

Sympatric Ecology of Five Species of Fossorial Snakes (Elapidae) in Western Australia

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ABSTRACT.—Snakes have very different ecologies and habits from other non-ophidian squamates (“lizards”); yet ecological data from sympatric populations of lizards are often used as models to explain resource partitioning in sympatric groups of all squamates. Most snake assemblages show greatest ecological divergence in use of dietary resources. We use dietary, spatial, and reproductive data in a clade of five sympatric snake species with similar ecologies to test previous assumptions of how snakes partition resources in a species-rich community. Species show dietary specializations, with species of *Simoselaps* and *Brachyuropis fasciolatus* feeding exclusively on lizards and *Brachyuropis semifasciatus* eating only squamate eggs. Some species show trends regarding differential habitat use; *Simoselaps bertholdi* and *B. semifasciatus* are habitat generalists, whereas the other species are not captured in flat areas between sand ridges. Time of peak activity is not partitioned seasonally because all species, except *B. fasciolatus*, are most active in December. Partitioning of dietary resources is a stronger structuring agent than is partitioning of habitat resources in this community as indicated by the amount of resource overlap. Diet is the most important dimension in explaining ecological divergence among these elapid species, in agreement with prior studies of resource partitioning in snake assemblages.

Squamates are useful model organisms in studying sympatric ecology (Pianka, 1969, 1971, 1973, 1974, 1975; Fitch, 1975; Shine, 1977; Huey et al., 1983). Most of these studies of sympatry include only non-ophidian squamates (“lizards”). Much remains unknown about how snakes partition resources within species-dense communities. Squamates are useful models in comparative ecological studies because (1) most species are relatively abundant, (2) they are easily trapped, and (3) most species eat prey whole, making identification of stomach contents manageable. Data on sympatric ecology of snakes, in relation to non-ophidian squamates, are generally lacking because snakes are less abundant, more cryptic, and often have empty stomachs. However, resource partitioning in the form of habitat, food, and time has been documented in several snake assemblages (Carpenter, 1952; Fouquette, 1954; Henderson, 1974; White and Kolb, 1974; Luiselli, 2006 and references therein). Snakes have different behavioral and ecological attributes compared to other lizards, and greater knowledge of sympatry in snakes could be useful in understanding complexities of community structure.

We present spatial, reproductive, and dietary data for five sympatric fossorial elapids of the *Simoselaps–Brachyuropis–Neelaps* clade from the Great Victoria Desert in Western Australia. Data

on ecologies of these five snakes are limited, and nothing is known about their behavior in sympatry. Previous studies (Shine, 1984; Scanlon and Shine, 1988; Strahan et al., 1998) have used museum specimens where individuals had been collected throughout their ranges, including many areas where the five species included in our study are not sympatric. Shine (1984) showed that *Brachyuropis semifasciatus* specialize on squamate eggs, whereas the other four species consume long, slender adult lizards, especially *Lerista* sp. (Scincidae) and various *Ctenotus* skink species. How and Shine (1999) conducted censuses of five *Simoselaps* species at 32 sites near Perth, Western Australia over 11 yr. Four species in their sample overlap with species in our assemblage, but not all species were found at every site. How and Shine (1999) emphasize differences among species and sexes in seasonal time of activity and species composition at different sites. Data on species differences in dietary or microhabitat preference in sympatry are not presented by How and Shine (1999), which are the emphases of our study. Here, we will test whether data on diets from these five snakes in sympatry agree with data presented by Shine (1984) where these five snakes were not necessarily sympatric. In addition, we present data on differential use of microhabitats on sand ridges, which were not provided by Shine (1984) and Scanlon and Shine (1988), and some data on reproductive ecology.

Resource dimensions are traditionally categorized as habitat, food, and time of activity

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TABLE 1. Species census and relative capture rates per 100 pitdays (= $[N/100p]$) through six census periods. * Lapse in trapping between 24 February 1990 and 5 September 1990.

Year	Trap days	Census period	Species										Total
			<i>S. anomalus</i>		<i>S. bertholdi</i>		<i>B. fasciolatus</i>		<i>B. semifasciatus</i>		<i>N. bimaculatus</i>		
			N	N/100p	N	N/100p	N	N/100p	N	N/100p	N	N/100p	
1978–79	none	30 JUL–13 MAR	0	-	2	-	1	-	3	-	0	-	6
1989–1991*	8646	8 OCT–6 MAR	47	0.54	13	0.15	0	0.00	12	0.14	1	0.01	73
1992	3885	30 JUL–15 DEC	25	0.64	13	0.33	5	0.13	0	0.00	0	0.00	43
1995–96	5714	12 SEP–8 FEB	31	0.54	10	0.18	2	0.04	17	0.30	2	0.04	62
1998	7600	14 SEP–5 DEC	34	0.45	20	0.26	8	0.11	14	0.18	6	0.08	82
2003	3849	9 SEP–5 DEC	0	0.00	4	0.10	6	0.16	5	0.13	5	0.13	20
Totals			137		62		22		51		14		286

(Pianka, 1973, 1975). In a comprehensive literature review of resource partitioning studies on amphibians and reptiles, Toft (1985) determined habitat as the most partitioned resource dimension in most taxa except amphibian larvae and snakes. Diet, in snakes, is the most important dimension in reducing ecological overlap among species. These data agree with previous reviews (Arnold, 1972; Schoener, 1977) that diet/predation is most important for ecological divergence in snake assemblages. Luiselli (2006) reviewed literature published on resource partitioning in snakes since Toft's review and concluded that diet is the most partitioned resource in 56.8% of studies. We will combine data on different resource dimensions to test whether diet is the most important resource dimension in this fossorial snake assemblage. Resource partitioning may not be a consequence of competition alone but may be influenced by variation in physiological and morphological constraints, response to predators (Toft, 1985), and historical constraints (Brooks and McLennan, 1991).

MATERIALS AND METHODS

Specimens were collected in the field by ERP using pit fall traps and by hand during 10 Austral spring and summer seasons over 25 yr between 1978 and 2003 (i.e., 1978–79, 1989–92, 1995–96, 1998, 2003). Table 1 outlines number of trapdays, census durations for individual collecting periods, and species census data. Not every trap is open during the entire census. The study site is a large, semipristine red sand desert in the Great Victoria Desert of southwestern Australia (28°12'S, 123°15'E). Topography is punctuated by large sand ridges with shallow rises and steep slopes, with interdunal flats covered mostly by spinifex grass with scattered marble gum trees. Vegetation on sandridges consists primarily of various shrubs (for further description of the study site, refer to

Pianka [1986:9–11]). Series of pit fall traps cover all habitats and areas of the ridges and flats at the study site. Designated microhabitats on sandridges and number of pit traps (N) at each location are crest (33 [top of ridge]), slope (9), base (24), and flat (11 [area between dunes]). Pit traps were checked 2–3 times daily. Snakes reported herein were found during early morning checks and, thus, are nocturnal. An associated pit fall trap number was recorded for every snake collected, providing data on microhabitat and position on sand ridges. Snakes were preserved and later dissected and analyzed for stomach contents, testes sizes in males, and numbers and volumes of eggs in females. All dissected parts, including stomach contents and eggs, were counted and measured by volume (nearest 0.1 cm³) and length (nearest 0.01 ml) and placed in separate containers from the whole snakes. Relative clutch mass (RCM) was calculated by dividing total egg volume by total adult body mass.

Relative importance of resource dimensions was determined by comparing niche overlaps, as calculated by Pianka (1973, 1974), among species. Dimensions having less overlap identify those dimensions that may be key to phenotypic divergence among species and, hence, ecological diversification.

RESULTS

Habitat Use.—Data on habitat use reveal that some species specialize on certain habitats, whereas others are more microhabitat generalists (see Fig. 1). *Simoselaps anomalus* were trapped 63% of the time on the crest area of sand ridges and less frequently on the three other areas of the ridges. *Simoselaps bertholdi* and *B. semifasciatus* were trapped an almost equal amount in each microhabitat. *Brachyurophis fasciolatus* and *Neelaps bimaculatus* were trapped nearly half the time on slopes but never on flat areas.

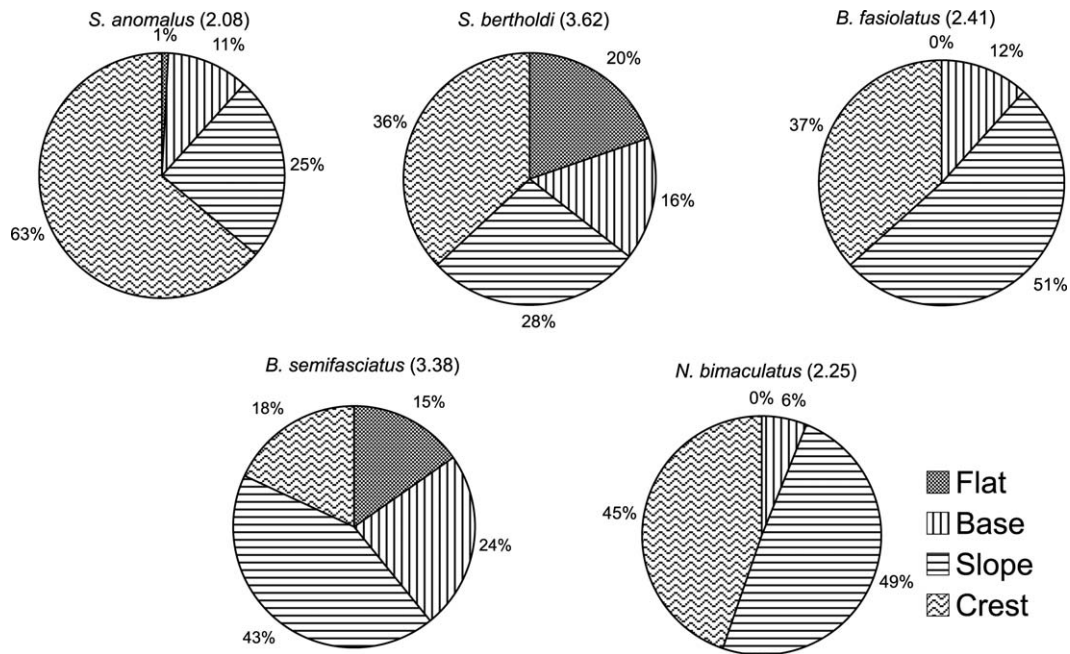


FIG. 1. Different regions of pie chart represent percentage of samples collected at one of four microhabitats as indicated in the legend (numbers in parentheses indicate niche breadths as calculated by the reciprocal of Simpson's diversity index, H' ($1 / \sum p^2$)). Capture rates are determined as proportions relative to number of pit traps in each microhabitat. Numbers of traps (N) at each microhabitat are Flat (11), Base (24), Slope (9), and Crest (33).

Diet.—*Simoselaps anomalus* and *S. bertholdi* consume almost exclusively (over 90%) *Lerista* sp. lizards. All fully intact *Lerista* in stomach contents were identified as *Lerista bipes*, which is distinguishable from other local *Lerista* species by the presence of two digits on its hind limbs. Many *Lerista* found in stomachs were partially digested or only contained autotomized tails, thus were unidentifiable to species level. All *Lerista* found in stomach contents were oriented head-first. The only stomach content identified in any specimen of *N. bimaculatus* was the tail of a *Ramphotyphlops* snake. *Brachyuropsis semifasciatus* ate almost exclusively squamate eggs, with the exception of one unidentifiable hard, amber-colored object. Eggs were identified as belonging to squamates because of the soft, leathery cover characteristic of most squamate eggs, and several eggs were discovered that still had embryos, recognizable as lizards, inside them (for diet summaries, see Table 2).

Reproduction.—Reproductive data, including testes sizes, egg numbers and egg volumes were measured in all five snake species (Table 3). In males of each species, testes size correlated positively with SVL and fresh body mass ($P < 0.002$). For gravid females of each species, neither egg number nor total egg volume correlated with SVL or mass ($P > 0.1$) except for *B. semifasciatus* where fresh body weight

correlated positively with total egg volume ($R^2 = 0.65$, $P < 0.001$). Mean clutch size (number of oviductal eggs) varied little among species (3–4.67). However, relative clutch mass (volume of eggs in proportion to total adult weight) varied more widely (3–13%) among species. Sex ratios in samples of all species were male biased (ranging from 61–86% among species), and percentages of females collected that bore oviductal eggs ranged widely from 17–100% among species (Table 4).

Comparisons of resource dimensions reveal diet as a greater structuring agent than habitat use. Treating individual species as cases, habitat niche overlap is significantly greater than dietary niche overlap (Wilcoxon signed-rank test, $W = 10$, $P < 0.005$; for all species pairwise comparisons, see Table 5). As a temporal dimension, seasonal activity does not vary substantially among species. Individuals of all species were collected most often in December except for *B. fasciolatus*, most of which were collected in November. Although all species are nocturnal, precise information is not available for exact activity time on a daily cycle.

DISCUSSION

Several features stand out in our diet and microhabitat data. First, *Lerista* make up 66% of

TABLE 2. Numbers and volumes of prey type (percentage of total amount consumed in parentheses) in the diet of each snake species. Also shows number and percentage of snakes found to have empty stomachs. * Indicates a negligible amount of food content in stomach.

Sp. / Diet	S. anomolus	S. bertholdi	B. fasciolatus	B. semifasciatus	N. bimaculatus	Totals
<i>Lerista</i> sp.	number 29 (96.7%)	14 (82.4%)	0	0	0	43 (66.2%)
	volume 7.95 (98.8%)	5.25 (90.5%)	0	0	0	13.2 (68.8%)
<i>Ctenotus</i> sp.	number 1 (3.3%)	1 (5.9%)	2 (100%)	0	0	4 (6.2%)
	volume 0.1 (1.2%)	0.45 (7.8%)	0.35 (100%)	0	0	0.9 (4.7%)
<i>Ramphotyphlops</i> sp.	number 0	0	0	0	1 (100%)	1 (1.5%)
	volume 0	0	0	0	0.1 (100%)	0.1 (0.5%)
Eggs	number 0	0	0	14 (93.3%)	0	14 (21.5%)
	volume 0	0	0	4.7 (95.9%)	0	4.7 (24.5%)
Invertebrates	number 0	1 (5.9%)	0	0	0	1 (1.5%)
	volume 0	0.1 (1.7%)	0	0	0	0.1 (0.5%)
Unidentified	number 0	1 (5.9%)	0	1 (6.7%)	0	2 (3.1%)
	volume 0	*	0	0.2 (4.1%)	0	0.2 (1.0%)
Empty stomachs	114 (83.2%)	47 (75.8%)	20 (90.9%)	36 (70.6%)	13 (92.9%)	230 (80.4%)
Total	number 137	62	22	51	14	286
	volume 8.05	5.8	0.35	4.9	0.1	19.2

prey by number (69% by volume) consumed by all snakes, with most being *L. bipes*. These data confirm data presented by Shine (1984) that *Lerista* compose a substantial dietary component in these species. *Lerista* and all five snake species in this study are fossorial, spending most of their time burrowing under or "swimming" through sand, which should result in a great chance of habitat overlap and for these animals to encounter one another. However, some snake species in this study are more fossorial than others, which may contribute to variation in overlap of resource use. *Neelaps bimaculatus* is more of a "swimmer" than a burrower (ERP, pers. obs.), and the other species vary in size of the rostral shield and morphology of countersunk jaw kinesis (Scanlon and Shine, 1988), which may indicate degree of fossoriality. Second, our data confirm Shine's (1984) conclusion that *B. semifasciatus* is a dietary specialist on squamate eggs.

In this assemblage, *B. semifasciatus* is the only complete dietary specialist but is a habitat generalist. Lack of dietary competition may enable *B. semifasciatus* to exploit food resources in all microhabitats, whereas other species specialize on sandridge crests. Alternatively, distributions of snake species may simply reflect either distributions of most commonly used dietary resources or loose substrate on sandridge crests more suitable for burrowing. From this same locality, Pianka (1996) reported *L. bipes* were caught most often in traps on sandridge crests (42.5%), less often on sandridge bases (38.8%), and much less often on slopes and flats (15 and 3.7%, respectively; *N* = 614). These data conform to the hypothesis that microhabitat use of elapid snakes tracks that of their prey. Finally, the only invertebrate consumed by any snake was one ant by *S. bertholdi*, which was likely consumed inadvertently along with a *Lerista*. *Ctenotus* skinks were also found to be a minor part of diets of the two *Simoselaps* species, differing from data given by Shine (1984), which show that *Ctenotus* make up a major prey source for all five snakes except *B. semifasciatus* (the egg specialist). It is not clear why snakes in this study consumed fewer *Ctenotus* skinks. Because these snakes are nocturnal and *Ctenotus* skinks are diurnal, it is peculiar that they were found so frequently in diets of snakes analyzed by Shine (1984). Temporal partitioning between these snakes and *Ctenotus* skinks may reduce interaction and, hence, predation of small skinks. However, at this study site, 13 *Ctenotus* skink species occur, including five that could be considered abundant. Given their abundance, we might expect more snake predation on *Ctenotus* skinks than observed in this study.

TABLE 3. Means and SE for SVL, clutch size (CS), and relative clutch mass (RCM) in proportion to weight for fecund/gravid females. Standard errors are not given for *Brachyuropis fasciolatus* and *Neelaps bimaculatus* because of our small sample sizes for these species.

Species	SVL (mm)	CS	RCM	N
<i>S. anomalus</i>	190.69 ± 2.06	3 ± 0.2	9% ± 1.86	13
<i>S. bertholdi</i>	255.67 ± 6.3	4.67 ± 0.49	13% ± 4.06	6
<i>B. fasciolatus</i>	285	3	6%	1
<i>B. semifasciatus</i>	304.8 ± 7.59	3 ± 0.24	3% ± 0.8	15
<i>N. bimaculatus</i>	405	4	9%	2

No single ecological parameter shapes an entire assemblage. Abundance and diversity for any group of organisms are likely influenced by more factors than analyzed here. However, a quantitative attempt can be made to answer which ecological dimensions are most important in shaping apparent ecological diversity within communities. Pairwise comparisons between species of habitat niche overlap and dietary niche overlap allow inference of which factors have greater effect on community structure (Pianka, 1973, 1974). Here, diet is a much greater structuring agent than is habitat use. These results match the consensus that most snake assemblages are structured by diet (Luiselli, 2006; Toft, 1985). However, some authors have questioned whether interspecific competition plays any significant role in structuring communities (for a concise argument, see Reichenbach and Dalrymple, 1980).

Our study suffers from several shortcomings. Most notably, we had low sample sizes for some species. *Brachyuropis fasciolatus* and *N. bimaculatus* are represented by only 22 and 14 specimens, respectively. Only two specimens of *B. fasciolatus* and one specimen of *N. bimaculatus* contained any stomach contents. Limited dietary data give a likely incorrect representation of resource use and dietary specialization in these two species. Another limiting factor in our study is that specimens were collected mostly during the Austral spring seasons, when abundance and activity are high and many animals were likely to be caught in pit fall traps. However, during Austral winter

collections in 1992, none of these snake species was ever found in a pit trap. Finally, although pit fall traps have been shown to be useful in catching squamates, especially cryptic species, they have many drawbacks (Enge, 2001). A major disadvantage of using pit fall traps is that one cannot elucidate the exact moment that an animal was trapped; therefore, one cannot know the animal's precise time of activity. One can only assume that an animal has been caught in a trap sometime since the trap was last checked. Along with this, data on temperature, humidity, and others are useless in understanding any correlation between such environmental factors and animal activity. Another drawback to pitfall traps is that some animals may die in traps as a result of environmental factors and predation and not preserve well. Finally, some individuals might be resistant to pit fall trapping methods. Further, one cannot undergo a thorough comparative ecological study without taking into account phylogeny (Felsenstein, 1985). Previous attempts have been made to reconstruct phylogenies of Australian elapids by using morphological (Keogh, 1999) and molecular data (Keogh et al., 1998) but do not include more than two species from the entire *Simoselap-Brachyuropis-Neelaps* clade. A more detailed phylogeny of this group will be required to sort out effects of ecology and historical inertia in determining behaviors and habits of these snakes.

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TABLE 4. Sex ratios as percentages of the population for each species including percentage of females that bore oviductal eggs. Percentages for some species do not add up to 100% because sex could not be determined for some small juveniles.

Species	Total (N)	% ♂ in pop.	% ♀ in pop.	% of fecund ♀
<i>S. anomalus</i>	137	0.8	0.15	0.65
<i>S. bertholdi</i>	62	0.61	0.39	0.17
<i>B. fasciolatus</i>	22	0.86	0.09	0.5
<i>B. semifasciatus</i>	51	0.65	0.35	0.83
<i>N. bimaculatus</i>	14	0.79	0.14	1
Total / Average	286	0.73	0.23	0.55

TABLE 5. Pairwise comparisons between each species indicating amount of habitat niche overlap (captures per trap in each microhabitat) on the top right of the diagonal and dietary niche overlap (based on number of prey items in diet) on the bottom left of the diagonal.

	<i>S. anomalus</i>	<i>S. bertholdi</i>	<i>B. fasciolatus</i>	<i>B. semifasciatus</i>	<i>N. bimaculatus</i>
<i>S. anomalus</i>	—	0.884	0.836	0.658	0.893
<i>S. bertholdi</i>	0.997	—	0.875	0.885	0.885
<i>B. fasciolatus</i>	0.034	0.071	—	0.9	0.989
<i>B. semifasciatus</i>	0	0	0	—	0.843
<i>N. bimaculatus</i>	0	0	0	0	—

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- Brachyuropis fasciolatus*: (WAM: R147028–R147037, R155061–R155066); (ERP: R833, R26866, R26868, R26889, R28099, R28214).
- Neelaps bimaculatus*: (WAM: R147069–R147076, R155075–R155079); (ERP: R23353).
- Simoselaps anomalus*: (WAM: R147077–R147141, R156514–R156527); (ERP: R22943, R22944, R22949, R23105–R23110, R23139, R23140, R23382, R23424, R23425, R23524, R23525, R23682, R23683, R23751, R23765, R23766, R23784, R24006, R24317, R24627, R25726, R25742, R25807, R25813, R25836, R25844, R25850, R25852, R25987, R26018, R26262, R26763, R27009, R27011, R27238, R27247, R27248, R27356, R27381, R27484, R27489, R27538, R27615, R27619, R2767, R27675, R27676, R27947, R27957, R27982, R28004, R28010, R28070, R28071, R28096, R28369, R32113, R32702, R33123, R33267, R33276, R33277, R33294, R33314, R33407, R33425, R33430, R33490, R33492, R33532, R33540, R33555, R33587, R34110, R34111).
- Simoselaps bertholdi*: (WAM: R147142–R147171, R155099–R155102, R156509–R156511), (ERP: R1236, R23110, R23374, R23453, R24493, R25729, R25846, R25987, R26108, R26157, R26243, R27226, R27266, R27267, R27364, R27366, R27389, R27394, R27443, R27485, R27491, R27537, R27946, R28293, R28594, R29166, R31231, R3246, R32610, R33775, R34004, R3645).

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APPENDIX 1

All specimens examined have been deposited in the Western Australia Museum (WAM). Specimens with ERP catalog numbers have not yet been cataloged by WAM. All lizards were collected by ERP; only the most recently collected specimens have been cataloged by WAM. The following catalog numbers are given separately for each species.