

# Ecological traits and conservation biology of five fossorial ‘sand-swimming’ snake species (*Simoselaps*: Elapidae) in south-western Australia

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## Abstract

Although small, nocturnal, fossorial snakes are a significant component of the reptile fauna in many parts of the world, their biology is poorly known. An 11-year pit-trapping study in urban bushland remnants near the city of Perth, Western Australia, provided data from > 500 captures of small fossorial snakes of the genus *Simoselaps*. The five species differed in relative abundances and in distribution, both among localities and among habitats within a single locality. For example, three saurophagous taxa (*Simoselaps bertholdi*, *S. bimaculatus*, *S. calonotos*) were most abundant in *Banksia* woodland, whereas two species that feed on reptile eggs (*S. semifasciatus*, *S. fasciolatus*) were most abundant in coastal heath. Capture rates for most species were low (for three of the five species, < one specimen captured per 1000 trapdays), and these taxa may be genuinely rare in most of the habitats that we surveyed. Activity patterns were highly seasonal, with little activity in winter or in midsummer. The two oophagous species showed a more restricted activity period (late spring–early summer) than did species with broader dietary habits. In the most abundant taxon (*Simoselaps bertholdi*), males were active mainly during spring (the mating season) and females during autumn, after oviposition. Capture rates and body condition of the captured snakes varied substantially among seasons and across years. Low capture rates mean that very prolonged surveys are needed to determine reliably whether or not a taxon occurs on any given site.

**Key words:** habitat use, activity patterns, sexual dimorphism, snake, Elapidae

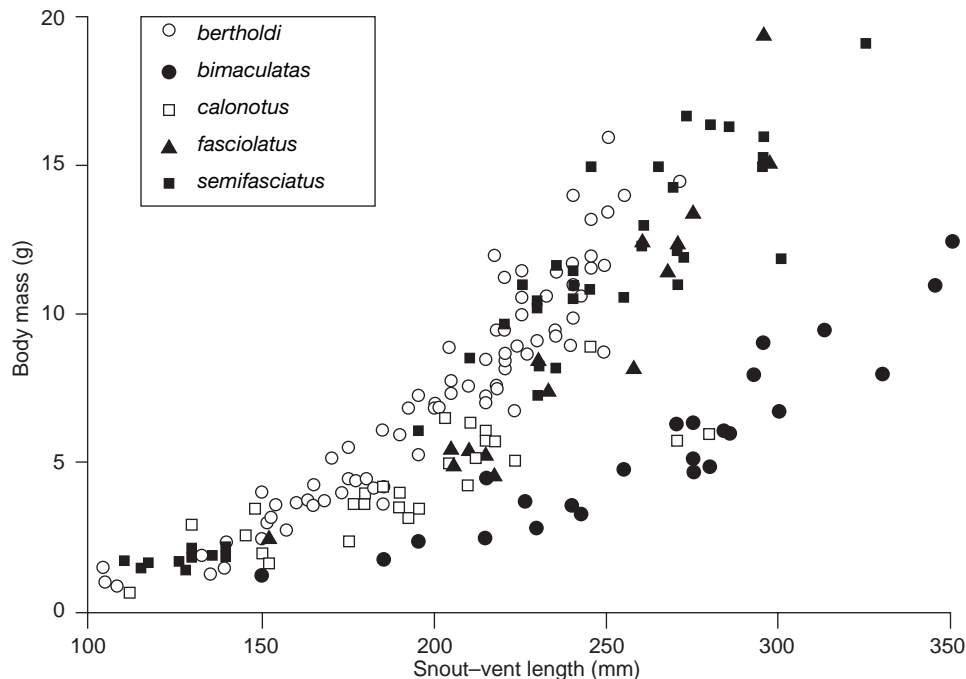
## INTRODUCTION

Available information on the ecology of squamate reptiles is strongly biased towards large or abundant species with attributes that facilitate scientific study (e.g. diurnal behaviour, occupancy of particular kinds of habitats). Thus, for example, phrynosomatid lizards have achieved the status of ‘model vertebrates’ because of their abundance and ease of observation (Huey, Pianka & Schoener, 1983; Vitt & Pianka, 1994), whereas most species of snakes remain unstudied because they tend to be highly secretive, cryptic and infrequently active (e.g. Seigel, 1993). In the same way, scientific studies on snakes have concentrated on large diurnal species that are frequently active above-ground (e.g. Seigel & Collins, 1993; Shine & Madsen, 1996). The many snake species that are small, nocturnal, and fossorial have attracted less attention. Although the development of miniature radiotransmitters has played

a crucial role in the scientific study of snake ecology, the technology is a mixed blessing. By making a subset of snake species (those large enough to carry telemeters) more accessible to research, radiotelemetry methods have discouraged work on smaller species.

This bias has had unfortunate consequences for conservation planning, because small fossorial species may be at particular risk from anthropogenic disturbance. These kinds of snakes are poorly suited to moving long distances across open areas, especially across artificial substrates that preclude burrowing. Surface activity may introduce dangers from predation (by introduced foxes and cats as well as native taxa) or desiccation. Thus, small fossorial species may be strongly disadvantaged by habitat fragmentation. More generally, the ecology of small snakes is of interest in its own right. Comparative analyses suggest that body size is a crucial variable for an organism’s ecology, with strong effects on trophic habits (e.g. size of ingestible prey), survival rates (e.g. vulnerability to predation), reproductive output (e.g. size and number of offspring), thermoregulation (e.g. heating and cooling rates) and habitat use (e.g. ability to penetrate small crevices)

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**Fig. 1.** Body shapes of the five *Simoselaps* species; note that *S. bertholdi* is extremely heavy-bodied whereas *S. bimaculatus* is very slender.

(Pough, 1980; Peters, 1983; Reiss, 1989). Perhaps for this reason, most of the truly fossorial 'sand-swimming' snakes are characterized by small body sizes; this adaptive zone may be unavailable to larger species (Pough, 1980). Information on the ecology of small 'sand-swimming' snakes is thus of considerable interest, especially for taxa that belong to poorly-known lineages, inhabiting areas where the ecology of snakes has attracted little scientific study. The present paper provides data on just such a lineage: fossorial elapid snakes inhabiting sandy habitats of south-western Australia. The information derives from a decade-long survey of the herpetofauna of bushland remnants around the city of Perth, in south-western Australia.

## STUDY AREAS AND METHODS

### Study species

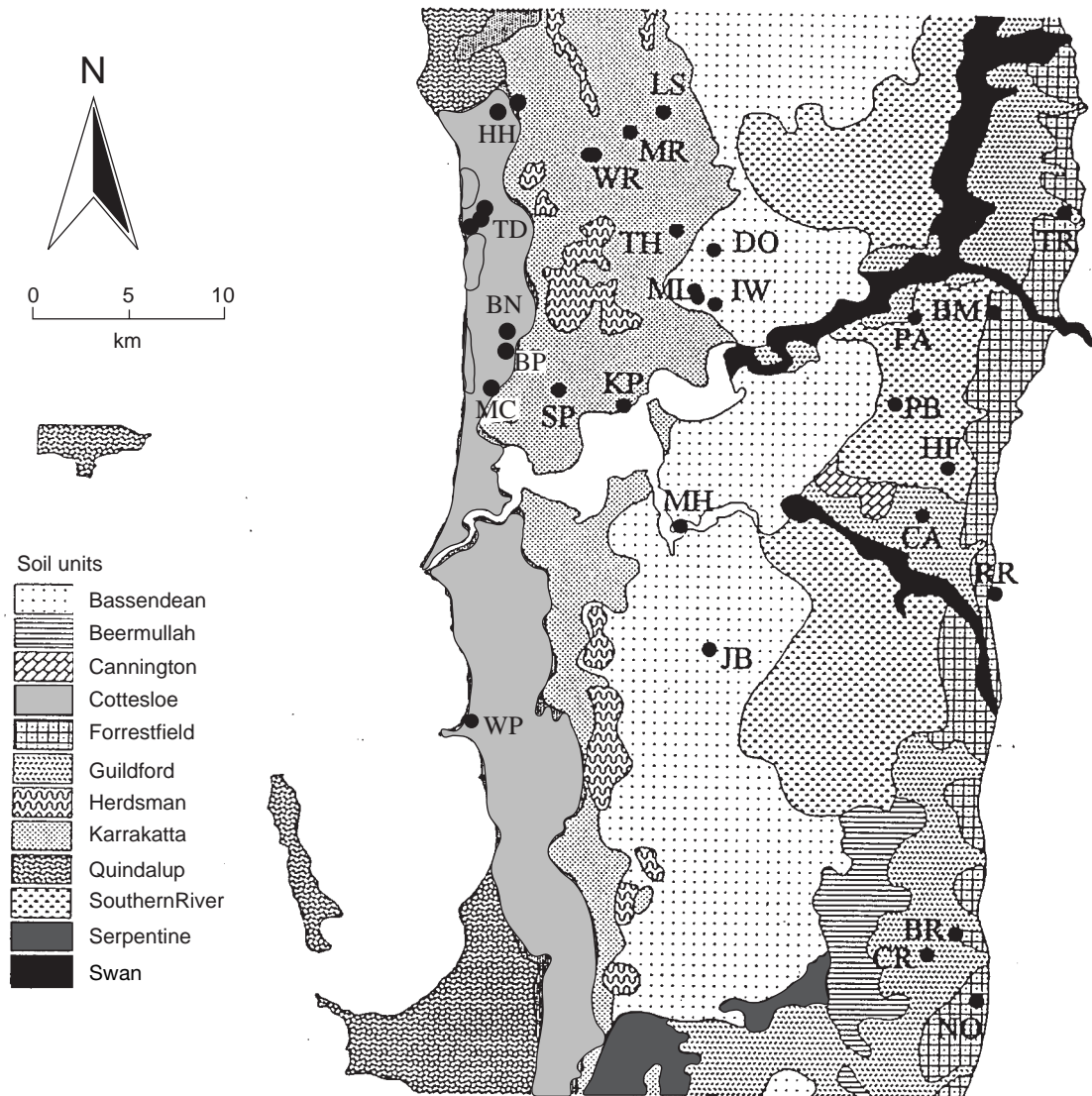
Five species of small fossorial elapid snakes occur in broad sympatry on the Swan Coastal Plain, on the west coast of Western Australia (How & Dell, 1990, 1993). We follow Cogger (1992) in treating these taxa as congeneric (within *Simoselaps*), but some of these species have previously been allocated to separate genera (*Neelaps*: Cogger, 1975), or combined with other taxa into a larger group (*Vermicella*: e.g. Storr, 1967, 1979; see Keogh & Smith, 1996; Keogh, Shine & Donnellan, 1998). This complex nomenclatural history reflects the considerable diversity within the group; for example, *S. bertholdi* is brightly banded in black and orange, whereas *S. bimaculatus* is brown. Morphologically, some of the *Simoselaps* species are strongly

convergent with 'sand-swimming' snakes of other desert areas, such as the American *Chilomeniscus*, *Chionactis*, *Gyalopion*, *Sonora* and *Tantilla* (Shaw & Campbell, 1974) and the African *Prosymna*, *Elapsoidea* and *Chilorhinophis* (Branch, 1988). The five *Simoselaps* species show more interspecific variation in body shape than occurs within most snake genera (and in some families). Figure 1 plots mass against body length, and shows that some of the taxa (e.g. *S. bertholdi*, *S. semifasciatus*) are very heavy bodied whereas *S. bimaculatus* is extremely slender. The other species are intermediate in shape. Published data on the ecology and reproductive biology of *Simoselaps* are based entirely on dissection of preserved specimens in museum collections (Shine, 1984; Clarke & How, 1995; Strahan, How & Dell, 1998). Given the heterogeneity of climates and habitats within the large geographic ranges of most of these taxa (Cogger, 1992), and the conservation concerns voiced about some of them (Cogger *et al.*, 1993), it is of interest to examine their ecology within a single region.

### Study area

Our data are derived from captures in fenced pitfall traps set out at 32 separate bushland locations around Perth. These locations were selected to represent the major landforms across the Swan Coastal Plain (McArthur & Bettenay, 1960), whereas the 75 sampling sites within these locations were chosen to represent the major vegetational types at each location. The distribution of all sampling locations is shown in Fig. 2.

Most locations were surveyed during a single year, but 6 locations were monitored for 3 successive years



**Fig. 2.** Distribution of 32 survey locations on the Swan Coastal Plain that were sampled between 1986 and 1997. BM Bushmead Reserve, BN Bold Park North, BP Bold Park, BR Brickwood Reserve, CA Cannington, CR Cardup Reserve, DO Dianella Reserve, HF Hartfield Park, HH Hepburn Heights, IW Inglewood Reserve, JK Jandakot Airport, KP Kings Park, LS Landsdale Farm School, MC Mount Claremont, MH Mount Henry, ML Mount Lawley, MR Marangaroo Reserve, NO Norman Road, PA Perth Airport North, PB Perth Airport South, RR Rushton Road Reserve, SP Shenton Park Bushland, TD Trigg Dune, TH Tuart Hill, TR Talbot Road Reserve, WP Woodman Point Reserve, WR Warwick Road. Major soil units are also indicated.

and Bold Park was sampled for 11 successive years. Bold Park, occupying 338 ha of native bushland and lying adjacent to the Indian Ocean west of Perth, thus provided most of our data. Within Bold Park, we surveyed 5 habitats which represented the principal vegetation types determined by Keighery, Harvey & Keighery (1990) for this location. These habitats were: (1) BP1 mixed coastal heath; (2) BP2 *Dryandra sessilis* shrubland; (3) BP3 *Banksia attenuata* / *B. menziesii* low woodland; (4) BP4 *Eucalyptus gomphocephala* (Tuart) woodland; (5) BP5 *Olearia* heath.

Sites BP1 and BP5 were located on Holocene sands of the near-coastal Quindalup Dune landform and the remainder (BP2, BP3, BP4) were located on the adjacent Pleistocene Cottesloe sands of the Spearwood Dune

landform. In addition, 8 near-coastal sites at Bold Park were sampled intensively for 12 months during 1988 by Jiang Wang Gao. We have used his unpublished *Simoselaps* capture data in conjunction with our own results to examine patterns of activity among the 5 species.

#### Methods

Traplines were checked and cleared each morning. Most locations were monitored for around 50 days during a single year with intensive sampling during spring and early summer. Sites and locations sampled before spring 1993 (locations BP, PA and CA) had fenced pitfall

**Table 1.** Locations (sizes in ha) in the Perth area where *Simoselaps* species have been captured during the survey of bushland remnants, 1986–1997. *N* = number of individual snakes trapped; *N*/100p, captures per 100 pitdays

Location	No. of pitdays	Species									
		<i>bertholdi</i>		<i>bimaculatus</i>		<i>calonotos</i>		<i>fasciolatus</i>		<i>semifasciatus</i>	
		<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p
BP (338)	34828	284	0.816	34	0.098	34	0.098	17	0.049	45	0.129
TD2 (8)	1674	25	1.493	–	–	4	0.239	–	–	–	–
MC (45)	1512	14	0.926	–	–	–	–	–	–	–	–
TD1 (22)	1674	8	0.478	–	–	–	–	–	–	1	0.060
SP (24)	3420	5	0.146	–	–	–	–	–	–	–	–
HH1 (43)	1431	4	0.280	–	–	–	–	–	–	1	0.070
TD4 (16)	963	3	0.312	–	–	1	0.104	–	–	–	–
KP (270)	8793	3	0.034	3	0.034	–	–	–	–	–	–
HH4 (20)	360	1	0.278	1	0.278	–	–	–	–	1	0.278
LS (16)	954	1	0.105	–	–	1	0.105	–	–	–	–
PA (250)	2232	–	–	2	0.090	–	–	–	–	–	–
TR (90)	1719	–	–	–	–	–	–	–	–	4	0.233
RR (10)	918	–	–	–	–	–	–	–	–	3	0.327
BN (12)	837	–	–	–	–	–	–	–	–	–	–
CA (35)	1116	–	–	–	–	–	–	–	–	–	–
PB (150)	1683	–	–	–	–	–	–	–	–	–	–
TH (9)	1044	–	–	–	–	–	–	–	–	–	–
IW (1)	522	–	–	–	–	–	–	–	–	–	–
MH (13)	954	–	–	–	–	–	–	–	–	–	–
JK (100)	954	–	–	–	–	–	–	–	–	–	–
WO (50)	1431	–	–	–	–	–	–	–	–	–	–
DO (4)	972	–	–	–	–	–	–	–	–	–	–
MR (28)	954	–	–	–	–	–	–	–	–	–	–
WR1 (14)	477	–	–	–	–	–	–	–	–	–	–
WR2 (29)	477	–	–	–	–	–	–	–	–	–	–
ML1 (1)	504	–	–	–	–	–	–	–	–	–	–
ML2 (2)	504	–	–	–	–	–	–	–	–	–	–
BM (19)	459	–	–	–	–	–	–	–	–	–	–
HF (25)	459	–	–	–	–	–	–	–	–	–	–
BR (43)	936	–	–	–	–	–	–	–	–	–	–
CR (75)	1404	–	–	–	–	–	–	–	–	–	–
NO (130)	918	–	–	–	–	–	–	–	–	–	–
Total		336		40		40		17		55	

traps consisting of 6 pitfall traps placed in a line between 7 and 8 m apart. Each pit trap consisted of a 17.5 cm diameter PVC pipe that was 60 cm deep and sealed at the bottom with flyscreen mesh. Drift fences were 50 m long flyscreen mesh (30 cm high but dug into the soil 5 cm) which crossed each of the 6 pitfall traps. From spring 1993 onwards, all sampling sites consisted of 20-l buckets as pitfalls arranged in a 3 × 3 grid and spaced 10 m apart; drift fences of 6–7 m were placed over the centre of each pitfall trap. Each pit set open for 24 h is referred to as a pitday.

Trapped reptiles were identified and measured for snout–vent length (SVL) and tail length (TL). Body mass was determined by weighing before release. Tail length was recorded routinely for the last 9 years of study so that the sex of individuals could be determined from their tail to body ratio (TBR: see Clarke & How, 1995). Based on Clarke & How's 1995 study, we assigned sex to field-caught snakes using the following criteria: males were those individuals with TBR ratios > 0.1122 (*S. bertholdi*), 0.0858 (*S. bimaculatus*), 0.1397

(*S. calonotos*), 0.1052 (*S. fasciolatus*) and 0.0929 (*S. semifasciatus*). Adults were distinguished from juveniles on the basis of SVL, with the minimum size at maturity for each taxon based on dissection of museum specimens by Shine (1984) and Strahan *et al.* (1998). Statistical tests were conducted using Statistix (1996). Significance levels ( $P < 0.05$ ) on group means were determined using the least significant difference (LSD) test.

## RESULTS

### Distribution and abundance

We recorded more than 500 captures of *Simoselaps*, comprised of 349 captures of Jan's banded snakes *S. bertholdi*, 40 captures of black-naped snakes *S. bimaculatus*, 40 captures of black-striped snakes *S. calonotos*, 17 captures of narrow-banded snakes *S. fasciolatus* and 55 captures of southern shovel-nosed snakes *S. semifas-*

**Table 2.** The number of individuals captured and the effort expended to trap the five *Simoselaps* species in the five habitats at Bold Park. Captures at other Bold Park sites monitored by Jiang (unpubl.) are also listed. *N* = number of captures; *N*/100p = captures per 100 pitdays

Location	No. of pitdays	Species									
		<i>bertholdi</i>		<i>bimaculatus</i>		<i>calonotos</i>		<i>fasciolatus</i>		<i>semifasciatus</i>	
		<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p
BP1	5817	55	0.946	7	0.12	4	0.069	10	0.172	22	0.378
BP2	2388	24	1.005	1	0.042	4	0.168	1	0.042	2	0.084
BP3	5817	94	1.616	11	0.189	12	0.206	3	0.052	5	0.086
BP4	5817	47	0.808	4	0.069	4	0.069	1	0.017	6	0.103
BP5	3429	28	0.817	8	0.233	6	0.175	2	0.058	6	0.175
Total	23268	248	1.066	31	0.133	30	0.129	17	0.073	41	0.176
Other	11560	36	0.311	3	0.026	4	0.035	0	0	4	0.035

*ciatus*. Undoubtedly, some of these records involve repeated captures of the same individuals. Because we did not mark the snakes, we cannot determine the magnitude of this effect. However, it is unlikely to affect any of our conclusions substantially, given the large area and long timescale of our study combined with the generally long intervals between successive captures of most species (see below).

The five species differed substantially in abundance and distribution across our study sites. Contingency table analysis of the data on numbers of captured animals (Table 1) shows that the relative abundances of each taxon varied among sites (excluding sites where no snakes were captured;  $\chi^2 = 128.07$ ,  $P < 0.0001$ , d.f. = 48). Because this test relies upon low expected values in many cells, we repeated it after combining data into larger categories. The result remained robust (comparing *S. bertholdi* vs the other species, in the three localities with largest sample sizes only:  $\chi^2 = 10.05$ ,  $P < 0.007$ , d.f. = 2). *Simoselaps bertholdi* was the most widespread species, captured at 10 of the 32 locations sampled (Table 1). The most restricted taxon was *S. fasciolatus*, known only from Bold Park (although it was recorded in all five sampling sites there). The three remaining species were trapped at between four and six locations each (Table 1).

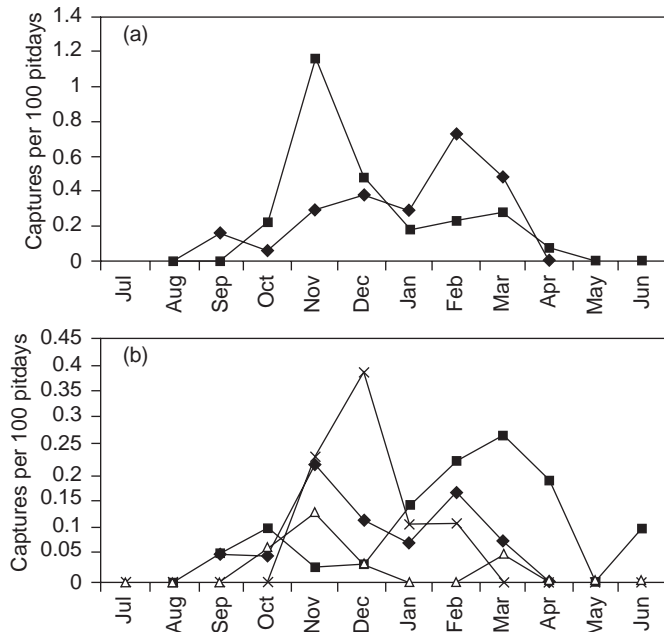
Most of the *S. bertholdi*, *S. calonotos* and *S. fasciolatus* were captured on the Quindalup Dunes or the Cottesloe sands of the Spearwood Dunes; *S. bimaculatus* and *S. semifasciatus* were recorded on other landform types and occupied a greater longitudinal range across the Swan Coastal Plain (Table 1). The highest rates of capture for *S. semifasciatus* were at locations TR and RR, on alluvia of the Ridge Hill Shelf landform to the east of the Swan Coastal Plain.

*Simoselaps bertholdi* was the most abundant snake that we encountered in these urban bushland remnants. However, even at locations where these animals were relatively abundant, our capture rates were low: on average, less than one individual per 100 pitdays. All other species were captured much less frequently, with an average of > 1000 pitdays required to capture a single individual of *S. bimaculatus*, *S. calonotos* or *S. fasciolatus*.

Because of these low rates of capture, long periods often elapsed between successive captures of *Simoselaps* species in Bold Park. For example, no *S. bimaculatus* individuals were captured for 35 months (3912 pitdays) between 10 December 1988 and 24 November 1991; *S. calonotos* was not captured for 32 months (4248 pitdays) between 12 February 1991 and 24 October 1993 and *S. fasciolatus* was not captured for 32 months (3912 pitdays) between 31 March 1991 and 21 November 1993. The rarity of capture of species in certain habitats is best illustrated by *S. fasciolatus*, a species captured only once at BP4 in 11 years of sampling that encompassed 5817 pitdays during 779 days of trapping in that habitat. These low probabilities of capture suggest that many locations and most sites were not trapped intensively enough for us to be confident that a given species was absent from the area (Table 1).

#### Distribution across habitats

The differences in distribution of the five *Simoselaps* species across our study sites (above, and see Table 1) suggest that the taxa may be using different habitats. To evaluate this possibility, we can look in more detail at the data from Bold Park, the most intensively studied area (34 798 pitdays of trapping over 11 years; 82.6% of all captures; see Table 2). This analysis confirms that the five *Simoselaps* species are found in different habitats (from Table 2, contingency table test comparing numbers of each species among habitats:  $\chi^2 = 41.07$ ,  $P < 0.001$ , d.f. = 16). The three saurophagous taxa (*S. bertholdi*, *S. bimaculatus* and *S. calonotos*) were encountered most frequently on *Banksia* woodland on the Cottesloe sands of the Spearwood Dune formation (site BP3). In contrast, the two oophagous species (*S. fasciolatus* and *S. semifasciatus*) were captured most often on coastal heath on the Quindalup Dune formation (BP1; see Table 2). Even after Bonferroni correction for multiple non-independent tests, the capture frequencies of these two latter taxa among habitat types were strongly correlated (data from Table 2)  $n = 5$  habitat types,  $r = +0.97$ ,  $P < 0.005$ ).



**Fig. 3.** Seasonal activity pattern expressed as number of captures per 100 pitdays in (a) *Simoselaps bertholdi* at Bold Park for males (■) and females (◆) and (b) *S. bimaculatus* (◆), *S. calonotos* (■), *S. fasciolatus* (△) and *S. semifasciatus* (x).

### Seasonal activity patterns

Activity (as judged by capture rates) was highly seasonal in all of the *Simoselaps* species (Fig. 3). The peak in activity for most species occurred during November and December, with a secondary peak in February. Very little activity was recorded between May to August (the austral winter, which is cool and wet in the Perth region; Seddon, 1972). Despite this overall similarity, however, there were strong differences among species in monthly rates of capture. Omitting data for the cooler months of April to August (when very few snakes were caught), contingency table tests reject the null hypothesis of similar monthly patterns of capture rates in the five species ( $\chi^2 = 76.19$ ,  $P < 0.0001$ , d.f. = 24). Most two-species comparisons using the same test were also highly significant; *S. calonotos* was the most atypical species in seasonal activity patterns, whereas *S. bertholdi* and *S. bimaculatus* were most similar to each other. Another way to clarify interspecific similarities and differences in monthly capture rates is to correlate capture rates of the different species among months (i.e. do months with high capture rates of one species, also give high capture rates for other taxa?). Again, this analysis emphasized the distinctiveness of *S. calonotos*; interspecific correlations of monthly capture rates were highly significant ( $P < 0.001$ ) for five of six comparisons not involving *S. calonotos*, but were all non-significant ( $P > 0.30$ ) for comparisons of capture rates between *S. calonotos* vs any other species.

Sample sizes for *S. bertholdi* were large enough for us to examine sex differences in activity. The two sexes of *S. bertholdi* at Bold Park showed markedly different activity patterns (Fig. 3; contingency table test as above:

$\chi^2 = 43.67$ ,  $P < 0.0001$ , d.f. = 6). Male activity peaked in spring (November–December), while female activity peaked in late summer (February–March). The combined result of these two patterns is that overall capture rates for this species exhibited two distinct peaks.

The two oophagous species (*S. fasciolatus* and *S. semifasciatus*) showed briefer periods of activity each year than did the other three saurophagous species (Fig. 3). To quantify this difference, we calculated the proportions of snake captures for each species in each month (Fig. 3). A more restricted period of activity should be reflected in a higher variance in this score (because many months will have zero readings, whereas others will have high values). An equality of variances test confirmed that variances in monthly capture rates were significantly higher in the two oophagous species than in the three saurophages ( $F_{21,32} = 3.09$ ,  $P < 0.007$ ).

### Annual activity patterns

There was marked variation among years in capture rates of *Simoselaps* at Bold Park (Table 3). The least variation in annual capture rates occurred in the most abundant species (*S. bertholdi*) and greatest variation in the rarest (*S. fasciolatus*). Thus, the coefficient of variation was inversely related to the mean frequency of capture of the species, although this correlation did not attain statistical significance (from Table 3:  $n = 5$  species,  $r = +0.84$ ,  $P = 0.07$ ). The magnitude of year-to-year variation was greater than would be expected under the null model of no significant annual variation in capture rates (for *S. bertholdi*, comparing numbers of successful vs unsuccessful pitdays per year:  $\chi^2 = 25.89$ ,  $P < 0.004$ , d.f. = 10).

Capture rates of the five species varied in different ways from year-to-year (contingency table test on data on captures from Table 3:  $\chi^2 = 63.74$ ,  $P < 0.01$ , d.f. = 40; and correlation analysis revealed no significant correlations between capture rates of any species-pair across the 11 years of the study; all  $P$ -values  $> 0.33$ ). Thus, the five *Simoselaps* species apparently respond differently to year-to-year variations in factors such as weather and prey availability. Precipitation data for November and December each year from Perth metropolitan weather records allowed us to investigate the situation further. These analyses supported the idea that the numbers of each *Simoselaps* species captured varied with rainfall; for example, drier conditions in spring and early summer increased the numbers of *S. calonotos* that were captured (November precipitation vs capture rate for *S. calonotos*;  $n = 11$  years,  $r = -0.75$ ,  $P < 0.006$ ) but decreased captures of *S. bertholdi* (December precipitation vs capture rate,  $n = 11$  years,  $r = +0.77$ ,  $P < 0.004$ ).

### Sex ratios and sexual dimorphism

Males were captured more often than females in all *Simoselaps* species at Bold Park (Table 4). This bias was

**Table 3.** Numbers of individual *Simoselaps* trapped during each year of the Bold Park survey and the trapping effort expended. *N* = number of snakes captured; *N*/100p = captures per 100 pitdays

Year	No. of pitdays	Species									
		<i>bertholdi</i>		<i>bimaculatus</i>		<i>calonotos</i>		<i>fasciolatus</i>		<i>semifasciatus</i>	
		<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p	<i>N</i>	<i>N</i> /100p
1986–87	480	6	1.250	2	0.417	1	0.208	–	0.000	1	0.208
1987–88	1320	22	1.667	3	0.227	4	0.303	2	0.152	1	0.076
1988–89	1344	21	1.563	1	0.074	3	0.223	2	0.149	6	0.446
1989–90	1680	10	0.595	–	0.000	5	0.298	–	0.000	2	0.119
1990–91	1344	18	1.339	–	0.000	3	0.223	3	0.223	4	0.298
1991–92	1176	23	1.956	2	0.170	–	0.000	–	0.000	2	0.170
1992–93	2232	22	0.986	2	0.090	–	0.000	–	0.000	6	0.269
1993–94	3204	28	0.874	6	0.187	6	0.187	2	0.062	11	0.343
1994–95	3744	30	0.801	3	0.080	5	0.134	1	0.027	1	0.027
1995–96	3744	34	0.908	4	0.107	1	0.027	6	0.160	5	0.134
1996–97	3060	34	1.111	8	0.261	2	0.065	1	0.033	2	0.065
Mean		1.186 ± 0.414		0.147 ± 0.123		0.152 ± 0.113		0.073 ± 0.082		0.196 ± 0.131	
CV%		34.9		84.0		74.5		112.3		66.6	

**Table 4.** Body sizes and dates of capture of five fossorial snake species on the Swan Coastal Plain. Table shows mean values for adult specimens, ±SD. SVL = snout–vent length (mm). Probability levels (\**P* < 0.05, \*\*\**P* < 0.001) for the existence of significant sexual size dimorphism are indicated for the smaller of the two sexes where significant dimorphism exists

	<i>bertholdi</i>	<i>bimaculatus</i>	<i>calonotos</i>	<i>fasciolatus</i>	<i>semifasciatus</i>
Male SVL (mm)	192.1 ± 15.2(140)***	289.2 ± 35.2(13)	201.0 ± 16.5(12)	265.2 ± 35.4(9)	249.3 ± 26.6(23)
Male SVL range (mm)	150–225	230–355	180–223	205–310	195–295
Minimum adult SVL (mm)	143	230	171	202	192
Female SVL (mm)	214.7 ± 25.7(69)	323.9 ± 61.2(9)	228.7 ± 41.4(6)	217.7 ± 14.2(3)	273.1 ± 38.1(9)
Female SVL range (mm)	165–270	243–411	190–280	205–233	230–325
Minimum adult SVL (mm)	164	237	186	205	196
Male mass (g)	6.47 ± 1.41(139)***	7.65 ± 3.97(13)	4.89 ± 1.04(12)	12.38 ± 5.68(9)	11.93 ± 2.76(23)
Male mass range (g)	3.10–9.80	2.89–18.50	3.60–6.40	4.60–20.50	6.10–16.40
Female mass (g)	8.78 ± 3.09(68)	10.32 ± 5.91(9)	5.15 ± 2.21(6)	6.13 ± 1.18(3)	13.53 ± 4.88(9)
Female mass range (g)	3.60–16.00	3.30–17.50	3.20–8.90	5.40–7.50	7.30–21.50
Earliest seasonal capture	18 September	12 September	21 September	11 October	11 November
Latest seasonal capture	8 May	27 March	23 June	31 March	13 February

statistically significant (i.e. different from a 50:50 sex ratio) for the species with the largest sample sizes (*S. bertholdi*,  $\chi^2 = 24.12$ ,  $P < 0.01$ , d.f. = 1; *S. semifasciatus*,  $\chi^2 = 6.13$ ,  $P < 0.05$ , d.f. = 1). Adult males averaged smaller than females in all of the species except *S. fasciolatus*, for which our sample was too small to establish adult sizes with confidence (Table 4; note that we captured a much larger *S. fasciolatus* individual (390 mm SVL, 38.5 g) of undetermined sex, early in the study). The sex difference in adult body lengths and masses was statistically significant for the most abundant species (*S. bertholdi*), but not for the other taxa (Table 4). Table 4 is based entirely on the Bold Park sample; slightly larger specimens of *S. bimaculatus* (421 mm SVL, 18.5 g) and *S. semifasciatus* (a female, 358 mm SVL and 24 g) were trapped at sites other than Bold Park.

The sexes within *Simoselaps* species differ in body shape as well as absolute size, with males tending to be more heavy-bodied than females at the same snout–vent length. For example, a heterogeneity of slopes test

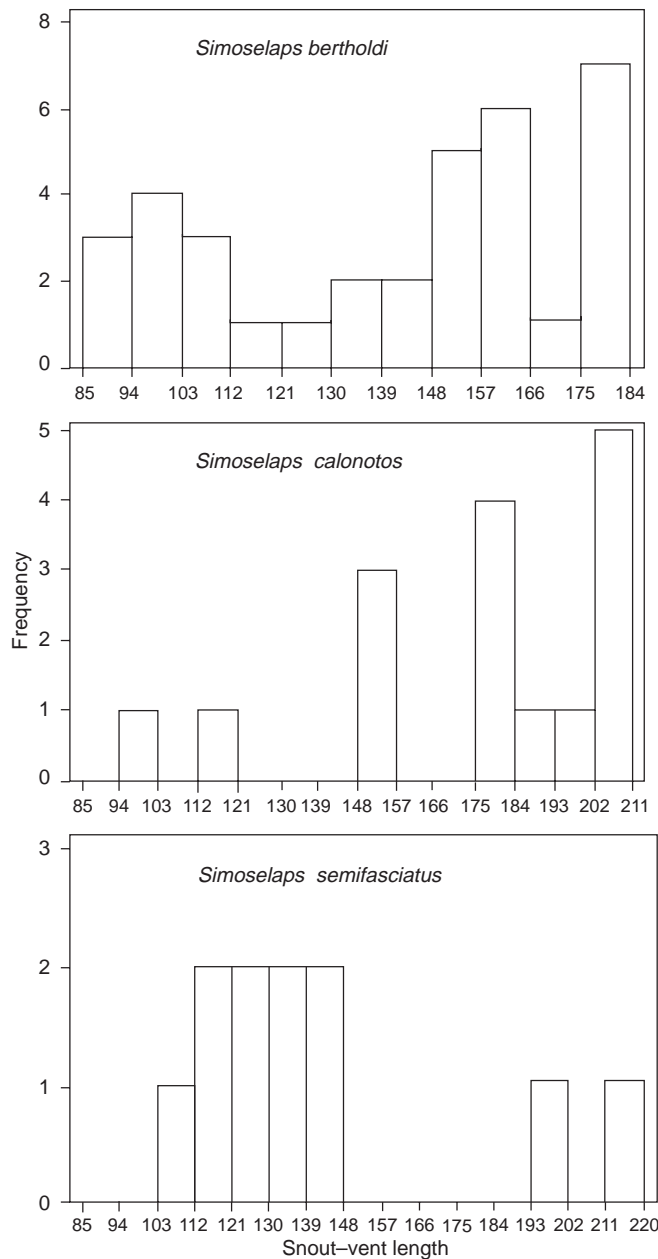
shows that the rate at which ln body mass increases with ln SVL is greater in male *S. bertholdi* than in female conspecifics (see Table 5; restricting attention to specimens < 225 mm SVL, to ensure overlap in sizes between the two sexes: slopes  $F_{1,200} = 9.58$ ,  $P < 0.003$ ). The sexes also differ in body shape in the slender-bodied *S. bimaculatus* (slopes  $F_{1,20} = 0.03$ ,  $P = 0.86$ ; intercepts  $F_{1,21} = 4.88$ ,  $P < 0.04$ ) and in *S. semifasciatus* (slopes  $F_{1,34} = 0.15$ ,  $P = 0.70$ ; intercepts  $F_{1,35} = 4.23$ ,  $P < 0.05$ ). However, we detected no sex difference in body shape in *S. calonotos* (slopes  $F_{1,20} = 0.23$ ,  $P = 0.64$ ; intercepts  $F_{1,21} = 0.52$ ,  $P = 0.48$ ).

#### Hatching and growth

The most direct information on reproductive seasonality comes from captures of gravid snakes, but we caught very few such animals (three *S. bertholdi* on 24 November, 29 November, 7 January; one *S. bimaculatus* on 24 December; one *S. semifasciatus* on 27 December).

**Table 5.** Values for the linear regression analyses, for *Simoselaps* populations from Bold Park, based on natural log transformed variables of snout–vent length (mm) and mass (g)

Species	Constant	Slope	N	F value	P	Adjusted r <sup>2</sup>
<i>bertholdi</i>						
Male	−13.289	2.875	275	2525.1	< 0.0001	0.9021
Female	−12.816	2.788	143	840.6	< 0.0001	0.8553
Male plus female	−13.923	2.988	89	1497.8	< 0.0001	0.9445
<i>bimaculatus</i>	−14.465	2.892	30	358.6	< 0.0001	0.9250
<i>calonotos</i>	−11.176	2.393	32	116.6	< 0.0001	0.7885
<i>fasciolatus</i>	−14.674	3.068	17	323.4	< 0.0001	0.9527
<i>semifasciatus</i>	−12.107	2.633	44	835.5	< 0.0001	0.9510



**Fig. 4.** The snout–vent length (SVL) distributions for *Simoselaps bertholdi*, *S. calonotos* and *S. semifasciatus* captured at Bold Park. Distributions extend up to an SVL of 20 mm above the minimum size at maturity for females and are for January–April for *S. bertholdi* and *S. calonotos* and November–December for *S. semifasciatus*.

Captures of hatchlings were more common, and provide an indication of dates of hatching. The smallest individuals of *S. bertholdi*, *S. calonotos* and *S. fasciolatus* were trapped from late summer to autumn (January–March), corresponding to the expected time of hatching if oviposition occurs in late spring–early summer (as has been shown from museum dissections: Shine, 1984; Strahan *et al.*, 1998). However, the smallest *S. bimaculatus* and *S. semifasciatus* individuals were trapped in October and December, respectively.

Snout–vent lengths of individual *S. bertholdi*, *S. calonotos* and *S. semifasciatus*, up to 20 mm longer than the minimum female SVL at maturity (Table 4) are plotted for the Bold Park populations in Fig. 4. For *S. bertholdi* and *S. calonotos*, captures between January and April are combined. These plots indicate that two nearly discrete cohorts of *S. bertholdi* (85–120 mm and 130–166 mm) are discernible during the hotter summer months. In turn, this result suggests that adult size is attained sometime in the third year of life. For *S. semifasciatus*, captures over the period of peak activity (November–December) are combined and suggest that only a single juvenile cohort is present (Fig. 4).

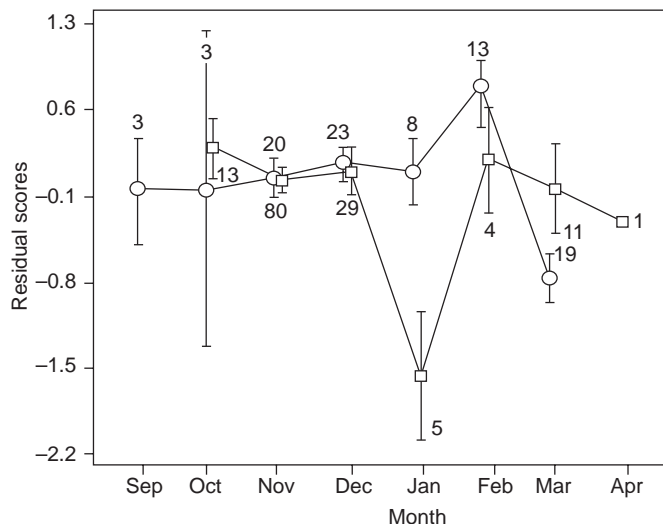
**Body condition indices**

To provide an index of body condition for each captured individual, we calculated residual scores from linear regressions of ln-transformed mass vs ln SVL, separately for each species. The body condition of the snakes was examined separately by sex for our analyses of *S. bertholdi* (because of significant sex differences in body shape – see above), but we combined sexes for analyses of the other species because the sex difference in these taxa was slight, and sample sizes were smaller.

**Month**

Male *S. bertholdi* showed similar body condition throughout the year, but with a significant decline in January. Female condition declined rapidly from February to March, presumably due to oviposition (Fig. 5). The condition indices of all species of *Simoselaps* in Bold Park showed substantial variation among





**Fig. 5.** Body condition of female (○) and male (□) *S. bertholdi* from Bold Park plotted against the months of capture. The body condition indices were calculated as the residual scores from the general linear regression of ln-transformed mass vs snout-vent length. The mean, standard error and sample size are shown.

seasons (Fig. 6). Most species decreased in condition over the period from spring to early summer, but *S. calonotos* showed the opposite pattern (Fig. 6).

### Year

A two-factor ANOVA (with sex and year as the factors, and condition index as the dependent variable) confirmed that the body condition of *S. bertholdi* differed between the sexes (as would be expected from the above analyses showing sexual dimorphism in body shape;  $F_{1,8} = 11.53$ ,  $P < 0.001$ ). More interestingly, the analysis revealed year-to-year variation in body shape within this species ( $F_{1,8} = 7.35$ ,  $P < 0.001$ ), with the sexes differing in their response to this temporal variation (interaction  $F_{8,190} = 3.04$ ,  $P < 0.004$ ). We also detected significant year-to-year variation in body condition in the next most abundant species, *S. semifasciatus* (one-factor ANOVA,  $F_{10,33} = 5.70$ ,  $P < 0.001$ ); sample sizes for the other taxa were too small for robust analysis. Correlation analyses revealed no significant correlations for body condition of one species vs another across the 11 years of the study, supporting the inference (from similar analyses on capture rates among years) that the five *Simoselaps* species respond in different ways to annual variation.

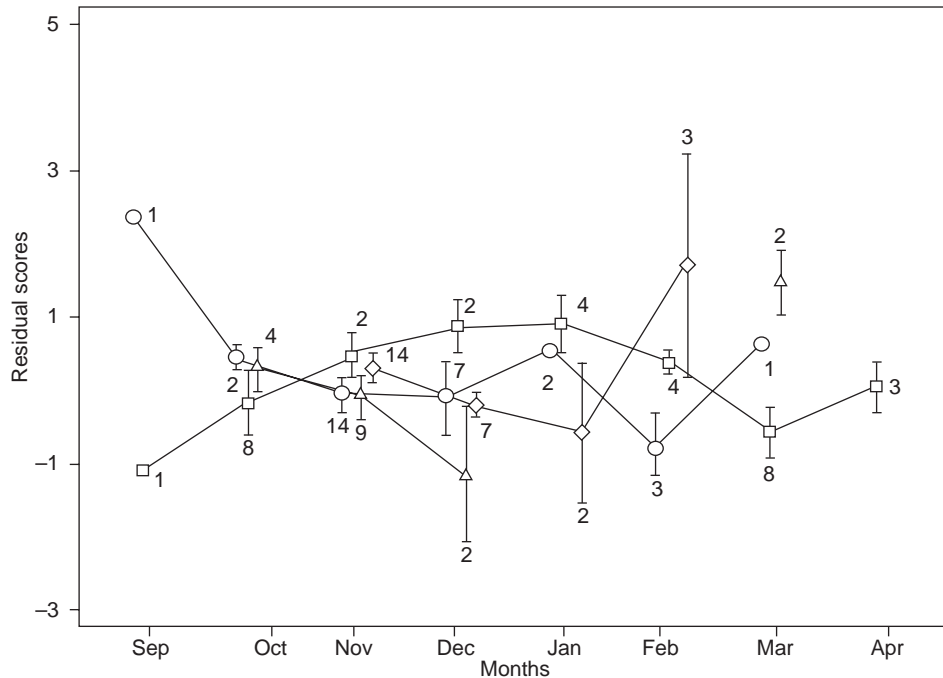
## DISCUSSION

*Simoselaps* of the Australian arid zone constitute a substantial adaptive radiation, in terms of both their morphological diversity and extensive geographic

ranges (e.g. Cogger, 1992). Unfortunately, like most species of small nocturnal fossorial snakes, *Simoselaps* have attracted little scientific attention. Dissection of museum specimens showed that the *Simoselaps* species are diverse ecologically as well as morphologically (Shine, 1984; Scanlon & Shine, 1988; Strahan *et al.*, 1998). Indeed, recent phylogenetic studies suggest that the genus may not be monophyletic (Keogh *et al.*, 1998). *Simoselaps* species appear to be relatively similar in reproductive biology (e.g. all are oviparous, and females exceed males in mean adult body size) but they differ interspecifically in feeding habits. Although most taxa feed on lizards, a few species feed only on reptilian eggs and display corresponding dentitional modifications (e.g. *S. semifasciatus*: Scanlon & Shine, 1988). Among the saurophagous taxa, some (e.g. *S. bertholdi*) specialize on surface-active species whereas others feed mainly on burrowing forms (e.g. *S. calonotos*: Strahan *et al.*, 1998). Our study, the first to be based on live *Simoselaps*, shows that this interspecific diversity extends to other ecological traits as well.

Based on records from 11 years of pit-trapping, we conclude that the various species of *Simoselaps*, although sometimes syntopic, display consistent interspecific differences in characteristics such as abundances, habitat preferences, seasonal patterns in activity and body condition, and the ways in which activity levels vary among years. The only previous information on habitat usage by these taxa, although anecdotal in nature (Storr, Smith & Johnstone, 1986; Cogger, 1992; Bush *et al.*, 1995), is broadly consistent with our results. For example, Bush *et al.* (1995) stated that all species except *S. semifasciatus* were common on the near-coastal dunes of the Swan Coastal Plain that supported heath with banksia/eucalypt woodland. The oophagous *S. semifasciatus* occurs throughout the sandy soils of the coastal plain and onto the gravelly soils of the adjacent Darling Range.

In the absence of detailed studies on the behaviour of these taxa, it is difficult to interpret the interspecific variation in habitat use. In a forthcoming paper, we will examine the degree to which the abundance of *Simoselaps* is associated with the availability of lizard prey. The current analysis does, however, provide some evidence to suggest that habitat selection is related to diet. For example, the two oophagous *Simoselaps* species (*S. semifasciatus* and *S. fasciolatus*) resemble each other in habitat use, but differ from the saurophagous species. The habitats selected by the oophagous taxa (heathlands) may somehow provide greater access to reptilian eggs than do other kinds of habitats on the Swan Coastal Plain. Similarly, *S. calonotos* has a distinct preference for habitats on the Quindalup and Spearwood dune systems – the more westerly (younger) ones that are also the preferred habitats of the fossorial lizards (such as *Aprasia repens*, *Lerista lineopunctulata* and *L. praepedita*) on which these snakes feed. The other *Simoselaps* species, which feed on more widely distributed non-fossorial lizard species, tend to be more widely distributed themselves. However, this putative



**Fig. 6.** Body condition of *S. bimaculatus* (○), *S. calonotos* (□), *S. fasciolatus* (△) and *S. semifasciatus* (◇) from Bold Park plotted against the months of capture. The body condition indices were calculated as the residual scores from the general linear regression of ln-transformed mass vs snout-vent length. The mean, standard error and sample size are shown.

link between the geographic distributions of predators and prey requires considerably more verification; the patterns we observe may reflect other biological attributes of these taxa.

Interspecific differences in the timing of activity are also clear-cut, and again may reflect diet as well as other factors. The two oophagous taxa, *S. fasciolatus* and *S. semifasciatus*, have briefer activity periods than do the other taxa. Activity of these species was largely confined to midsummer (Fig. 3, and see above for statistical tests). This restriction of activity fits well with their feeding on reptilian eggs, which are available only at this time (this is the peak period of oviposition in lizards from the Mediterranean climate of southwestern Australia: Chapman & Dell, 1985; How, Dell & Wellington, 1986, 1990). Interestingly, Shine (1984) had predicted that activity periods should be briefer in the oophagous *Simoselaps* species than in their saurophagous congeners, but his analysis of museum records failed to reveal any such difference. With the benefit of a data set derived from a restricted locality where the taxa are syntopic, we can validate Shine's original prediction. His failure to detect this trend presumably resulted from combining specimens from wide geographic areas and collected by various methods such that seasonal patterns in activity were impossible to detect.

Most temperate-zone snakes display highly seasonal patterns of activity (e.g. Gibbons & Semlitsch, 1987; Gregory, Macartney & Larsen, 1987). The highly restricted seasonal activity of *S. fasciolatus* and *S. semifasciatus* suggests that prey availability plays an important role in this respect (see above), and the bimodal activity patterns of the other species also fit this

hypothesis. On the Swan Coastal Plain, lizard prey are most available in spring (when many lizards are breeding, and thus may be unusually vulnerable: e.g. Shine, 1980) and autumn (when newly-hatched lizards are present in large numbers: Bamford, 1986). However, climatic conditions may also exert a direct effect. Activity during cooler months of the year may be precluded by low body temperatures, and activity during summer may be constrained by the hot dry summers of the Perth region. Small snakes are generally reluctant to move about under hot dry conditions, perhaps because of their vulnerability to desiccation (Barbour, Harvey & Hardin, 1969). A similar bimodality in seasonal activity patterns is common among snake species that inhabit hot regions (Gibbons & Semlitsch, 1987).

Our data on sex ratios and body condition reinforce the significance of seasonal variation for these small fossorial animals. Most species except *S. calonotos* showed a slight decline in condition over the reproductive season, with an increase later in the summer (Fig. 6). Sex ratios also varied strongly through time, at least in the species for which we had sufficiently large samples to evaluate this trend. The overall male-biased sex ratio (Table 4) accords with previous studies that reported sex ratios of museum specimens (Shine, 1984; Clarke & How, 1995), but our more detailed study shows that sex-ratio estimates are very sensitive to the time of year at which samples are taken. Males are captured frequently in spring, presumably because mate-searching involves extensive movements (e.g. Gibbons & Semlitsch, 1987; Gregory *et al.*, 1987; Madsen *et al.*, 1993). In contrast, females dominate

samples taken later in the year, as they move about to recoup body condition after oviposition (Gibbons & Semlitsch, 1987; Fig. 6).

Most of the life-history traits that we measured were consistent across species. For example, males are smaller than females in most or all *Simoselaps* species (Table 4), and the appearance of hatchling-sized snakes in autumn (Fig. 4) suggests that females oviposit in early summer. Museum dissections confirm this supposition (Shine, 1984; Strahan *et al.*, 1998). The only possible exception to this reproductive timing is *S. semifasciatus*, for which hatchlings were not found until late spring (Fig. 4). It is unclear whether this represents an interspecific difference in reproductive timing (perhaps related to the highly seasonal food supply of *S. semifasciatus*) or is a result of the brief seasonal activity of this species. Our inference on age at maturation (from Fig. 4) fits well with Shine's (1984) suggestions, based on similar kinds of data. Although size distributions provide a less reliable basis for such inferences than do longitudinal data from individually marked animals, the technique probably works relatively well for species with relatively synchronous reproduction and relatively slow growth (Vitt & Vangilder, 1983). The inferred age at maturation for *S. bertholdi* (24–36 months) is similar to that described for many other snake species, including several larger elapid taxa from eastern Australia (Parker & Plummer, 1987).

Our results have three main implications for the conservation of these snakes. These involve: (1) the logistics of detecting the presence of these taxa; (2) the population densities of most species; (3) information on the biology of one taxon, *S. calonotos*, that has been classified as being of significant conservation concern (Cogger *et al.*, 1993).

### Logistics of detection

We captured remarkably few specimens of most species, despite the long duration of the study and the large numbers of traps employed at many sites (e.g. Table 1). For most species, > 1000 pitdays were needed to catch a single animal, and > 1 year often passed between successive captures of a species. The timing of trapping is also crucial. Trapping during some parts of the year (especially winter) was completely uninformative about the presence of *Simoselaps* (Fig. 3). Also, overall capture rates were much lower in some years than in others (Table 3). Additionally, the five species had considerably different responses (in terms of capture rates and body condition) to year-to-year variation in weather and other factors (note the lack of significant interspecific correlations for both of these variables). This result has an obvious methodological implication: the kinds of short-term faunal surveys that are often used to 'establish' a species' presence or absence are inadequate for taxa such as most *Simoselaps* species and for many other taxa (How, 1998). Not only does one need to trap for extraordinarily long periods in order to detect any *Simoselaps*

species at all; but also, which species is first detected may depend as much upon local environmental conditions as upon underlying abundances of the different taxa.

Legislation over much of Australia requires faunal surveys to be carried out before the approval of applications to degrade natural habitats for commercial purposes. Judging from our experience, it may require thousands of pitdays to detect all of the *Simoselaps* species living in such an area (Table 1). The time and expenses required for such efforts are formidable, but shorter-term surveys will provide an incomplete picture of the fossorial reptile communities present on any such site. Unfortunately, we doubt that *Simoselaps* are unique in this respect; not surprisingly, many of the taxa of conservation concern are naturally rare and many are predators that are high in the food chain.

### Population densities

Our low capture rates suggest that these small snakes may occur at very low population densities. The alternative possibility is that the snakes are difficult to catch, but we doubt that this can be the entire explanation. Capture rates of these small snakes from pit-traps are generally as high as those from any other collecting technique of which we are aware. We do not know movement patterns or foraging modes of these small snakes, but at least some of them (the oophagous taxa) must be active searchers rather than ambush foragers, and hence would be expected to be vulnerable to pit-trapping. If the snakes were abundant, we would expect occasional records of very large numbers, in the course of activities such as bulldozing or flooding. We are unaware of any such reports, and the Western Australian Museum collections do not include any large series of specimens obtained under such circumstances. Indeed, a recent realignment of the highway adjacent to our study site at Bold Park failed to detect any *Simoselaps* in front of the bulldozers. Additionally, the patterns of relative abundance of the five species from our trapping study mirror that from Shine's (1984) examination of museum specimens that had been collected over a broad area, a long time, and a diversity of methods. Thus, we suspect that some *Simoselaps* species are genuinely rare animals; most occur over very broad areas, but at low population densities over much of this range. This possibility has obvious implications for conservation planning, and we advocate additional survey work, using mark-recapture techniques, to provide estimates of absolute population densities of these animals.

### The biology of *S. calonotos*

One of the species that we studied (*S. calonotos*) is listed as being of significant conservation concern (Cogger *et al.*, 1993). The other four species that we studied have wide distributions across central and western Australia

(Cogger, 1992), whereas *S. calonotos* has a very restricted geographic distribution in the more mesic south-western coastal region, over a latitudinal range of around 200 km from Mandurah to Lancelin (Storr *et al.*, 1986; however, there is a recent report of a specimen from much farther north, near Dongara: G. Harold, pers. comm.). This region has higher human population densities and has suffered more anthropogenic disturbance than have the more remote desert areas. Our trapping data suggest that *S. calonotos* occurs at similar population densities to most of the other *Simoselaps* species on the Swan Coastal Plain (Table 1). However, it is most abundant on the near coastal dunes of the Swan Coastal Plain (How & Dell, 1994; this study), the landforms that are the focus of the greatest residential and industrial development in Western Australia due to their proximity to the Indian Ocean. *Simoselaps calonotos* is distinctive within the genus in its dietary specialization on fossorial rather than surface-active lizards (Strahan *et al.*, 1998) and its seasonal activity patterns. Its continued activity through summer (most captures January–April, and one in June, Fig. 3) contrasts markedly with other *Simoselaps* species and it has the most extended period of activity of the species examined, indicating that there are long periods each year when these animals are likely to be affected by surface disturbance (Fig. 4). Several analyses in our study point to the biological distinctiveness of *S. calonotos*, for example, it is the only species not to display sex differences in body shape.

Habitat fragmentation has a pronounced impact on the persistence of most reptile populations in the winter rainfall areas of Western Australia, such that the greatest diversity of lizard species is associated with larger patches of remnant bushland (Kitchener *et al.*, 1980; How & Dell, 1994). On the Swan Coastal Plain, the greatest richness and abundance of small fossorial snakes occurs in bushlands on the Quindalup and Spearwood dune systems adjacent to the west coast. These near-coastal dunes coincide with an area of great environmental impact in Western Australia associated with habitat fragmentation for urbanization and industrialization. These developments, coupled with an increasing frequency and intensity of fires in urban bushlands and increasing cat populations, will have a severe impact on the persistence of *Simoselaps* populations in areas where these snakes are both regionally and locally uncommon. The same coastal landforms preferred by *Simoselaps* species occur on the adjacent large offshore islands (Rottnest and Garden) that have been isolated from the mainland for around 7000 years. However, no *Simoselaps* species occur on these islands (Storr *et al.*, 1986), suggesting that long-term persistence of viable populations may require areas of suitable habitat > 2000 ha.

We need to develop appropriate techniques for the study of these small, cryptic and virtually non-observable animals. Radiotelemetry has made it relatively easy to identify crucial habitat features for large surface-

active species of snakes that are threatened by anthropogenic disturbance (e.g. Webb & Shine, 1997), but the task is much more difficult with these miniature burrowing taxa. Most of the species that we studied are difficult even to detect in an area, let alone characterize ecologically. The same is likely to be true for other small 'sand-swimming' snakes, of various phylogenetic lineages, that comprise a substantial component of reptile biodiversity in many other arid-zone regions. In consequence, most of what we know about these kinds of animals comes from dissections of preserved specimens, or occasional captures of active animals in pit-traps (this study) or on the roads at night (e.g. Rosen & Lowe, 1994). New techniques are urgently needed if we are to learn enough about these animals to plan effectively for their conservation.

In summary, our study provides the most detailed data yet available on the biology of small fossorial elapid snakes. Our results reveal major interspecific differences in habitat usage among the five *Simoselaps* species, and suggest that most of these species occur at low population densities over much of the Swan Coastal Plain. These ecological attributes have important implications for the conservation of *Simoselaps* in an area that is the focus of major habitat alteration. For example, strongly seasonal patterns in sex-ratios, activity and body condition indicate that the impact of habitat disturbance on snake populations will depend on the timing as well as the magnitude of perturbations.

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## REFERENCES

- Bamford, M. J. (1986). *The dynamics of small vertebrates in relation to fire in Banksia woodland near Perth, Western Australia*. Unpubl. PhD thesis, Murdoch University.
- Barbour, R. W., Harvey, M. J. & Hardin, J. W. (1969). Home range, movements and activity of the eastern worm snake, *Carphophis amoenus amoenus*. *Ecology* **50**: 470–476.
- Branch, W. R. (1988). *A field guide to the snakes and other reptiles of southern Africa*. Cape Town: Struik.
- Bush, B., Maryan, B., Browne-Cooper, R. & Robinson, D. (1995). *A guide to the reptiles and frogs of the Perth region*. Perth: University of Western Australia Press.
- Chapman, A. & Dell, J. (1985). Biology and zoogeography of the amphibians and reptiles of the Western Australian wheatbelt. *Rec. West. Aust. Mus.* **12**: 1–46.
- Clarke, V. & How, R. A. (1995). Body dimensions in *Simoselaps* and *Vermicella* (Elapidae): a method of determining sex in natural populations. *Rec. West. Aust. Mus.* **17**: 69–72.
- Cogger, H. G. (1975). *Reptiles and amphibians of Australia*. Sydney: Reed Books.
- Cogger, H. G. (1992). *Reptiles and amphibians of Australia*. 2nd edn. Sydney: Reed Books.
- Cogger, H. G., Cameron, E. E., Sadlier, R. A. & Egger, P. (1993). *The action plan for Australian reptiles*. Australian Nature Conservation Agency. Endangered Species Program Project No. 124.
- Gibbons, J. W. & Semlitsch, R. D. (1987). Activity patterns. In *Snakes: ecology and evolutionary biology*: 396–421. Seigel, R. A., Collins, J. T. & Novak, S. S. (Eds). New York: Macmillan.
- Gregory, P. T., Macartney, J. M. & Larsen, K. W. (1987). Spatial patterns and movements. In *Snakes: ecology and evolutionary biology*: 366–395. Seigel, R. A., Collins, J. T. & Novak, S. S. (Eds). New York: Macmillan.
- How, R. A. (1998). Long-term sampling of a herpetofaunal assemblage on an isolated urban bushland remnant. *J. R. Soc. W. A.* (in press).
- How, R. A. & Dell, J. (1990). Vertebrate fauna of Bold Park, Perth. *West. Aust. Nat.* **18**: 122–131.
- How, R. A. & Dell, J. (1993). Vertebrate Fauna of the Perth Metropolitan Region: Consequences of a Changed Environment. In *Urban bushland management*: 24–47. Hipkins, M. (Ed.). Perth: Australian Institute of Urban Studies.
- How, R. A. & Dell, J. (1994). The zoogeographic significance of urban bushland remnants to reptiles in the Perth region, Western Australia. *Pac. Conserv. Biol.* **1**: 132–140.
- How, R. A., Dell, J. & Wellington, B. D. (1986) Comparative biology of eight species of *Diplodactylus* gecko in Western Australia. *Herpetologica* **42**: 471–482.
- How, R. A., Dell, J. & Wellington, B. D. (1990). Reproductive and dietary biology of *Nephrurus* and *Underwoodisaurus* in Western Australia. *Rec. West. Aust. Mus.* **14**: 449–459.
- Huey, R. B., Pianka, E. R. & Schoener, T. W. (1983). *Lizard ecology: studies of a model organism*. Cambridge: Harvard University Press.
- Keighery, G. J., Harvey, J. & Keighery, B. J. (1990). Vegetation and flora of Bold Park. *West. Aust. Nat.* **18**: 100–122.
- Keogh, J. S. & Smith, S. A. (1996). Taxonomy and natural history of the Australian bandy-bandy snakes (Elapidae: *Vermicella*) with a description of two new species. *J. Zool. (Lond.)* **240**: 677–701.
- Keogh, J. S., Shine, R. & S. C. Donnellan. (1998). Phylogenetic relationships of terrestrial Australo-Papuan elapid snakes (sub-family Hydrophiinae) based on cytochrome *b* and 16S rRNA sequences. *Mol. Phyl. Evol.* **10**: 67–81.
- Kitchener, D. J., Chapman, A., Dell, J., Muir, B. G. & Palmer, M. (1980). Lizard assemblages and reserve size and structure in the Western Australian wheatbelt – some implications for conservation. *Biol. Conserv.* **17**: 25–62.
- McArthur, W. M. & Bettenay, E. (1960). The development and distribution of soils on the Swan Coastal Plain, Western Australia. *CSIRO Soil Publication* No. 16.
- Madsen, T., Shine, R., Loman, J. & Hikansson, T. (1993). Determinants of mating success in male adders, *Vipera berus*. *Anim. Behav.* **45**: 491–499.
- Parker, W. S. & Plummer, M. V. (1987). Population ecology. In *Snakes: ecology and evolutionary biology*: 253–301. Seigel, R. A., Collins, J. T. & Novak, S. S. (Eds). New York: Macmillan.
- Peters, R. H. (1983). *The ecological implications of body size*. Sydney: Cambridge University Press.
- Pough, F. H. (1980). The advantages of ectothermy for tetrapods. *Am. Nat.* **115**: 92–112.
- Reiss, M. J. (1989). *The allometry of growth and reproduction*. Cambridge: Cambridge University Press.
- Rosen, P. C. & Lowe, C. H. (1994). Highway mortality of snakes in the Sonoran desert of southern Arizona. *Biol. Conserv.* **68**: 143–148.
- Scanlon, J. & Shine, R. (1988). Dentition and diet in snakes: adaptations to oophagy in the Australian elapid genus *Simoselaps*. *J. Zool. (Lond.)* **216**: 519–528.
- Seddon, G. (1972) *Sense of place*. Perth: University of Western Australia Press.
- Seigel, R. A. (1993). Summary: future research on snakes, or how to combat 'lizard envy'. In *Snakes: ecology and behavior*: 395–402. Seigel, R. A. & Collins, J. T. (Eds). New York: McGraw-Hill.
- Seigel, R. A. & Collins, J. T. (1993). *Snakes: ecology and behavior*. New York: McGraw-Hill.
- Shaw, C. E. & Campbell, S. (1974). *Snakes of the American West*. New York: Alfred A. Knopf.
- Shine, R. (1980). 'Costs' of reproduction in reptiles. *Oecologia (Berl.)* **46**: 92–100.
- Shine, R. (1984). Ecology of small fossorial Australian snakes of the genera *Neelaps* and *Simoselaps* (Serpentes, Elapidae). In *Vertebrate ecology and systematics—a tribute to Henry S. Fitch*: 173–183. Seigel, R. A., Hunt, L. E., Malaret, L. & Zuschlag, N. I. (Eds). Kansas: Mus. Nat. Hist., Univ. Kansas. Spec. Publ.
- Shine, R. & Madsen, T. (1996). Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. *Physiol. Zool.* **69**: 252–269.
- Statistix (1996). *Analytical software*. St Pauls: Minnesota.
- Storr, G. M. (1967). The genus *Vermicella* (Serpentes, Elapidae) in Western Australia and the Northern Territory. *J. Proc. R. Soc. W. A.* **50**: 80–92.
- Storr, G. M. (1979). Revisionary notes on the genus *Vermicella* (Serpentes, Elapidae). *Rec. West. Aust. Mus.* **8**: 75–79.
- Storr, G. M., Smith, L. A. & Johnstone, R. E. (1986). *Snakes of Western Australia*. Perth: West. Aust. Mus.
- Strahan, N. R., How, R. A. & Dell, J. (1998). Reproduction and diet in four species of burrowing snakes (*Simoselaps* spp.) from south-western Australia. *Rec. West. Aust. Mus.* **19**: 57–63.

- Vitt, L. J. & Pianka, E. R. (1994). *Lizard ecology: historical and experimental perspectives*. Princeton: Princeton University Press.
- Vitt, L. J. & Vangilder, L. D. (1983). Ecology of a snake community in northeastern Brazil. *Amphib.-Reptilia*, **4**: 273–296.
- Webb, J. K. & Shine, R. (1997). Out on a limb: conservation implications of tree-hollow use by a threatened snake species (*Hoplocephalus bungaroides*: Serpentes, Elapidae). *Biol. Conserv.* **81**: 21–33.