

## IS THE FLORIDA SAND SKINK (*PLESTIODON REYNOLDSI*) A DIETARY SPECIALIST?

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**ABSTRACT:** We examined the question of whether an apparently restricted diet qualifies the Florida sand skink (*Plestiodon reynoldsi*) as a dietary specialist. We gathered diet data from the three existing sources, added new data from individuals that we collected, and used these data to calculate measures of dietary diversity. We compared the diet of *P. reynoldsi* with those of 25 species of skinks, nine species of fossorial squamates, and six species of lizards and snakes found in habitats similar to those occupied by *P. reynoldsi*. We estimated diet choice indirectly and applied standards of specialization drawn from the literature. In every regard, the Florida sand skink did not seem to have a restricted diet. Dietary diversity values for the species are near the center of the distribution of values for skinks and for the species found in similar habitats. The species has a higher than expected  $H'$  value, based on the identity of its main prey, and the highest or nearly highest dietary diversity values among the fossorial species examined. The diet of the species did not stabilize over the course of four diet studies; rather, the cumulative number of prey types taken nearly doubled. We suggest that the apparently restricted diet of *P. reynoldsi* reflects the restricted prey choices provided by its foraging sites. A major problem in studying dietary specialization is the lack of data on prey availability and therefore a lack of solid information on diet choice.

**Key words:** Diet choice; Dietary diversity; Dietary specialization; Florida sand skink; *Plestiodon reynoldsi*

THE FLORIDA sand skink, *Plestiodon* (formerly *Neoseps*) *reynoldsi*, is a federally threatened species precinctive to central Florida, USA. Individuals spend much of their lives below ground, “swimming” through loose sand. Most aspects of the life history of this species are not well understood (Campbell and Christman, 1982; McCoy et al. 1999; E. D. McCoy, 2010; unpublished data; Penney et al., 2001; Telford, 1959). Analysis of gut contents has been performed only three times (Cooper, 1953; Myers and Telford, 1965; Smith 1977, 1982). Myers and Telford (1965) suggested that *P. reynoldsi* has a highly restricted diet for a lizard and that it forages while burrowing. These suggestions were reinforced by Smith (1977, 1982), and have been accepted in many accounts not in the primary literature (Conant and Collins, 1991; McDiarmid, 1978; US Fish and Wildlife Service, 1999). Other accounts, however, although based largely upon the same data, indicate otherwise. For example, Moler (1992: 136) stated that individuals forage in “... surficial plant debris ... where they find their prey, consisting of spiders, ant lions, termites, beetle larvae, and other small invertebrates.”

It is not unreasonable to expect that a lizard morphologically adapted for a largely subterranean existence would have a restricted diet. Modifications for locomotion in a dense medium might constrain trophic features such as gape size (Andrews et al., 1987; Pough et al., 1997; Webb et al., 2000). Furthermore, what is known of the diets of other fossorial squamates, such as amphisbaenians (e.g., Cruz Neto and Abe, 1993; Webb et al., 2000) and Australian skinks of the genus *Lerista* (e.g., Pough et al., 1997), indicate that these species eat the same soft-bodied prey, termites and beetle larvae, as does *P. reynoldsi*. In subterranean locations where termites and beetle larvae are extraordinarily abundant, the sheer numbers alone could promote dietary specialization (Emlen, 1966; MacArthur and Pianka, 1966; Schoener, 1971; Sih and Christensen, 2001). Nevertheless, it seems that terms such as restricted diet and dietary specialist typically are associated with *P. reynoldsi* without clear specification of what is meant by them. Having a restricted diet and being a dietary specialist are not one in the same: a species could have a restricted diet because it specializes on a subset of available resources, but also simply because the diversity of available prey is limited (Ferry-Graham et al., 2002). In either case,

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the key element is a restricted diet; and to determine whether *P. reynoldsi* indeed is a dietary specialist, we must first determine whether it actually has a restricted diet.

The term dietary specialist has meaning only in a relative sense (Ferry-Graham et al., 2002; Fox and Morrow, 1981; Futuyma and Moreno, 1988); likewise, so does the term restricted diet. To determine whether *P. reynoldsi* has a restricted diet, we must specify what the term means, how restriction should be measured, and what other species should be used for comparison. In its most basic sense, a specialist is a species with a relatively narrow niche breadth (Futuyma and Moreno, 1988), and we accept use of narrow niche breadth as an indication of dietary restriction. Although designation of specialists is not necessarily based upon quantifiable attributes of a species (Futuyma and Moreno, 1988), we use niche metrics to measure dietary restriction. We use other skinks (possible evolutionary, phylogenetic specialization; Ferry-Graham et al., 2002), fossorial squamates (possible mechanistic specialization; Ferry-Graham et al., 2002), and squamates found in similar habitats (possible ecological specialization; Ferry-Graham et al., 2002) as the groups against which the relative degree of dietary restriction of *P. reynoldsi* is judged.

#### MATERIALS AND METHODS

Data on the diet of *P. reynoldsi* were gathered from the three existing sources (Cooper, 1953; Myers and Telford, 1965; Smith, 1977, 1982). We added new data from individuals that died in traps in 2007 and 2008, at sites in the southern half of the species' distribution. Most previous data have come from the northern half of the species' distribution. Fifteen individuals were collected at Archbold Biological Station (ABS), Highlands County (27° 10' 50" N, 81° 21' 00" W), near the southern end of the geographical range. Collection occurred primarily in inopina oak scrubby flatwoods on satellite sand. Fourteen individuals were collected near Davenport, Polk County (28° 10' 50" N, 81° 33' 55" W), in scrubby sandhill comprised mostly of scrub oak, live oak, palmetto, and grasses. Dissections were accomplished with the aid of a light microscope,

and the contents of the stomach and intestines were stored in ethanol. Food items were identified with assistance from M. Deyrup (ABS).

We measured several aspects of dietary diversity, including diet breadth, of *P. reynoldsi* and other species (see below) based on categories of arthropod prey. We were careful to use individuals of the consumer species as the sampling units in measuring dietary diversity, because these individuals are independent samples. The food items taken by each individual are not independent samples. Dietary specialization logically should be approached from the consumer's perspective (Ferry-Graham et al., 2002), and taking this perspective also avoids the practical problem of sacrificial pseudoreplication (Hurlbert, 1984; Krebs, 1989). The unfortunate consequence of measuring dietary diversity in the way that we do is the apparent loss of information bound up in the relative abundances of the food items that were consumed. Indices used in herpetology simply to describe diets, such as those of Powell et al. (1990) and James (1991), typically incorporate relative abundances of food items; and, if they were used to assess dietary restriction or specialization, they would "save" the information bound up in the relative abundances but would do so at the risk of sacrificial pseudoreplication. In the absence of an estimate of true preference (i.e., use relative to availability on a per capita basis) and availability, one instance of a food item in a stomach is equivalent to, say, five items of another food item in the stomach, because the consumer has shown identical preference for the two items, as far as we can tell from available information.

The diet data were placed into a matrix with the rows being 23 categories of terrestrial arthropod prey: Chilopoda, Diplopoda, Colembola, Thysanura, Orthoptera, Phasmida, Dermaptera, Blatteria, Mantoidea, Isoptera, Homoptera, Hemiptera, Neuroptera larvae, Coleoptera, Coleoptera larvae, Mecoptera, Diptera, Diptera larvae, Lepidoptera, Lepidoptera larvae, Hymenoptera, Formicidae, and Arachnida. Arthropods with aquatic larvae, such as Plecoptera and Trichoptera, were not included. The diet of each predator

species was composed of a number of categories (=S). The columns of the matrix were the predator species, with the entries being numbers of individuals of each species with particular diet items in their guts. Each column was summed to yield the total diet for each species, and then each entry in the column was divided by the total diet to yield a proportional contribution of each diet category to the total diet. We used the results to calculate Shannon–Wiener diversity ( $H'$ ) and evenness ( $J'$ ), the latter value being a measure of diet breadth. We also calculated Levins' measure of diet breadth ( $B$ ), which is less sensitive than  $H'$  to rare prey items, and Berger–Parker dominance ( $D$ ), which is the percentage composition of the most common diet item.

Based on the measures of dietary diversity, we determined the position of *P. reynoldsi* relative to other species. We compared *P. reynoldsi* with (1) skinks (25 species), (2) fossorial squamates (nine species: four skinks; four amphisbaenians, a group highly adapted for subterranean existence; and one small athropodivorous fossorial snake that co-occurs with *P. reynoldsi* and may be expected to show a high degree of diet specialization; see Cobb, 2004; Smith, 1982), and (3) species found in habitats similar to those in which *P. reynoldsi* occurs (six species: three skinks, two other lizards, and one snake).

To examine the possible specialization of *P. reynoldsi* further, we assessed diet selection. We wanted to know whether *P. reynoldsi* takes certain food types out of proportion to their availabilities, but data on food availability have not been gathered for *P. reynoldsi* nor for most other species (but see Chen and Jiang, 2006; Freeman, 1997; James, 1991; Tocher, 2003). We used two indirect methods of assessing diet selection, which provide imperfect but useful information. First, we constructed a measure of gut fullness (total diet [see above]/number of consumer individuals) and compared the results among the 25 species of skinks, under the assumption that the greater the mean number of food items in the gut, the greater the general food availability for that species. Second, we compiled a list of main diet items, by using the criterion of James (1991; those categories making up

>10% of the diet by either number or volume and consumed by >20% of the individuals), and then we again compared the results among the 25 species of skinks, under the assumption that the narrower the range of main diet items, the more restricted the diet. The use of this method carries some risk of pseudoreplication. The arrays of main diet items are made up of variable numbers and identities of food categories, and we arranged the arrays from simple to complex with principal component analysis, using PRIMER software (Clarke and Gorley, 2006), and then we correlated the ordering with dietary diversity. This procedure helped to reveal commonalities among the diets of species with similar levels of dietary diversity. To determine whether a different standard for specialization would still identify the same species as specialists as did the previous method, we applied the 80% standard suggested by Costa et al. (2008; specialists are species in which a single food category represents 80% or more of its diet volumetrically). The use of this method also carries some risk of pseudoreplication.

## RESULTS

Previous examinations indicate that the diet of *P. reynoldsi* consists principally of soft-bodied insects, such as termites, antlions, and beetle larvae, with occasional ingestion of small spiders, roaches, and adult beetles (Table 1). Our new examination, however, suggests a greater variability (Table 2). Gut contents from 14 of the 29 individuals had identifiable specimens. Insects were the only arthropod prey items found among the gut contents, and both hard- and soft-bodied forms were present.

Among the gut contents in the new examination were two previously unrecorded diet items. One specimen of Florida harvester ant (*Pogonomyrmex badius*) was found in an individual captured at ABS. This is the first report of any ant in the natural diet of *P. reynoldsi*, although Ashton and Ashton (1991; R. E. Ashton, personal communication) reported consumption of ants by captive specimens. Individuals of *P. reynoldsi* occasionally are found in nests of the Florida harvester ant at ABS (M. Deyrup, personal communica-

TABLE 1.—Previously available data on the diet of *Plestiodon reynoldsi*. M = Myers and Telford (1965), C = Cooper (1953), and S = Smith (1982). Question mark (?) indicates that the number is unknown, as the author presented only presence information.

Prey type (order, family)	No. individuals			No. prey items		
	M	C	S	M	C	S
Solpugida	1			1		
Pseudoscorpionida		1			1	
Araneae						
Lycosidae			3			
Salticidae	3			3		
Coleoptera	4			4		
Coleoptera (larvae)	13			14		
Elateridae/Tenebrionidae	22	?	3	29		33.3%
Scarabaeidae	9			10		
Isoptera		?				
Rhinotermitidae	9		2	148		63.3%
Lepidoptera (larvae)						
Tortricidae	2			3		
Blatteria	2			2		
Diptera (larvae)		1			1	
Neuroptera (larvae)						
Myrmeliontidae	1	2		1		

tion). ABS possesses a rich ant fauna of 102 species, of which 20 are found commonly in the inopina oak scrubby flatwoods (Deyrup and Trager, 1986). One specimen of scaly bush cricket (*Cycloptilium* sp.) was found in an individual captured at ABS. This is also the first report of any cricket in the diet of *P. reynoldsi*. The scaly bush cricket does not burrow underground and is most often found

in the leaf litter (M. Deyrup, personal communication).

Incidentally, we found nine of 29 individuals to have at least one adult of the nematode *Parapharyngodon ocalaensis* in the colon. *Plestiodon reynoldsi* is the type host for this parasite (Bursey and Telford, 2002). Myers and Telford (1965) found a nematode parasite then identified as *Thelandros* sp. (Oxyuridae)

TABLE 2.—Identifiable prey items taken by 14 individuals of *Plestiodon reynoldsi* at Archbold Biological Station and Davenport, Florida.

Prey type (order, family, subfamily or species)	No. individuals	No. prey items
Hymenoptera, Formicidae		
<i>Pogonomyrmex badius</i> (Florida harvester ant)	1	1
Orthoptera, Gryllidae		
<i>Cycloptilium</i> sp. (scaly bush cricket)	1	1
Coleoptera, Aclopidae		
<i>Geopsammodius relictillus</i> (subterranean scarab)	4	5
Coleoptera, Elateridae (larvae)	1	2
Coleoptera, Tenebrionidae (larvae)	4	5
Alleculinae (comb-clawed beetle, larvae)	2	2
Lepidoptera, Acrolophidae		
<i>Acrolophus</i> sp. (tubeworm moth, larva)	1	1
Neuroptera, Myrmeleontidae		
<i>Brachynemurus</i> sp.(common antlion, larva)	1	1

TABLE 3.—Diet data for 25 species of skink, four species of amphisbaenians (AM), and three southeastern US nonskink lizard and snake species (SE). Fossorial species are in bold. N = number of individuals, S = number of diet categories, H' = Shannon–Wiener diversity, J' = Shannon–Wiener evenness, B = Levins' diet breadth, and D = Berger–Parker dominance. Numbered species have two records. \* = fecal samples (whole or part), \*\* = number of individuals without prey unknown.

Species	N	S	H'	J'	B	D	Source
<b><i>Tantilla relicta</i></b> (SE)	124	2	0.39	0.56	1.30	0.81	Smith, 1982
<b><i>Lerista labialis</i></b>	52	3	0.90	0.82	2.10	0.64	Greenville and Dickman, 2005
<b><i>Cercolophia roberti</i></b> (AM)	150	6	1.03	0.57	2.04	0.67	Cruz Neto and Abe, 1993
<b><i>Lerista lineopunctulata</i></b>	21**	5	1.20	0.75	2.50	0.55	Pough et al., 1997
<i>Lerista macropisthopus</i>	50**	6	1.23	0.69	3.06	0.51	Pough et al., 1997
<i>Leiopisma telfairii</i>	59*	7	1.29	0.66	2.73	0.56	Pernetta et al., 2005
<b><i>Lerista connivens</i></b>	28**	6	1.31	0.73	2.88	0.38	Pough et al., 1997
<b><i>Monopeltis anchietae</i></b> (AM)	55	6	1.31	0.73	3.06	0.47	Webb et al., 2000
<b><i>Amphisbaena mertensii</i></b> (AM)	36	6	1.41	0.79	3.30	0.48	Cruz Neto and Abe, 1993
<i>Oligosoma grande</i>	167*	10	1.44	0.63	2.40	0.62	Tocher, 2003
<i>Plestiodon inexpectatus</i>	24	6	1.46	0.81	3.96	0.30	Hamilton and Pollack, 1961
<i>Oligosoma nigriplantarae</i>	10*	6	1.48	0.83	3.72	0.35	Freeman, 1997
<b><i>Zygaspis quadrifrons</i></b> (AM)	100	8	1.49	0.72	3.44	0.53	Webb et al., 2000
<i>Oligosoma maccanni</i>	29*	8	1.59	0.76	4.40	0.35	Freeman, 1997
<i>Ctenotus fallens</i>	28**	8	1.64	0.79	5.44	0.26	Pough et al., 1997
<i>Plestiodon egregius</i>	280	15	1.65	0.61	3.90	0.34	Hamilton and Pollack, 1958; Mount, 1963
<b><i>Plestiodon reynoldsi</i></b>	96	9	1.65	0.75	3.87	0.45	Cooper, 1953; Myers and Telford, 1965; Smith, 1977, 1982; this study
<i>Mabuya longicaudata</i>	61	11	1.70	0.71	4.40	0.35	Huang, 2006
<i>1Ctenotus pantherinus</i>	14	7	1.74	0.89	4.69	0.33	Twigg et al., 1996
<i>Aspidoscelis sexlineatus</i> (SE)	100**	9	1.75	0.80	4.23	0.43	Hamilton and Pollack, 1961
<i>Ctenotus piankai</i>	50*	13	1.76	0.69	5.07	0.34	James, 1991
<i>Ctenotus grandis</i>	68	9	1.82	0.83	5.13	0.30	Twigg et al., 1996
<i>1Ctenotus pantherinus</i>	86*	15	1.88	0.69	5.70	0.37	James, 1991
<i>2Mabuya agilis</i>	18	8	1.92	0.92	5.52	0.28	Rocha et al., 2004
<i>Sceloporus undulatus</i> (SE)	60**	11	1.93	0.80	5.28	0.35	Hamilton and Pollack, 1961
<i>3Ctenotus helenae</i>	28	9	1.97	0.90	6.39	0.23	Twigg et al., 1996
<i>Abelpharus kitaibelii</i>	41**	11	1.97	0.82	5.61	0.28	Herczeg et al., 2007
<i>Mabuya macrorhyncha</i>	95**	12	1.98	0.66	5.52	0.33	Vrcibradic and Rocha, 1996
<i>Oligosoma ottagense</i>	78*	10	1.99	0.87	6.00	0.26	Tocher, 2003
<i>Egernia coventryi</i>	47	12	1.99	0.80	5.04	0.31	Clemman et al., 2004
<i>Eumeces chinensis</i>	113	10	2.00	0.87	5.40	0.28	Chen and Jiang, 2006
<i>3Ctenotus helenae</i>	73*	16	2.28	0.82	6.72	0.23	James, 1991
<i>2Mabuya agilis</i>	33**	16	2.36	0.85	8.96	0.21	Vrcibradic and Rocha, 1996
<i>Ctenotus quattuordecimlineatus</i>	212*	16	2.37	0.85	8.16	0.21	James, 1991
<i>Ctenotus leonhardii</i>	87*	17	2.52	0.89	12.24	0.14	James, 1991

in 30 of 82 individuals, and Cooper (1953) found an unnamed roundworm parasite in three of four individuals.

The several measures of dietary diversity are related to one another (Table 3). For the 25 species of skinks, strong positive correla-

tions were found between S and H' ( $r_s = 0.81$ ,  $P < 0.01$ ,  $n = 28$ ), S and B ( $r_s = 0.72$ ,  $P < 0.01$ ,  $n = 28$ ), H' and J' ( $r_s = 0.53$ ,  $P < 0.01$ ,  $n = 28$ ), H' and B ( $r_s = 0.92$ ,  $P < 0.01$ ,  $n = 28$ ), and J' and B ( $r_s = 0.55$ ,  $P < 0.01$ ,  $n = 28$ ). A strong positive correlation also exists

TABLE 4.—Main diet items for 22 species of skinks, arranged from least to greatest  $H'$ . Prey types, from left to right, are Isoptera, Coleoptera larvae, Coleoptera adults, Blatteria, Diptera, Orthoptera, Arachnida, Hemiptera, Lepidoptera larvae, Chilopoda, ants, Homoptera, Lepidoptera adults, and Thysanura.

Species	Prey type													
	IS	CL	CO	BL	DI	OR	AR	HE	LL	CH	AN	HO	LE	TH
<i>Lerista labialis</i>	X													
<i>Lerista lineopunctulata</i>			X											
<i>Lerista macropisthopus</i>				X										
<i>Leiopisma telfairii</i>				X										
<i>Lerista connivens</i>		X	X											
<i>Oligosoma grande</i>					X									
<i>Plestiodon inexpectatus</i>				X			X							
<i>Oligosoma nigriplantarum</i>					X		X							
<i>Oligosoma maccanni</i>						X			X					
<i>Ctenotus fallens</i>				X						X				
<i>Plestiodon egregius</i>							X	X						
<i>Plestiodon reynoldsi</i>			X											
<i>Ctenotus pantherinus</i>		X			X						X			
<i>Ctenotus piankai</i>	X					X	X	X						
<i>Ctenotus grandis</i>	X										X			
<i>Ctenotus pantherinus</i>		X			X			X			X			
<i>Mabuya agilis</i>					X		X	X				X		
<i>Ctenotus helenae</i>	X					X								
<i>Abelpharus kitaibelii</i>				X				X					X	
<i>Mabuya macrorhyncha</i>								X						
<i>Eumeces chinensis</i>			X										X	
<i>Ctenotus helenae</i>	X		X	X		X	X			X				
<i>Mabuya agilis</i>		X			X	X		X						
<i>Ctenotus quattuordec</i>	X			X		X	X	X						X
<i>Ctenotus leonhardii</i>	X		X	X		X	X				X			X

between sample size ( $N$ ) and  $S$  ( $r_S = 0.61$ ,  $P < 0.01$ ,  $n = 28$ ), indicating that  $S$  is influenced by the number of predator individuals examined (i.e., that it is sample size dependent), although the same is not true for the measures of diet breadth,  $H'$  and  $B$  (cf. Pianka, 1986). With the data ranked from least to greatest  $H'$ , *P. reynoldsi* is 12th among the 25 species of skinks in  $H'$ , eight in  $J'$ , and ninth in  $B$ . Among the nine fossorial species, *P. reynoldsi* has the greatest  $H'$  and  $B$  and is seventh in  $J'$ . Among the six species occurring in similar habitats, *P. reynoldsi* is third in  $H'$  and  $J'$  and second in  $B$ .

The indirect diet choice analyses revealed several important patterns. A reasonably strong positive correlation was found between gut fullness (total diet/number of consumer individuals) and  $S$  ( $r_S = 0.37$ ,  $P = 0.05$ ,  $n = 28$ ), indicating that  $S$  probably is influenced by the availability of prey. We could detect no strong tendency for lizard species with high-volume prey items, such as vegetation and

vertebrates, in their guts to have relatively low diet diversities; so, gut fullness in the strict sense (i.e., based on volumetric capacity) does not seem to limit diet choice (cf. Lima et al., 2000). We also could detect no strong correlation between mean snout–vent length of the species of skinks and any of our measures of dietary diversity. For *P. reynoldsi* alone, cumulative  $S$  increased from 5 to 9 over the course of the four diet studies (Cooper, 1953; Myers and Telford, 1965; Smith, 1977, 1982; this study). Gut fullness was the same, approximately 1.00, for all four studies, however, suggesting that the increase in  $S$  was not the result of differences in general availability of prey.

Principal component analysis yielded an ordering of diets (principal component 1) that was strongly positively correlated with  $H'$  ( $r_S = 0.61$ ,  $P < 0.01$ ,  $n = 22$ ). Main diet items for 22 of the 25 species are displayed in Table 4, arranged from least to greatest  $H'$ . From this arrangement, it can be seen that species with



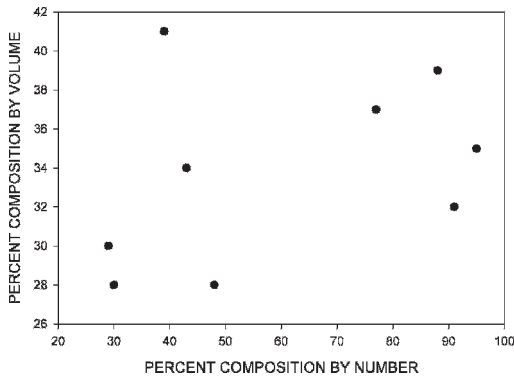


FIG. 1.—Comparison of two measures of diet composition for nine species of skink.

relatively low  $H'$  values—which often also are fossorial—tend to feed on a few, similar prey categories, whereas species with relatively high  $H'$  values tend to feed on a larger and broader array of prey categories. It also can be seen that species with relatively high  $H'$  values often use Orthoptera and Arachnida as main diet items, but they also seem to bet-hedge when possible by using Isoptera, a highly reliable food source when other prey items are scarce (e.g., James, 1991; Pough et al., 1997). *Plestiodon reynoldsi* has a higher  $H'$  value than would be expected from the identity (Coleoptera larvae) of its main diet item.

Among the 25 species of skinks, only the diets of two species of *Ctenotus* (James, 1991; Twigg et al., 1996) had numerical percent compositions exceeding 80%. No species of this genus, however, seemed particularly specialized based on the analysis of main diet items (Table 4). The calculated percent composition of the most frequent prey type in the diet of *P. reynoldsi* is 64%, based on numeric data. Volumetric data are not available to compare the species to the 80% standard for specialization, but it would be unusual for percent composition based on volumetric data to exceed percent composition based on numeric data (Fig. 1; note that in all cases, the points are near or below the isometric line, indicating that percent composition by number, is equal to or greater than the corresponding percent composition by volume and that the range of composition by number is 29–95%, whereas the range for composition

by volume is only 28–41%); so, 64% defines a reasonable upper limit for a calculation based on volumetric data. Incidentally, among the nine fossorial species and six species sharing similar habitats with *P. reynoldsi*, only the diets of the four amphisbaenians (Cruz Neto and Abe, 1993; Webb et al., 2000) and the snake *Tantilla relicta* (Smith, 1982) had numerical percent compositions exceeding 80%.

## DISCUSSION

Based on our analysis, we did not find compelling evidence that *P. reynoldsi* has a particularly restricted diet. Dietary diversity values for the species are near the center of the distribution of values for skinks, most of which are considered dietary generalists. Similarly, *P. reynoldsi* places approximately in the middle of the distribution of B values compared with 33 species of desert skinks (Pianka, 1986). *Plestiodon reynoldsi* has a relatively high  $H'$  value for a species whose only main diet item is Coleoptera larvae. The species also has the highest  $H'$  and B values, and nearly highest  $J'$  value, among the nine fossorial species examined; and values near the center of the distribution of dietary diversity values for the six species coexisting in southeastern US habitats. As data from four successive studies were added, the cumulative number of prey types taken by *P. reynoldsi* nearly doubled, even as gut fullness remained constant.

*Plestiodon egregius* is a syntopic congener of *P. reynoldsi* (Smith, 1977, 1982) that has been suggested to be a more generalized feeder than *P. reynoldsi*, but our analysis does not bear out this view. Smith (1982) compiled diet data on a large number ( $n = 83$ ) of individuals of *P. egregius*, but we could not use these data in our analysis because he combined cockroaches and crickets together in the same diet category. If we make the assumption that the ratio of cockroaches to crickets is approximately 2 to 1, then Smith's (1982) data match Mount's (1963) data, which we did use, closely. Our analysis indicates that the dietary diversity of *P. egregius* is very similar to that of *P. reynoldsi*, even though the number of diet categories taken by *P. egregius*

is substantially larger (18 versus 9). Although *P. egregius* takes a large number of prey categories, its diet consists largely of roaches, crickets, and arachnids. In this latter respect, it actually may be considered more of a specialist than *P. reynoldsi* (cf. the fossorial *Typhlosaurus* spp. in Pianka, 1986).

Our analysis showed that the number of prey types taken by skinks in general is influenced by the number of predator individuals examined and probably also by availability of prey. These findings reinforce the conclusion that skinks tend to be dietary generalists, taking prey items largely as a function of their availabilities (Luiselli, 2008). Dietary diversity can therefore be expected to be relatively high where prey diversity is relatively high and relatively low where it is not (James, 1991; Mount, 1963). Dietary diversity can, in turn, be expected to increase with increasingly mesic conditions, because of increasing availabilities of prey (James, 1991; also see Pianka, 1986). For example, the diet of *Oligosoma grande*, which occurred in a variety of dune habitats, was substantially less diverse than the diet of *O. ottagense*, which occurred only in wet swales in the same area (Tocher, 2003). Clearly, microhabitat choice is important in influencing dietary diversity (also see Pianka, 1986; Vrcibradic and Rocha, 1996). Furthermore, skinks often shift their diets to reflect changing availabilities of prey, both temporally and spatially (Duffield and Bull, 1998; Eifler and Eifler, 1999; James, 1991; Pianka, 1986). Many species of skinks seem to broaden their diets when given the opportunity, and what we have learned about *P. reynoldsi* suggests that it does the same. The apparently restricted diet of *P. reynoldsi* probably reflects the restricted prey choices provided by its foraging sites (cf. Attum et al., 2004; Myers and Telford, 1965). For example, although all previous studies reported termites as the most abundant, or one of the most abundant, food items for *P. reynoldsi*, we did not find termites in the guts of our specimens; perhaps because termite colonies simply are not common at our study sites. Likewise, the presence of diet items such as the scaly bush cricket suggests the potential importance of the litter layer as a source of prey items for *P. reynoldsi* at our study sites

(cf. Moler, 1992; Telford, 1959), perhaps because belowground prey items are not common. These findings reinforce the general observation that a species that seems specialized locally may be generalized over its entire range (Fox and Morrow, 1981; Werner and Sherry, 1987).

Because we cannot show that *P. reynoldsi* has a particularly restricted diet, the question of dietary specialization may be moot. But suppose that a dietary specialist would need to satisfy three criteria, at a minimum: consistently use the same set of food items (based on identity, size, or some other attribute); use a set of food items that differs from the spectrum of available items; and occupy only locations that supply precisely the required spectrum of food items, or at least a substantial portion of it. We can envision the possibility that *P. reynoldsi* could satisfy these criteria to some degree, despite the results of our analysis, because the process of specialization is so complex (Ferry-Graham et al., 2002). We suggest that any attempts to examine potential dietary specialization of *P. reynoldsi* further should be aware of three important considerations raised by our study.

The first consideration is the absence of sound data on food availability. Although such data are notoriously difficult to obtain, without them it is simply impossible to determine whether a species meets two of the three basic criteria for dietary specialization that we have suggested. Food availability is more than simply what one can count in the environment. One also must know about factors such as rates of encounter, detection ability, and capture ability (Ferry-Graham et al., 2002).

The second consideration is the possibility of biased sampling, which could lead to failure to recognize specialization when it actually exists. The following are four examples from our study. First, we used relatively coarse diet categories, and the coarseness of the categories may have masked finer scale choices made by the lizard species (Luiselli, 2008). Second, although we selected studies from the literature only by the type of data they contained, we ended up using a relatively restricted set of lizard species, particularly a large number of species of the Australian genus *Ctenotus*, and these species may not



reflect the general pattern of dietary diversity in skinks accurately. Third, our use of a mix of study types, ranging from small samples taken in local habitat patches to large samples taken in broad geographic regions could have influenced conclusions about relative degrees of specialization (Gainsbury and Colli, 2003; Magnusson and Silva, 1993), again masking the pattern of diet choice. Although such concerns are valid, we note that the diet categories match those used in previous studies and are at the level upon which statements about dietary specialization in *P. reynoldsi* have been based and that we have no reason to suspect that the lizard species and study types that we selected are not representative. Fourth, our gut contents samples came from individuals retrieved from traps, and it is possible that an individual in a trap may have consumed a particular food item only because the two were confined together. This last example is representative of a general class of sampling problems (e.g., Peterson and Black, 1994) that have no simple solution. One way to begin to assess the importance of this potential sampling bias in diet studies may be to determine how often food items found in guts also are found alone in traps.

The third consideration, which also could lead to failure to recognize specialization, is incorrect identification of the basis of diet specialization. *Plestiodon reynoldsi* might specialize not based on prey taxonomy but on some other attribute, such as size (e.g., Chen and Jiang, 2006). Lizard body size tends to be related to the size of prey taken (Costa et al., 2008; Lima et al., 2000). One would expect, therefore, that some relationship might exist between lizard body size and dietary diversity, because larger lizard species could take a broader size spectrum of prey items, but we found no strong correlation between snout-vent length and any of our measures of dietary diversity for the species of skinks that we studied. The lack of correlation may reflect a tendency for larger lizard species to exclude small prey items actively (Costa et al., 2008). Alternatively, it may reflect a more complex relationship between predator and prey size in lizards, involving absolute predator head length, relative predator head length, or both

(e.g., Costa et al., 2008; Pough et al., 1997). We are currently investigating the relationships among morphometrics, gape size, and prey size in *P. reynoldsi*.

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