, B26715, B26771, B26772, B26774, B26796, B26803, B26830, B26856, B26906, B26918, B26930, B26974, B27014, B27016, B27218, B27308, B27310, B27453, B27494, B27500, B27509, B27582–B27583, B27625, B27679, B27902, B27914, B27928, B27962, B27963, B28016, B28102, B28104, B28172, B28191, B28193, B28200, B28224, B28294, B28327, B28373–B28374, B28479, B28489, B28497, B28501, B28505, B28515, B28529, B28532, B28554, B28567, B28570, B28730, B28747, B28754, B28765, B28771, B28780, B28793, B28801–B28802, B28805–B28806, B28809, B28820, B28822, B28827, B28831–B28832, B28844, B28846, B28854, B28904–B28906, B28910–B28912, B28915, B28918–B28919, B28950, B28953–B28954, B28956, B29023, B29038, B29130, B29264, B30872, B31402, B31420, B31478, B31482, B31506, B31524, B31673, B31686, B31700–B31701, B31735, B31810, B31897, B31929, B31963, B32128, B32166, B32172, B32276, B32299, B32305, B32744, B32814, B32838, B32844, B32862, B32900, B32997–B32998, L26409, L26427, L26435, L26445, L26448, L26461–L26463, L26479, L27042, L27049, L27122, L27181, L27699, L27790, L27825, L27827, L27846, L27876, L28440, L28447, L28466, R26703, R26800, R27400).

Ctenotus piankai: (WAM: R155769, R155771–R155786, R155788–R155802, R155805, R155807–R155821, R156078, R169425, R169427–R169430); (ERP: B2035–B2037, B2040, B2083, B2106, B2113, B2166, B2171, B2194, B2203, B2258, B2260, B2285, B2303, B2309, B2315–B2317, B2332, B2333, B2374, B2405, B2424, B2449, B2478, B2488, B2490, B2493, B26566, B26607, B26699, B26701, B26795, B26814–B26815, B26819, B26844, B26849, B26854, B27015, B27017, B27025, B27029, B27199, B27202, B27206, B27300, B27302, B27304, B27336, B27337–B27339, B27372, B27432, B27434–B27435, B27464, B27523–B27525, B27559, B27561, B27575, B27592, B27611, B27652, B27656, B27892–B27893, B27895, B27897, B27906, B27908, B27921, B27923, B27937, B27964, B27970, B28019, B28022, B28053, B28064, B28065, B28066, B28106, B28156–B28157, B28159–B28160, B28162, B28192, B28201, B28241, B28242, B28257, B28269, B28271, B28279, B28283, B28307–B28308, B28326, B28358–B28359, B28362, B28742, B28744, B28777, B28804, B28817, B28857, B28914, B28952, B29184, B29265, B29311, B30292, B30750, B30757, B31407, B31425, B31427, B31455, B31479, B31496–B31497, B31561, B31661, B31668, B31692, B31738, B31754, B31790, B31811, B31813, B31855, B31858, B31982–B31983, B32007–B32008, B32048, B32050, B32061, B32091, B32092, B32095, B32149, B32153–B32154, B32157, B32159, B32162, B32209–B32211, B32230, B32232–B32233, B32268, B32290, B32292, B32304, B32323, B32326, B32330, B32337–B32341, B32381–B32383, B32428, B32498–B32499, B32520, B32527, B32570, B32572, B32576, B32617, B32620, B32624, B32682, B32685, B32723, B32725, B32749, B32781, B32791, B32810, B32816, B32830, B32833, B32834, B32835, B32858–B32859, B32866, B32906, B32920, B32947, B32979, B32986, L26406, L27079, L27081, L27084, L27088, L27117, L27123, L27150–L27151, L27192, L27700, L27713, L27717, L27767, L27768, L27782–L27783, L27813, L27836, L27838–L27839, L27842–L27843, L27863, L28380, L28382, L28400, L28403, L28406, L28421–L28423, L28439, L28465, R26678, R26693, R27007, R27257, R27288, R27294, R27373, R27378, R27423, R27457, R27510,

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Ctenotus quattuordecimlineatus: (WAM: R155978–R155990, R169813–R169816, R169861, R169867); (ERP: B2033, B2107, B2111, B2169, B2198, B2208, B2209, B2247, B2252, B2256, B2308, B2452, B26605, B26805, B26949, B27275, B27301, B27340, B27371, B27470, B27520, B27915, B28052, B28321, B28483, B28785, B28842, B29292, B30285, B30322, B30327, B30719, B30763, B30798, B31392, B31474, B31480, B31628, B31737, B31757, B32045–B32046, B32049, B32089–B32090, B32097, B32148, B32165, B32288, B32293, B32430, B32432, B32472, B32524, B32573, B32629, B32839, B32896–B32897, B32940, B32950, B32989, L26396–L26397, L26402, L26405, L26410, L26413–L26414, L26416–L26417, L26419, L26422, L26426, L26436, L26440, L26442–L26444, L26453, L26457, L26464–L26465, L26467, L26471–

L26472, L26481, L26487–L26488, L26490, L26492, L27030–L27031, L27070, L27077, L27108, L27112, L27114, L27118, L27143–L27145, L27149, L27152, L27154, L27158–L27159, L27161, L27183–L27184, L27187, L27189, L27196, L27685, L27687, L27691, L27693, L27707–L27708, L27722–L27723, L27734, L27753, L27760, L27761, L27774, L27777, L27779, L27781, L27784–L27785, L27787, L27810–L27811, L27815, L27817–L27818, L27835, L27844–L27845, L27862, L27864, L27875, L27878–L27881, L27885, L28395–L28397, L28399, L28401–L28402, L28408, L28415–L28419, L28425, L28427, L28430, L28434, L28441, L28467, R26547, R26614, R26640–R26641, R26723, R26750, R26754–R26756, R26788–R26789, R26798, R26875–R26876, R26911, R26914–R26915, R26942, R26945, R26954, R26956–R26958, R26992, R27246, R27250, R27293, R27296, R27343, R27345, R27374, R27420, R27428, R27436, R27456, R27458, R27461, R27511, R27515–R27516, R27566, R27649, R27670, R27978, R27988, R27990, R27999, R28037, R28094, R28110, R28114, R28116, R28184, R28229, R28254, R28256, R28263, R28273, R28275, R28305, R28306, R28315, R28318, R28344).