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Intraspecific Variation in Thermoregulation, Movements and Habitat Use by Australian Blacksnakes, *Pseudechis porphyriacus* (Elapidae)

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ABSTRACT.—Radiotelemetric studies of snake behavior often have been based on few animals, monitored in single study areas for short periods of time. A four-year study involving three widely separated study areas, in which 44 blacksnakes (*Pseudechis porphyriacus*) were radio-tracked for an average of 90 days each, revealed unexpectedly high variability in habitat use, activity levels, daily movements and activity ranges. Significant variation was documented among individual snakes, between sexes, among seasons, among years, and among study areas.

The only characteristic that showed little variation was activity temperature range: active blacksnakes maintained body temperatures of 28 to 31°C over a variety of seasons, study areas, and ambient temperatures. This constancy was apparently achieved by varying behavioral characteristics, especially activity levels and times.

Activity ranges varied from 0.02 ha to over 40 ha in different snakes, and were larger in males during the mating season. Reproductive activity declined or ceased in two populations during a severe drought. The behavioral flexibility exhibited by *P. porphyriacus* makes it difficult to describe "typical" behavior for this species, and suggests that many previous radiotelemetric field studies of snakes should be interpreted with caution.

Detailed data on natural history are available for only a few species of snakes, because most snakes are highly secretive and thus are difficult to locate or observe in the field. The low probability of relocating individuals makes it difficult to apply conventional capture-mark-recapture techniques, except with enormous effort and over long periods of time (e.g., Fitch, 1960, 1963, 1975). The development of miniature radiotransmitters has provided an alternative methodology, and radiotelemetric field studies of thermoregulation, movements and habitat use have now been carried out on snakes of the families Acrochordidae, Boidae, Colubridae, Elapidae, and Viperidae (Table 1). Most of these studies have reported short-term data on small numbers of animals from a single study area, so that the extent of geographic and temporal variation in these natural history variables remains unknown.

The present study describes radiotelemetric studies on three geographically separated populations of a widespread species: the large proteroglyphous (elapid) blacksnake, *Pseudechis porphyriacus*, of eastern Australia. This species is loosely associated with riparian habitats throughout its range (Cogger, 1983), but is found in habitats as diverse as montane creeks, coastal sand-dune swamps, and major rivers in the semi-arid continental interior. *P. porphyriacus* is well-suited to telemetric studies by virtue of its large body size, diurnal habits, generally inoffensive nature and low venom toxicity.

MATERIALS AND METHODS

Study Areas.—All three study sites are in New South Wales, but differ greatly in climates, vegetational characteristics, topography and habitats:

(1) The Macquarie Marshes (148 E, 32 S) are close to the western geographic limit of *P. porphyriacus*, as nearby areas are too arid for this species. The Marshes occupy approximately 5000 km² of low-lying land in the semi-arid zone. The land is flat, with sparse vegetation and considerable soil erosion due to grazing by domestic livestock (cattle and sheep) and feral pigs. Summers are hot (mean daily air temperature is approximately 27°C in January, 11°C

TABLE 1. Published studies using radiotelemetry of free-ranging snakes. "Duration of tracking" refers to data for individual snakes, not the entire length of the study.

Family	Species	Number of snakes	Mean duration of tracking	Number of study areas	Authority
Acrochordidae	*Acrochordus arafurae*	15	2–24 days	1	Shine and Lambeck, 1985
Boidae	*Boa constrictor*	1	12 days	1	Montgomery and Rand, 1978
	Aspidites melanocephalus	2	1–3 days	2	Johnson et al., 1975
	Liasis amethystinus	1	1 day	1	Johnson, 1973
Colubridae	*Nerodia fasciata*	9	1–5 days	1	Osgood, 1970
	N. taxispilota	4	1–5 days	1	Osgood, 1970
	Natrix natrix	10	≃90 days	1	Madsen, 1984
	Nerodia sipedon	4	20 days	1	Fitch and Shirer, 1971
	Pituophis melanoleucus	2	3 days	1	Fitch and Shirer, 1971
	Elaphe obsoleta	5	9 days	1	Fitch and Shirer, 1971
	E. obsoleta	7	≃5 months	1	Weatherhead and Charland, 1985
	Coluber constrictor	12	38 days	1	Fitch and Shirer, 1971
	Thamnophis sirtalis	8	22 days	1	Fitch and Shirer, 1971
	Lampropeltis calligaster	2	13 days	1	Fitch and Shirer, 1971
	L. triangulum	4	16 days	1	Henderson et al., 1980
	Coluber constrictor	9	11–65 days	1	Brown and Parker, 1976
	Masticophis taeniatus	2	5–15 days	1	Parker and Brown, 1972
	M. taeniatus	14	4–81 days	1	Parker and Brown, 1980
	Pituophis melanoleucus	10	3–72 days	1	Parker and Brown, 1980
	Leptophis depressirostris	1	8 days	1	Nickerson et al., 1978
	Spilotes pullatus	1	6 days	1	Nickerson et al., 1978
	Chironius carinatus	1	6 days	1	Henderson et al., 1976
	Helicops angulatus	1	8 days	1	Henderson et al., 1976
Elapidae	*Austrelaps ramsayi*	1	30 days	1	Shine, 1979
	Notechis scutatus	3	25–46 days	1	Shine, 1979
	Pseudechis porphyriacus	2	1–44 days	1	Shine, 1979
Viperidae	*Agkistrodon contortrix*	20	3–16 months		Reinert, 1984
	A. contortrix	20 (?)	2 months (?)	1	Sanders and Jacob, 1981
	A. contortrix	32	22 days	1	Fitch and Shirer, 1971
	Crotalus horridus	3	23 days	1	Fitch and Shirer, 1971
	C. horridus	21	3–16 months	1	Reinert, 1984
	C. horridus	3	4–9 months	1	Brown, 1982
	C. horridus	5	≃2 months	1	Brown et al., 1982
	C. horridus	21	3–16 months	1	Reinert et al., 1984
	C. atrox	83	?	1	Landreth, 1973
	C. viridis	6	≃6 months	1	Jacob and Painter, 1980
	C. viridis	3	30–60 days	1	Duvall et al., 1985
	Sistrurus catenatus	25	up to 50 days	2	Reinert and Kodrich, 1982
	Trimeresurus flavoviridis	12	1–25 days	1	Ikeda et al., 1978
	T. flavoviridis	45	1–34 days	1	Wada et al., 1980

in June). Blacksnakes are found in paddocks close to rivers, creeks, and canals in this area.

(2) The Jamison Valley (151 E, 34 S) appears to be "typical" temperate montane habitat for blacksnakes. This valley, in the Great Dividing Range 50 km west of Sydney, has been cut through a sandstone plateau by the Jamison River. The river is a clear fast-running stream with wide sandy banks. Although there are extensive grassy areas close to the stream (maintained through grazing by cattle and feral horses), these give way to thick sclerophyllous forest on the steep surrounding hills. Summers are warm (mean daily temperature 25°C in January, 11°C in June).

(3) Coomonderry Swamp (151 E, 34 S) is a coastal hind-dune swamp 100 km south of Sydney, and only 2 km from the ocean.

TABLE 2. Snout-vent lengths (cm, $\bar{x} \pm$ SE, range below in parentheses) and body masses (g, $\bar{x} \pm$ SE, range below in parentheses) of blacksnakes, *Pseudechis porphyriacus*, in three study areas.

	Males			Females		
	N	SVL	Mass	N	SVL	Mass
Macquarie Marshes	61	104.8 ± 2.0 (54–140)	479 ± 127 (220–1088)	16	103.8 ± 3.8 (72–140)	443.3 ± 58.0 (360–555)
Jamison Valley	25	100.0 ± 1.7 (83–115)	400 ± 22 (232–603)	21	91.4 ± 2.2 (66–104)	287.2 ± 18.3 (107–432)
Coomonderry Swamp	16	131.2 ± 5.7 (73–152)	1241 ± 130 (134–2038)	18	110.2 ± 1.9 (96–122)	581.3 ± 32.1 (324–776)

The swamp covers 10 km^2 and is surrounded by dense shrubby vegetation. Apart from small grassy areas, the ground within 100 m of the water's edge is covered by large (up to 20 m) clumps of *Ghania* tussock. Bracken fern (*Pteridium*) covers the ground in drier areas, with emergent *Banksia, Grevillea, Acacia, Melaleuca* and *Eucalyptus.* The climate is slightly cooler than in the other study areas (mean daily temperature 22°C in January, 6°C in June).

Blacksnakes from the Jamison Valley population were much smaller than those in the other two populations (Table 2).

General Methods.—Snakes were captured by hand, or by Pilstrom tongs. All snakes were measured (snout–vent length, ±1 cm) and weighed (±1 g). Snakes were released at the exact site of capture less than 3 days after capture (usually, less than 24 h). Different types and sizes of transmitters were used (see below), but most transmitted at 150–152 mHz, and gave effective ranges of 0.2 to 2.0 km using handheld receivers and antennae (Telonics TR2E and RA-2AK). Transmitters were encapsulated in a paraffin-Elvax mixture, and most were surgically inserted in the peritoneal cavity immediately posterior to the stomach (see Brown and Parker, 1976, for methods), under inhalation anaesthesia with Fluothane. Some transmitters were placed inside dead mice and fed to snakes (see below), and others were force-fed to captured snakes. Temperature-sensitive transmitters were calibrated before and after use in waterbaths, against a certified thermometer (±0.1°C). Body temperatures of telemetered snakes were estimated by measuring inter-pulse intervals with Telonics TDP-2 digital processors, and calculating temperatures from quadratic equations fitted to the calibration points. Most temperature data came from readings taken at the time a snake was located, but signals were recorded automatically with a Telonics chart recorder system for one week in October and one week in December at the Jamison Valley site (one reading per snake each 30 minutes).

Detailed maps of each study area were prepared from aerial photography combined with ground survey. Whenever a snake was located, its exact position was recorded on the relevant map. Movements by radio-tagged snakes were determined from the maps. Straight-line distances between successive locations were used unless direct observation had revealed a different route, or the straight-line route was physically impossible (e.g., up a vertical cliff). Such corrections were rarely needed, and usually minor. Home ranges were calculated using the minimum convex polygon technique, with and without correction factors for sample size (Jennrich and Turner, 1969).

During the course of the study (1980 through 1984), several changes were made in equipment, methods, and sampling frequency. Differences in methodology used in the three study areas are described below.

(1) Macquarie Marshes—Data were gathered during three visits to the study area, each visit being of two to three weeks in duration (November 1980, December 1980, November 1981). Transmitters used were TT-IU-160 (J. Stuart Enterprises: 55 × 20 mm, 38 g) and Mini-Mitter Model T (27

• no visits over all seasons.???

mHz: 30 × 13 mm, 10 g). Four transmitters were force-fed to snakes, and the others were inserted in freshly-killed mice which were then dangled in front of foraging blacksnakes. In most cases the "bait" was seized and eaten immediately. Two snakes were monitored in spring 1980, seven in spring 1981, and four in summer 1980. Additional blacksnakes were captured, paint-marked for individual recognition, and released within 10 min at the site of capture.

(2) Jamison Valley—Following initial capture of snakes and transmitter insertion in October 1982, telemetered snakes were located at weekly intervals until May 1983. Two types of transmitters were used. UL 81Ts (Austec Electronics Ltd.: 45 × 15 mm, approx. 25 g) giving 10 months life, were inserted surgically in five blacksnakes. Smaller units (TT-1GE: J. Stuart Enterprises: 65 × 12 mm, 12 g) were inserted surgically in six blacksnakes, removed after 2 months, and replaced with the same transmitters force-fed to the snakes. These were regurgitated after two to five weeks, and no further data were gathered on these animals.

(3) Coomonderry Swamp—Transmitters (SS-1: Biotrack Ltd.: approx. 45 × 15 mm, 18 to 39 g, depending on battery size) were surgically inserted in 20 blacksnakes in October–November 1983, and the study area visited at intervals of six weeks until May 1984. At each visit, all radio-tagged snakes were captured so that a blood sample could be taken for isotopic assessment of feeding rates (Shine, in prep.) prior to release.

Results

The years during which these studies were conducted—1980 to 1984—came toward the end of one of the most severe and prolonged droughts recorded in New South Wales. The effects of the drought were most evident in the inland site (Macquarie Marshes), where more than 50% of grasses and shrubs in the study area died between the first and last studies. Blacksnake populations also were affected. Although reproductive activities (mating, male combat) were evident in spring 1979 (Shine et al., 1981) and 1980, these had ceased by spring 1981, and all snakes dissected at that time (7 telemetered, 4 non-telemetered) had gonads much smaller than those seen in reproductive animals (Shine, 1977). Many snakes were emaciated, with no abdominal fat bodies, and population numbers appeared to have fallen substantially. Although the vegetation of the coastal study areas superficially seemed to be less affected, many of the Jamison Valley snakes were non-reproductive during the period of the study. Specimens from Coomonderry Swamp continued reproductive activity.

Sample sizes and sampling frequencies differed among areas: the Macquarie Marshes study consisted of intensive observation over short time periods, whereas the other studies provided limited data at each monitoring period, but regular sampling at intervals of six weeks (Coomonderry) or one week (Jamison Valley). The durations of time for which snakes were radio-tracked (see below) show great differences among individual specimens and among areas, because of varying durations of trips, and transmitter malfunction or regurgitation. In total, 138 snake-days of telemetry are available from the Macquarie Marshes (comprising 733 locations of 13 snakes), 1150 snake-days from the Jamison Valley (229 locations of 11 snakes) and 2653 snake-days from Coomonderry Swamp (108 locations of 20 snakes).

Habitat Use.—Radio-tracked snakes provided extensive data on the types of habitats used in each study area (Table 3). Snakes were found in a wide variety of habitats, and used several different types of shelter. Geographic variation was evident, with habitat use differing significantly among areas (R × C *G*-test from Sokal and Rohlf, 1981: $G = 532.1$, $P < 0.001$; pairwise comparisons: Marshes-Jamison, $\chi^2 = 266.1$, 5 df, $P < 0.001$; Marshes-Coomonderry, $\chi^2 = 331.4$, 4 df, $P < 0.001$; Jamison-Coomonderry, $\chi^2 = 158.1$, 6 df, $P < 0.001$). Logs were the main refuges used by blacksnakes in the Macquarie Marshes and in the Jamison Valley, although snakes in the latter area also often used abandoned mammal burrows (probably made by rabbits). Coomonderry snakes usually sheltered in the thick grass clumps (*Ghania*) abundant in the area, but also were often

TABLE 3. Frequency of habitat use by radio-tracked blacksnakes, *Pseudechis porphyriacus*, in three study areas. "Sample size" refers to number of observations.

	Macquarie Marshes		Jamison Valley		Coomonderry Swamp	
	Male	Female	Male	Female	Male	Female
Sample size	304	374	113	98	69	33
Habitat types						
Grass	0.20	0.08	0.18	0.11	0.65	0.73
Logs	0.56	0.89	0.42	0.53	0.13	0.06
Rocks	0	0	0.12	0.09	0	0
Mammal nests	0	0	0	0	0.17	0.21
Burrows	0	0	0.22	0.20	0.04	0
Open ground	0.21	0.03	0.03	0.01	0	0
Debris	0	0	0.03	0.04	0	0

found in mammal dreys among grass and bracken fern (Table 3). These mammal dreys were at ground level, and about the size and shape of a football. Based on their size and on fur found within dreys, they were probably built and used by bandicoots (*Isoodon macrurus*) and native bushrats (*Rattus fuscipes*). The only time that significant numbers of snakes were found on bare open ground was in male snakes in the Macquarie Marshes (Table 3). This was also the only category in which any differences between the sexes in habitat use were evident (proportion of males versus females on open ground versus other habitats, in the Macquarie Marshes: 2 × 2 contingency table, $\chi^2 = 54.1$, 1 df, $P < 0.001$). Male and female snakes also did not differ in their proximity to waterbodies (Jamison Valley—♂♂ N = 119, $\bar{x}$ distance = 113.9 m, SE = 20.3; ♀♀, N = 100, $\bar{x}$ = 78.7 m, SE = 7.8; Coomonderry Swamp—♂♂, N = 81, $\bar{x}$ = 62.1 m, SE = 7.2; ♀♀, N = 40, $\bar{x}$ = 60.6, SE = 11.9).

Seasonal shifts in habitat use by blacksnakes were evident in studies conducted in the Macquarie Marshes. Most snakes seen in spring 1980 were on open ground within 2 m of a canal running through the study area (see Shine et al., 1981 for description of the canal). On the next visit to the area one year later, recent flooding had caused growth of thick grass in paddocks surrounding the canal, and almost all blacksnakes seen were in this grassy area more than 50 m from the canal. On subsequent visits under drought conditions, all of this grass had died, and most blacksnakes were relatively inactive and remained close to shelter sites (logs).

Even in cases where snakes are found in a single, superficially homogeneous, habitat type, the distribution of snakes is unlikely to be random. A good example of this comes from analysis of the exact sites of capture of 67 snakes along the banks of a canal in the Macquarie Marshes in spring 1980 (see above). The banks were virtually bare of vegetation, had a constant slope, and seemed to vary little along the canal. However, capture localities for snakes were highly clumped, and were correlated with the proximity to the canal of woodland, rather than open paddocks. Snakes were rarely seen beside the canal in any areas where the fringe of the woodland reached to within 500 m of the canal ($\bar{x}$ = 5.1 snakes per km, in a total of 4.6 km), but snakes were abundant in areas where the trees were more than 500 m from the water ($\bar{x}$ = 23.2 snakes per km, in 1.9 km).

Movements.—Radio-tracked snakes did not wander randomly, but occupied definite "activity ranges." One consistent feature of many telemetered snakes was their return to specific shelter sites within their activity range. For example, one Jamison Valley female used the same log as a retreat on three occasions, with intervals between uses of six days (and a movement of at least 230 m before return) and 21 days (and at least 600 m movement). One male returned to a specific shelter hole after a movement of 1 km over 21 days. The subjective impression gained from movements of all snakes was that they were thoroughly familiar with major topographic features within their activity ranges, often moving from one shelter site directly to another apparently far beyond direct line-of-sight.

Distances moved by radio-tracked snakes were highly variable. The largest data base on daily movements comes from the Macquarie Marshes. During the first study in this area (spring 1980) two large radio-tracked male snakes moved, on average, over 300 m each day (means of 347 and 374 m, range 0 to 1090 m). Thirteen marked but non-telemetered males (SVLs 100 to 130 cm, $\bar{x}$ = 116 cm) moved similar distances ($\bar{x}$ = 382 m, range 2–1220 m per day) during the same period of study. However, subsequent visits to the same area revealed much smaller average daily displacements (summer 1980—mean daily movements 7, 13, 48 and 64 m in four telemetered snakes, 5 and 15 m in two other snakes; spring 1981—means of 3, 4, 7, 7, 23, 24, and 29 m in telemetered snakes.

This variability in daily displacements resulted in estimated activity ranges varying greatly among individual snakes (Table 4). Minimum convex polygons ranged from 0.02 to 46.0 ha for adult blacksnakes, and correction for differing sample sizes did little to reduce this variability (Table 4). Considerable differences were evident even among similarly-sized snakes studied in the same area at the same time (e.g., Jamison Valley—activity ranges of 1.0 and 33.0 ha from two males of SVLs 107 and 108 cm). This variability renders further analysis difficult. Variances in home ranges among study areas are highly heterogeneous (F_{max} = 8.51 on 3, 7 df, $P < 0.05$), and could not be rendered homogeneous by any of the usual transformations, thus precluding parametric tests. Use of the non-parametric Kruskal-Wallis one-way analysis of variance by ranks suggested that significant differences in snake home ranges existed among the three study areas (χ^2 = 12.28 on 2 df, $P < 0.002$) but this result was primarily due to the small home ranges of most Macquarie Marshes snakes. As these were monitored for much shorter time periods than were snakes in the other two areas, the differences probably reflect methodology rather than significant biological phenomena. Home ranges of male blacksnakes (N = 20, $\bar{x}$ = 9.60 ha, SD = 12.62) averaged larger than those of females (N = 13, $\bar{x}$ = 2.37 ha, SD = 4.02), but cannot be directly compared because of the significant among-sites variation. There are no consistent differences evident between males and females monitored at the same site over the same time period (Table 4). Overall, the area of the activity range (corrected for sample size) correlated significantly with snake SVL (N = 33, $r = 0.52$, $P < 0.01$), but within study areas the same correlation was significant only in the Macquarie Marshes (N = 9, $r = 0.87$, $P < 0.01$). Even the latter result was primarily due to the fact that the two largest snakes were the only ones studied in the first year of the work (1980), when movements were very extensive.

Activity Patterns.—Whenever a telemetered snake was located, it was recorded as either "active" (exposed) or under cover. The proportion of snakes that were active when located averaged 23% in the Jamison Valley, 40% in the Macquarie Marshes, and 54% at Coomonderry Swamp. These differences among areas were significant (3 × 2 contingency, χ^2 = 32.6, 2 df, $P < 0.001$).

Because of the sampling schedule used, the Macquarie Marshes provided the most complete data for comparisons of activity levels in snakes at different seasons. The proportion of times a snake was "active" at the time it was located averaged 66% in spring and 9% in summer, a significant seasonal difference (χ^2 = 260.7, 1 df, $P < 0.001$). More detailed analysis shows that the higher activity level in spring than summer was true both in males (73% versus 3%, χ^2 = 110.5, 1 df, $P < 0.001$) and in females (43% versus 11%: χ^2 = 44.7, 1 df, $P < 0.001$). Although females tended to be more active than males in summer, the difference between sexes was not significant at this time of year (χ^2 = 3.48, 1 df, $P = 0.06$). However, males were much more active than females during spring (χ^2 = 25.9, 1 df, $P < 0.01$).

Snakes were recorded as being active at times from 0630 to 2130 h (Fig. 1). The proportions of animals active at each hour of the day did not differ significantly from the null hypothesis of equal proportions

TABLE 4. Activity ranges of radio-tracked blacksnakes, *Pseudechis porphyriacus*, in three study areas. SVL = snout-vent length (cm). N is number of observations. Home range corrected for differing sample sizes by method of Jennrich and Turner (1969).

		Snake			Activity Range		
Study area	Season	Sex	SVL	N	Time period (days)	Minimum polygon (ha)	Corrected minimum polygon (ha)
Macquarie Marshes	Spring	Male	130	22	11	26.5	55.1
		Male	140	22	11	46.0	95.6
		Male	107	26	13	0.2	0.4
		Male	96	28	14	0.9	1.8
		Male	120	26	13	1.0	2.0
		Male	101	30	15	0.02	0.04
		Female	112	26	13	0.8	1.5
		Female	105	26	13	0.02	0.04
		Female	112	24	12	0.05	0.1
	Summer	Male	110	48	8	0.5	1.1
		Female	114	48	8	0.3	0.7
		Female	98	42	7	0.05	0.1
		Female	121	36	6	0.1	0.3
Jamison Valley	Spring plus Summer	Male	102	10	47	1.2	3.5
		Male	107	16	63	1.0	2.4
		Male	95	22	112	1.3	2.8
		Male	102	28	189	16.8	31.5
		Male	114	17	105	2.2	5.3
		Male	108	29	182	33.0	60.9
		Female	98	26	116	1.8	3.5
		Female	86	19	79	3.4	7.6
		Female	102	16	58	4.9	11.2
		Female	101	15	50	1.0	2.5
		Female	95	20	79	3.2	7.0
		Female	98	14	70	0.5	1.4
Coomonderry Swamp	Spring plus Summer	Male	140	11	340	7.1	22.6
		Male	140	11	340	17.8	56.4
		Male	144	6	240	8.3	47.3
		Male	139	9	340	2.2	8.1
		Male	125	6	240	9.6	54.4
		Male	147	8	210	7.2	29.5
		Male	144	10	340	9.1	31.1
		Female	118	5	120	14.7	110.1

throughout the day for the samples from Jamison Valley (10 × 2 contingency, $\chi^2 = 10.5$, 9 df, $P = 0.31$) or Coomonderry Swamp (12 × 2 contingency, $\chi^2 = 16.3$, 11 df, $P = 0.13$). However, significant hourly variation in snake activity was evident in the Macquarie Marshes data. In spring, snakes were more active in the morning than in the afternoon (against a null hypothesis of equal numbers in each hour, 14 × 2 contingency, 13 df, $P < 0.001$) whereas in summer, snakes were active only in the morning and evening (15 × 2 contingency, $\chi^2 = 76.2$, 14 df, $P < 0.001$).

Thermoregulation.—Transmitter malfunction prevented temperature measurements at Coomonderry Swamp, but data are available for the other two areas. Body temperatures of radio-tracked snakes, and ambient (air) temperatures, are shown in Fig. 2, based on 501 readings from 13 snakes in the Macquarie Marshes, and 476 readings from 11 snakes in the Jamison Valley. Both minima and maxima for air temperatures were higher in summer than in spring at each site, and air temperatures in summer were higher in the Marshes than in Jamison Valley. Despite these differences in the thermal environment, the body temperatures of radio-tracked blacksnakes

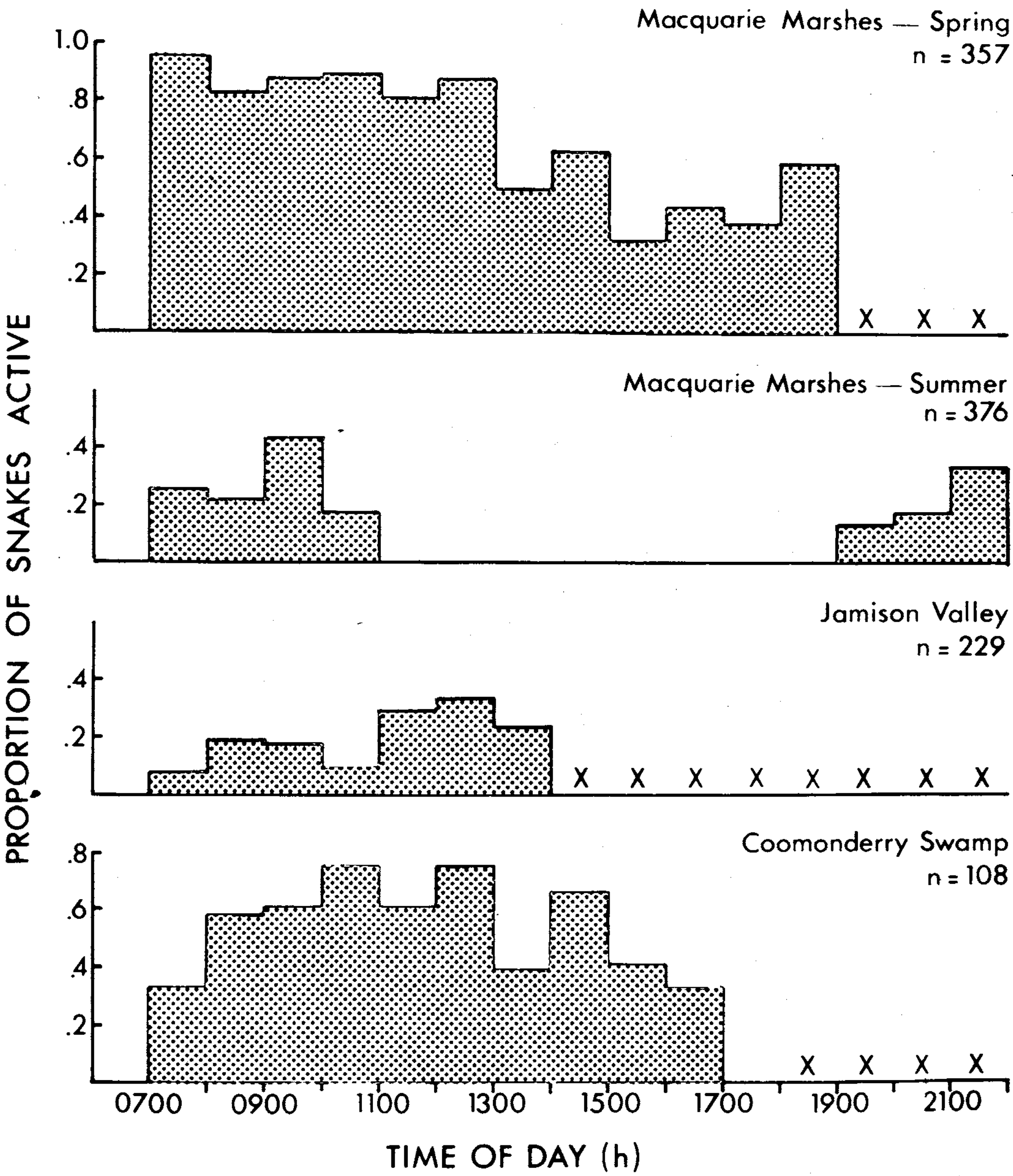

FIG. 1. Proportion of telemetered snakes active (not under cover) when located at different times of day, in three study areas. Data from spring and summer are shown separately for Macquarie Marshes. Time periods marked with crosses have insufficient data to warrant plotting (N < 3).

were similar among all four samples, and were generally within the range 28–31°C (Fig. 2). Body temperatures were relatively low at emergence, but average temperatures rose rapidly to reach the 28–31°C level by mid-morning (Fig. 2). The rate of cooling in the evening was slower than the rate of heating in the morning (Fig. 2). Thus, snake temperatures were usually higher than air temperatures in cool weather (true for 28 of 35 hourly means at ambient temperatures less than 30°C), and lower than air temperature in hot weather (true for 16 of 17 hourly means at ambient

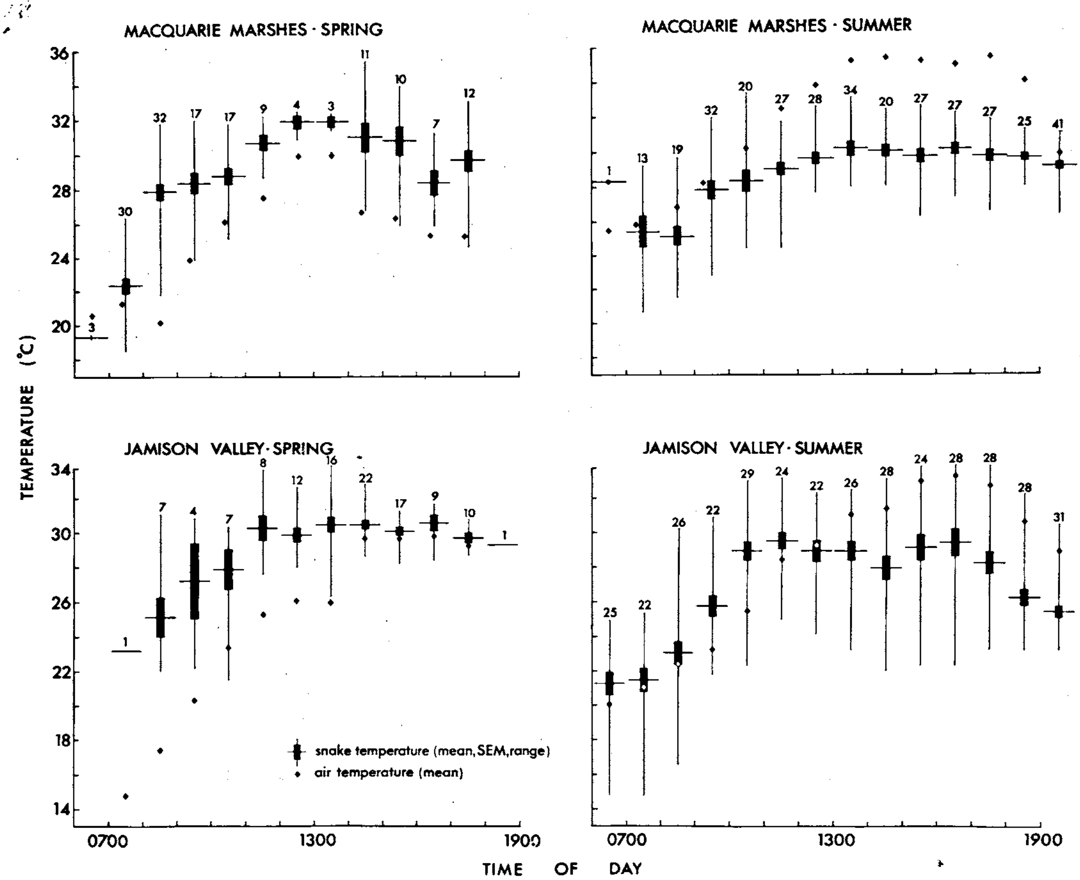

FIG. 2. Air temperatures, and body temperatures of telemetered blacksnakes, in two study areas and two seasons. Data for all specimens in each study period combined to give hourly mean temperatures; sample size shown above range bars. Diamonds show mean air temperatures for each hourly period.

temperatures greater than 30°C: Fig. 3). This difference is significant ($\chi^2 = 22.6$, 1 df, $P < 0.001$).

Related to this is a trend for mean hourly snake temperatures to be generally higher than air temperatures in spring (true in 22 of 24 cases: Fig. 3) but not in summer (snakes warmer at 7 of 28 hourly means). This difference between seasons is significant ($\chi^2 = 20.7$, 1 df, $P < 0.001$), and is not due entirely to the warmer weather in summer: at similarly low air temperatures, snakes tended to be much warmer in spring than in summer (Fig. 3). There is no evidence to suggest that opportunities for basking at a given air temperature are different in spring than in summer. Hence, the most likely explanation is that snakes bask more consistently in spring, when high body temperatures may be difficult to attain (note that the proportion of snakes out in the open when located was much higher in spring than in summer (Table 3).

DISCUSSION

The data presented above are of interest from two different perspectives—what they reveal about the biology of *Pseudechis porphyriacus* and problems that they identify in the interpretation of previous telemetric studies of snakes.

Despite the highly variable nature of the results gathered in the present study, some clear findings emerge on *Pseudechis* biology. For example, although *P. porphyriacus* is usually described as "riparian" (e.g., Cogger, 1983), telemetered snakes often

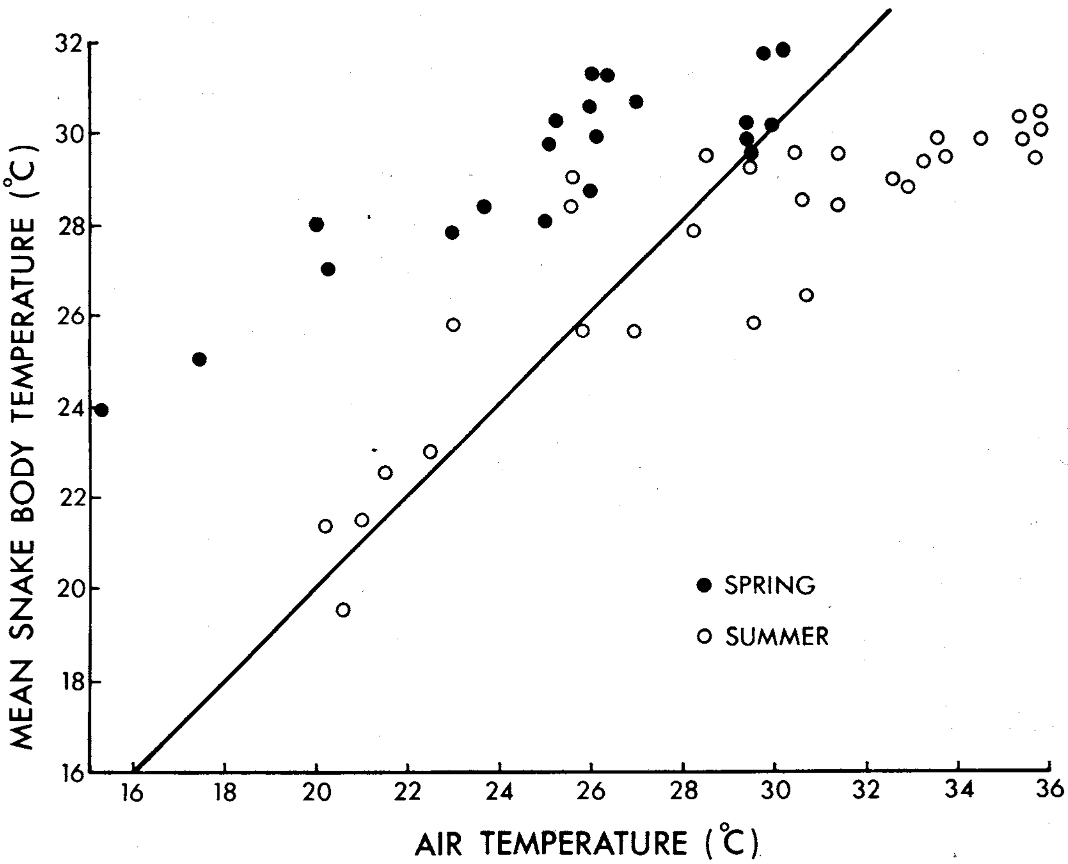

FIG. 3. Mean body temperatures of snakes for each hour of the day, compared to air temperatures (data from Fig. 2). Dots show data from spring, circles show data for summer. Samples from Macquarie Marshes and Jamison Valley combined. The line connects points where air temperatures equal body temperatures.

ranged far from streams or swamps (mean distances to water averaged about 60 to 100 m: see above). Mean activity temperatures were consistent both geographically and seasonally, and fell within the range 28–31°C. The observed temperatures also were similar to those reported in previous studies of this species in the field (Shine, 1979) and laboratory (Witten, 1974; Heatwole, 1976; Heatwole and Johnson, 1979; Lillywhite, 1980). This consistency offers a strong contrast to the variability seen in most other behavioral attributes studied. The snakes' ability to maintain these temperatures over a wide range of ambient temperatures (Fig. 2) reflects behavioral flexibility. Modification of activity times (Fig. 1) and postures (Heatwole and Johnson, 1979) result in different rates of heating under different thermal regimes (Fig. 3).

Movement patterns are more difficult to interpret. The extensive movements of male snakes in one sample (Maquarie Marshes, spring 1980) presumably were due to reproductive activity: both telemetered males spent time with females, and one was seen attempting to mate. The data on these specimens also emphasize the ability of *P. porphyriacus* to cover great distances; although they were only monitored for 11 days, their home ranges (27 and 46 ha) were far larger than those reported from long-term studies of any other snake species (0.002 to 12.2 ha from Parker and Brown's 1980 review of 14 species) except European grass snakes (21.2 ha: Madsen, 1984). The extensive movements of these two telemetered blacksnakes cannot be attributed to disturbance by handling. The transmitters were voluntarily ingested (inside 3 mice offered to the snakes), and neither snake was handled until the end of the study. Also, daily movements by the two telemetered snakes were very similar to those recorded for thirteen marked but non-telemetered specimens (see Results).

Many of the behavioral characteristics studied varied greatly among individual snakes, among years, among study areas, and between sexes. Some of this variation was an inevitable consequence of differences among years, sites, and seasons in weather, habitat availability, and probably food supply. Two major influences may have been: (i) the prolonged drought, which may have reduced snake movements and modified habitat usage by discouraging foraging activity (because prey were scarce, and the snakes in poor condition) and preventing reproductive activity (because of insufficient energy reserves); and (ii) the effects of telemeter implantation, and of the presence of the telemeter in the body cavity. Several snakes lost weight consistently during the time they were monitored, perhaps because of these effects.

The present study is based on data from 44 radiotracked blacksnakes, each monitored for an average of 90 days, and distributed among three widely separated study areas. Previous telemetric studies of snakes have usually involved far fewer specimens (often, six or fewer), in a single study area, monitored for a short period of time, often only a week or two (Table 1). I do not wish to denigrate these studies (some of my own are included!), because there is no doubt that intensive monitoring for short periods can yield valuable insights. However, the generality of the results must be questioned. The present study reveals extensive variation within a single species in most of the ecological attributes studied. For example, both habitat use and the size of the activity range have been found to vary strongly among individual snakes, among study areas, among seasons within a study area, and between successive years at the same location. The degree of activity, and the times of day at which activity occurred, also varied significantly between seasons and among sites.

These data indicate that a short-term study with relatively few specimens, in a single area, may grossly underestimate the range of "typical" behavior patterns in any given species. In particular, the variations observed with time (among seasons and years), as well as in space (among study areas) suggest that much of the variation represents behavioral flexibility of individual animals rather than genotypic differences between populations. These results indicate that caution is needed in interspecific comparisons of behavior from such studies:

(i) Two species cannot be properly compared unless their variability in these characteristics is known. Large sample sizes in short-term studies will not solve the problem, because much of the relevant behavioral variation probably is a response to environmental variation: long-term studies in more than one area are required.

(ii) Interspecific differences, even if they are consistent, should not be uncritically interpreted as genetically-fixed local adaptations to differences in environment. More likely, such behavioral differences may be due to direct responses to the respective environments by individual organisms. Studies of sympatric species (e.g., Reinert, 1984) are the best solution to this problem.

(iii) Broad comparisons between areas, even between populations of a single species, are fraught with uncertainty because of biases in the relative "observability" of specimens in different habitats (e.g., Weatherhead and Charland, 1985) and seasonal and geographic variations in activity levels. These may invalidate non-telemetric data on habitat use or population densities: note that in some seasons, less than 10% of snakes were active, on average, when located telemetrically.

The extent of variation observed in the present study may not be typical of other species of snakes. Certainly, *P. porphyriacus* is unusual in the wide range of conditions of habitat and climate under which it lives, and perhaps in its pronounced geographic variation in body size (Table 2). The effects of severe drought, involving cessation of reproductive activity by the snakes, also may have generated much of the variation in snake behavior. Nonetheless, numerous other factors—including subtle year-to-year climatic variation—may significantly affect many snake populations, and it would be dangerous to treat the *Pseudechis* data as an exceptional case. Additional long-term studies on other species, with large sample sizes and multiple study areas, are sorely needed.

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