

# Synchrony in capture dates suggests cryptic social organization in sea snakes (*Emydocephalus annulatus*, Hydrophiidae)

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**Abstract** Complex sociality is widespread in lizards, but the difficulties of directly observing social interactions in free-ranging snakes have precluded such studies for most snake species. However, a type of data already available from mark-recapture studies (dates of capture and recapture of individually marked animals) can reveal social substructure within snake populations. If individuals associate with each other in social groups, we expect synchrony in the dates of capture and recapture of those animals. A field study of turtle-headed sea snakes (*Emydocephalus annulatus*) in New Caledonia reveals exactly this phenomenon. For example, animals that were captured on the same day in one year often were recaptured on the same day the following year. Analysis rejects non-social interpretations of these data (such as spatial-temporal confounding in sampling, intrapopulation heterogeneity in cues for activity), suggesting instead that many individual sea snakes belong to ‘social’ groups that consistently move about together. The phenomenon of capture synchrony during mark-recapture studies can provide new insights into the occurrence and correlates of cryptic social aggregations.

**Key words:** aggregation, mark-recapture, reptile, sociality, turtle-headed sea snake.

## INTRODUCTION

Traditional views of squamate reptiles (lizards and snakes) as relatively asocial animals have come under strong challenge in recent years (Lanham & Bull 2004). Studies on a diverse array of lizard taxa have provided strong evidence of individual recognition (Bull *et al.* 2000, 2001) and long-term patterns of association among specific individuals including family-based social groupings (O'Connor & Shine 2003; Osterwalder *et al.* 2004; Stow & Sunnucks 2004), across-year monogamy (Bull 2000) and complex social interactions among individuals pursuing alternative social tactics (Comendant *et al.* 2003). Far fewer studies have been conducted on snakes, reflecting logistical difficulties associated with studies on these animals (Seigel 1993; Shine & Bonnet 2000). However, even for snakes there is accumulating evidence that social interactions among individuals exert a significant influence on spatial ecology. For example, individuals appear to avoid each other in some species (Webb & Shine 1997; Fitzgerald *et al.* 2002; Whitaker & Shine 2003) whereas closely related individuals (sisters) aggregate in others (Clark 2004).

Aggregations of snakes have been reported in many taxa, but typically have been ascribed a non-social

function. For example, the trend for large numbers of snakes to gather in overwintering sites (communal dens) generally has been attributed to a scarcity of sites offering suitable thermal conditions (Gregory 1982). Similarly, aggregations of reproductive female snakes have been interpreted as by-products of the spatial distribution of important resources such as nesting sites or suitable thermoregulatory opportunities (Graves & Duvall 1995). Nonetheless, such aggregations might also reflect direct social interactions among individuals.

How can we determine whether or not sociality is common among snakes? Anecdotal reports of interactions among individuals (e.g. Carpenter 1984) are of significant value in this respect, but most snakes are difficult to observe in the wild. Is there any way to infer social organization based simply on the types of data most commonly available from field studies of snakes – that is, records of the capture and recapture of individually marked animals? Any such method might enable a broader array of taxa to be assessed in this respect, based on already-completed mark-recapture studies as well as future work. In this paper we propose a method to infer the existence of social structure within snake populations, based on recapture records of marked animals. Our premise is that if individuals within the population form social groups, we are likely not only to capture these animals at the same time, but also, some period later, to recapture

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them at the same time. Thus, the temporal distribution of such encounters will be non-random, with capture dates of pairs or groups of individuals clustering in the recapture sequence more than would be expected by chance. We illustrate this approach with data on sea snakes, a group for which logistical impediments to direct behavioural observations are particularly severe.

We stress that examining synchrony among individual animals is not a new idea. Many investigators have examined the degree to which activity is synchronous among individuals within foraging groups (e.g. Conradt 1998; Ruckstuhl 1999), and such synchrony has been recognized as a potential problem in generating non-independence in the statistical analysis of mark-recapture data (Anderson *et al.* 1994). Co-occurrence of individuals in space has been the most common criterion for inferring the presence of pair bonds, family groups, and so forth (e.g. Bull 2000; O'Connor & Shine 2003; Osterwalder *et al.* 2004; Stow & Sunnucks 2004). The novelty of our approach is to extend this analysis to infer social structure from the temporal patterning of recaptures within a sample of mobile individuals encountered several months apart within a small study area.

## METHODS

### Study species and area

Turtle-headed sea snakes (*Emydocephalus annulatus*, Hydrophiidae) are medium-sized (to 80 cm snout-vent length (SVL)) entirely aquatic venomous snakes, widely distributed through shallow-water coral-reef habitats in the Indo-Pacific (Cogger 1975; Ineich & Laboute 2002). These snakes feed entirely on the eggs of demersal-spawning fishes (gobies and blennies) and have greatly reduced venom glands and fangs (Voris 1966). We have conducted behavioural and ecological research on this species at two adjacent beaches, 500 m apart (Baie des Citrons and Anse Vata) in Noumea, New Caledonia (22°16'S, 166°26'E) to clarify mating systems, foraging biology, locomotor performance and intraspecific habitat partitioning (Shine *et al.* 2002, 2003a; Shine 2005). Both of our study areas are 50 m long and extend up to 30 m from shore. They consist of shallow (0–4 m) water over coral reefs, rocks and coral rubble (see Shine *et al.* 2003b for a detailed description).

### Mark-recapture study

In January 2004, we collected active snakes by snorkelling for 20 min at each site each day for 11 days.

Any active snakes were easily visible in the clear shallow water, and none of these slow-swimming animals ever evaded capture after being sighted. Twenty minutes was sufficient for us to locate most or all of the animals that were active in our study areas at the time of our dive. The snakes were captured by hand, and immediately returned to our field laboratory a few hundred metres away for processing. Each snake was measured and weighed, sexed (by hemipenial eversion) and individually marked by implanting a microchip under the skin on the lateral surface, 5 cm anterior to the cloaca. A small section of scales was trimmed on the snake's tail to reveal the underlying white connective tissue, which provided a strong contrast to the surrounding black scales. This mark was easily visible underwater, enabling us to recognize snakes that had been processed on that trip. Such snakes were not recaptured during the sampling period, so that we have data only for the initial date of capture of each animal on each annual trip. Many of these animals were seen on subsequent dives, but were not captured and thus, not identified. We returned to the study area in January 2005 and repeated the procedure (again, sampling for 11 days), thereby recapturing many of our animals 12 months after their initial capture and marking. These recapture records (in each case, the first time the snake was seen in each of the 2004 and 2005 sampling periods) provide the data set for the current analysis.

### Analysis of recapture data

We tabulated the dates of initial capture and recapture for the recaptured snakes, and enumerated the frequencies of each combination of capture and recapture dates. To avoid excessive numbers of empty cells (Sokal & Rohlf 1981), we combined data for consecutive days with low numbers of captures or recaptures. Thus, capture periods ranged from 1 to 6 days for the first trip, and 1 to 4 days for the second trip (Table 1). We then used log-linear analyses to test the null hypothesis of equal distributions of recapture dates compared to initial capture dates. If snakes travel together, we expect clustering with some combinations of dates represented by zeroes and a few by high numbers. If snakes do not form consistent associations with other individuals, the distributions of capture and recapture dates should be random – and thus, we would expect both fewer zeroes, and fewer high numbers. Because this procedure required combining capture dates (and hence potentially obscuring patterns), we also calculated the disparity (in days) between initial capture dates of all pairs of snakes within each sampling year, and compared these two sets of disparity scores between years. If particular snakes consis-

**Table 1.** Dates of initial capture and recapture of turtle-headed sea snakes (*Emydocephalus annulatus*) in two study sites in Noumea, New Caledonia

	Initial capture date				
	16 January 2004	17 January 2004	18 January 2004	19–25 January 2004	26 January 2004
Recapture date					
18 January 2005	1	1	1	<b>3</b>	2
19 January 2005	2	0	1	0	<b>4</b>
20 January 2005	1	<b>3</b>	2	1	0
21–22 January 2005	2	0	<b>5</b>	<b>3</b>	1
26–29 January 2005	2	<b>3</b>	0	2	0

Each snake was initially caught and marked in January 2004, then recaptured in January 2005. Only the date of initial capture within each year is known. Data for successive capture periods (days) with low numbers of captures were combined to avoid excessive numbers of zero records. Clusters of three or more snakes that were captured and recaptured synchronously are shown in boldface font.

tently associated with each other, we expected that snakes that were caught at about the same time in the first year should be recaptured at about the same time in the second year. The null hypothesis of no association suggests that the interval between capture dates in the first year should not be correlated with the interval between capture dates of the same pair of snakes in the second year.

Because these analyses revealed ‘clusters’ of snakes, we also examined the phenotypic traits (sex, body size) of those individuals, to ask if such animals differed in any way from the ‘non-cluster’ snakes, or whether animals in one cluster differed from those in others. All statistical tests were conducted using Statview 5 (SAS Institute 1998); assumptions such as normality and homogeneity of variances were tested prior to analysis.

## RESULTS

### General observations

We observed 0–27 snakes per dive session, including recently marked animals that we did not attempt to recapture. We caught 0–20 ‘new’ animals per session. A few animals were found inactive, sheltering under coral or boulders, but >95% were found as they moved slowly but almost continuously across the reef (see Shine *et al.* 2003a for data on rates of movement, frequency of stops, etc.). Courtship and mating are restricted to winter in this population (Shine 2005), so our January (midsummer) samples did not include any reproductive activity. Many animals were found singly (>5 m from any other snake) but we also encountered groups of two, three or four animals <1 m apart. On some survey periods, most snakes were in groups of this kind. Observations of such groups for

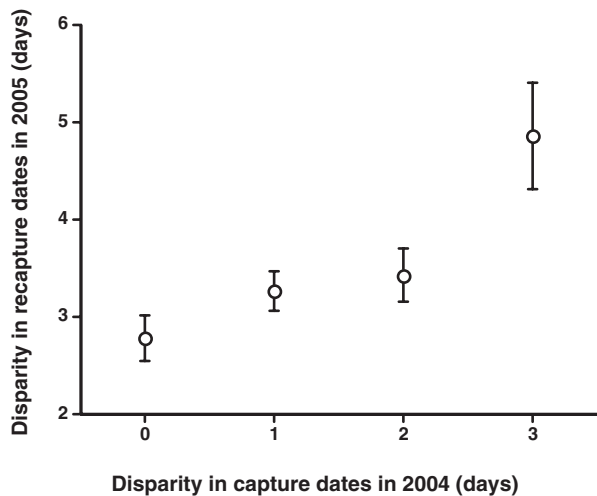
up to 5 min did not reveal any overt interactions between these animals, and the aggregations tended to disperse over the course of this period. If snakes encountered each other they tongue-flicked briefly and then recommenced foraging (investigating substrate crevices for fish nests: Shine *et al.* 2003a).

### Patterns of synchrony in capture

Analysis of the data in Table 1 rejected the null hypothesis of no association between capture date and recapture date (log-likelihood ratio test,  $\chi^2 = 36.61$ , d.f. = 16,  $P < 0.003$ ). This result reflects the existence of ‘clusters’ of co-occurring animals. For example, four snakes originally caught on 26 January 2004 were all recaptured on 19 January 2005, and five snakes caught on 18 January 2004 were all recaptured on 21 and 22 January 2005 (Table 1). An alternative way to examine these data is to compare the number of days between initial captures for any pair of animals to the number of days between recapture of those animals the following year. A positive relationship was apparent. Snakes that were captured at about the same time, generally were recaptured at about the same time (comparing disparities between captures in successive years, for 0–3 days between recaptures,  $r = 0.17$ ,  $n = 432$ ,  $P < 0.0003$ ; see Fig. 1).

### Phenotypic traits of snakes

Because about half of the recaptured snakes were attributable to clusters of three or more co-occurring animals (boldface font in Table 1), we can ask whether these ‘clustered’ snakes differ in phenotypic traits from those caught in other groups, or from the remainder of the sample (i.e. snakes that did not fall into any



**Fig. 1.** Disparities in dates of initial capture (in January 2004) compared to disparities in dates of recapture (in January 2005) for turtle-headed sea snakes, *Emydocephalus annulatus*, in the Noumea area of New Caledonia. Data are shown for the percentage of pairs of snakes in each recapture cohort (e.g. both caught the same day = 0; caught one day apart = 1) for snakes caught from zero to four days apart on the initial (January 2004) trip. Sample sizes (pairs of snakes, left to right) = 118, 175, 101 and 38.

identifiable cluster). For simplicity, we define a 'cluster' as any group of three or more snakes that were captured and recaptured together (i.e. within the same session) in both years.

#### Sex ratio

Contingency-table analysis revealed no significant differences in sex ratio between clusters ( $\chi^2 = 7.84$ , d.f. = 5,  $P = 0.17$ ) nor any difference between 'cluster' and 'non-cluster' animals ( $\chi^2 = 0.00$ , d.f. = 1,  $P > 0.99$ ). Sex ratios of the six recognizable clusters ranged from 100% male (3 male, 0 female) to 100% female (3 female, 0 male), with the other four clusters containing animals of both sexes.

#### Body size

Female turtle-headed sea snakes grow larger than males ( $F_{1,37} = 8.13$ ,  $P < 0.008$ ), but we detected no significant differences in mean body size between 'cluster' snakes *versus* 'non-cluster' conspecifics ( $F_{1,37} = 0.44$ ,  $P = 0.51$ ), nor any significant interaction between aggregation status and sex ( $F_{1,37} = 0.32$ ,  $P = 0.57$ ). Similarly, there were no consistent size differences between snakes in different clusters ( $F_{5,15} = 1.04$ ,  $P = 0.99$ ).

#### Location

Because we have two study sites a few hundred metres apart, we can see if a single 'cluster' always consists of snakes that actually live in the same place. For this analysis, we restricted the analysis to snakes captured on the same days (not sets of consecutive days, when conditions may have changed between sampling times). This leaves four groups, and in every case the snakes within a 'cluster' were captured in the same site (three groups each of three snakes at Baie des Citrons, one group of four snakes at Anse Vata), a result that strongly falsifies the null hypothesis of random assortment ( $\chi^2 = 13.00$ , d.f. = 3,  $P < 0.005$ ).

## DISCUSSION

This analysis was prompted by two puzzling observations in the course of fieldwork on *E. annulatus* in New Caledonia: the tendency for snakes to be found in groups (albeit with no overt social interaction) and for such groups to consist of individuals that had been found together on a previous occasion several months previously. Although sample sizes were small, the patterns were clear: these 'clusters' occurred more often than expected by chance, and were variable in composition (e.g. a given cluster included animals of both sexes and a range of body sizes). Does this synchrony in dates of capture and recapture provide evidence of social organization, or are other explanations more plausible? Several mechanisms might generate the patterns we have seen, but most can be dismissed based on other data. We outline these alternatives below, because any analysis of mark-recapture data needs to consider these possibilities before concluding anything about sociality.

#### Confounding of spatial and temporal factors during sampling

Imagine a system where animals are philopatric, perhaps territorial. If only part of the study site is searched on any given day, animals that occupy adjacent home ranges will tend to be captured (and recaptured) at about the same time. This explanation cannot account for the synchronous capture-recapture phenomenon in *E. annulatus*. First, each study site was small (maximum dimension 50 m), and we crossed and recrossed it many times during each survey. Second, these snakes forage almost constantly and do so by moving virtually continuously across the entire site, at a speed of about  $2 \text{ m min}^{-1}$  (Shine *et al.* 2003a). Thus, synchrony in capture dates cannot be due to small home ranges combined with spatially restricted capture effort.



### Heterogeneity in sampling conditions combined with heterogeneity in vulnerability to capture

If sampling occurs over a range of conditions, a given capture episode may occur at a time when one subset of the population is unusually catchable because of their responses to the conditions at the time. For example (i) animals of different ages, sexes or reproductive condition may be active (and thus, catchable) under different weather conditions. In many ectotherm species, times of activity may differ between adults and juveniles (e.g. Sun *et al.* 2000; Lever 2001) or between adult males and females (King & Duvall 1990), or be affected by reproduction (especially pregnancy: Shine 1979; Charland & Gregory 1990). (ii) In philopatric taxa, specific weather conditions may differentially affect catchability of individuals that live in particular habitats. For example, rainy weather may bring fossorial animals towards the soil surface (where they are more easily catchable) in some soil types but not others, depending upon water penetration (R. Shine, unpubl. data 1995). (iii) If individuals differ in their vulnerability to capture (perhaps because of differing camouflage or escape tactics), the weather conditions at the time of sampling may influence catchability differentially for different individuals. These effects may be most pronounced in ectotherms, where body temperatures influence mobility. Thus, animals that are unusually fast, or live in places where escape is usually easy, may be vulnerable only in unusually cold conditions where they are unable to move fast enough to flee successfully. (iv) Finally, some mark-recapture studies collect animals by an array of methods (e.g. pit-traps, hand-capture), which may substantially bias the kinds (sizes, sexes, etc.) of animals that are caught (Caughley 1977; Caughley & Sinclair 1994). If the amount of effort allocated to these alternative methods differs through time, then this heterogeneity might generate synchrony in collection dates of specific individuals that were vulnerable to the same collection technique.

This explanation also is unlikely in the case of *E. annulatus*. First, our previous work on this population has shown that an individual's body size, sex and reproductive status (pregnant *vs.* non-pregnant) have little effect on its habitat selection, movement patterns or activity (Shine *et al.* 2003b). All size classes of turtle-headed sea snakes eat similar prey, so that there is little spatial subdivision within the foraging population (Shine *et al.* 2003b). Second, there is little thermal stratification within the study area, nor significant day-to-day variation in water temperature over the course of the sampling sessions (Shine *et al.* 2003b). Thus, different effects of temperature or rainfall on animals of different sizes or colours (mediated by factors such as thermal inertia of larger or darker individuals) do not apply to this

system (Shine *et al.* 2003b). Other factors doubtless vary, however, such as freshwater input and the abundance of food and potential predators. We have no information on these topics, but evidence militates against this hypothesis:

1. If ecological heterogeneity related to body size or sex drove the synchrony, then clusters should consist of animals of the same size or sex; this was not the case. More generally, analysis of our data showed no significant day-to-day variation in traits such as sex ratios or mean body sizes among the captured snakes.
2. If individuals tend to be captured synchronously because of commonalities in their response to specific ambient conditions, 'clusters' of snakes should encompass animals from both study areas. That is, the apparent 'cluster' would contain individuals that were so far apart that no direct social connection was feasible. Our data falsify this possibility, because all clusters contained animals from either one or the other study site; none contained individuals from both areas.
3. All of our snakes were captured the same way (hand-collection), so temporal shifts in capture effectiveness for different kinds of individuals cannot explain our results.
4. Lastly, *E. annulatus* swim very slowly (Shine & Shetty 2001; Shine *et al.* 2003a) and all individuals that are seen are captured, so that our capture rates are not biased by differential ability of snakes to avoid capture.

Hence, the most plausible explanation for the synchronous capture and recapture of individuals within the study population is some form of long-term (or seasonal) social bond among small groups of snakes. This explanation also accords well with our frequent observations of three or four individuals in close proximity, despite the lack of any obvious behavioural interactions among those animals. The function of any such aggregative behaviour, let alone the apparent stability of group composition, remains obscure. Studies on captive rattlesnakes have revealed a tendency for closely related individuals (sisters) to aggregate (Clark 2004), hinting at kin-based social systems. Our working hypothesis for *E. annulatus* is that these animals travel to the study area from deeper water in small groups, disperse while feeding, and then join up again at some later time prior to returning to our mark-recapture sites. This species forages in deep as well as shallow water in New Caledonia (to 30 m: Ineich & Laboute 2002), so that the functional significance of the groupings may relate to deep-water ecology rather than any phenomena in the shallow-water areas searched in this study.

We encourage other workers to examine their mark-recapture records for synchrony in the times they encounter specific individuals. If such synchrony

is evident, the next step is to evaluate alternative explanations, as outlined above. Even if the synchrony has a non-social cause, the existence of significant temporal 'clusters' of individuals is an interesting phenomena in and of itself. For example, such heterogeneity invalidates assumptions of capture homogeneity critical to some analytical methods for inferring demographic traits from mark-recapture data (Caughley 1977). This problem is well-known, and methods have been developed to correct for the resulting over-dispersion in capture dates when deriving estimates of population traits (Anderson *et al.* 1994; Mantyniemi & Romakkaniemi 2002). An analysis of synchrony might also reveal correlations between weather conditions and the sex ratio or size structure of population samples, patterns of potential significance both to methodology (i.e. ways of obtaining unbiased population samples) and to ecological issues such as predation vulnerability (Sun *et al.* 2000).

More excitingly, such analyses might reveal hitherto-unsuspected complexity in the social organization of animals such as snakes, in which social interactions are so difficult to observe in nature. Such analyses may be most useful for taxa in which alternative explanations for capture synchrony (such as extreme philopatry and spatially heterogeneous sampling effort) are unlikely to be viable. Some of the best systems may be those in which animals move about widely through the landscape, but are frequently encountered in relatively high densities and especially, in recognizable aggregations. For example, do particular individuals tend to co-occur in mating aggregations of natricine colubrids (Luiselli 1996; Prosser *et al.* 2002), in groups of gravid females in viviparous colubrids, elapids, vipers and rattlesnakes (Stevens 1973; Shine 1979; Plummer 1981; Graves & Duvall 1995) or in small colubrids aggregated in retreat sites during inactivity (Gregory 2004) or captured together in funnel traps? Individual recognition is clearly widespread within lizards, the sister-group to snakes (Bull *et al.* 2000, 2001; O'Connor & Shine 2004), and recent research has documented that the vomeronasal system of snakes can provide very detailed information about conspecifics, even from substrate-deposited trails (LeMaster *et al.* 2001; LeMaster & Mason 2002, 2003; O'Donnell *et al.* 2004; Shine *et al.* 2005). Movement patterns of radio-tracked individuals within snake populations reveal active avoidance of conspecifics (Webb & Shine 1997; Fitzgerald *et al.* 2002; Whitaker & Shine 2003), and we believe that analyses of synchrony in capture-recapture records have the potential to expand significantly our knowledge of snake sociality, while simultaneously deriving additional value from these hard-won data sets.

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## REFERENCES

- Anderson D. R., Burnham K. P. & White G. C. (1994) AIC model selection in overdispersed capture-recapture data. *Ecology* **75**, 1780–93.
- Bull. C. M. (2000) Monogamy in lizards. *Behav. Process.* **51**, 7–20.
- Bull. C. M., Griffin C. L., Lanham E. J. & Johnston G. R. (2000) Recognition of pheromones from group members in a gregarious lizard, *Egernia stokesii*. *J. Herpetol.* **34**, 92–9.
- Bull. C. M., Griffin C. L., Bonnett M., Gardner M. G. & Cooper S. J. B. (2001) Discrimination between related and unrelated individuals in the Australian lizard *Egernia striolata*. *Behav. Ecol. Sociobiol.* **50**, 173–9.
- Carpenter C. C. (1984) Dominance in snakes. *Univ. Kansas Mus. Nat. Hist. Spec. Publ.* **10**, 195–202.
- Caughley G. (1977) *Analysis of Vertebrate Populations*. John Wiley and Sons, New York.
- Caughley G. & Sinclair A. R. E. (1994) *Wildlife Ecology and Management*. Blackwell Scientific Publications, Boston.
- Charland M. B. & Gregory P. T. (1990) The influence of female reproductive status on thermoregulation in a viviparous snake, *Crotalus viridis*. *Copeia* **1990**, 1089–98.
- Clark R. W. (2004) Kin recognition in rattlesnakes. *Proc. Roy. Soc. Lond. Ser. B* **271**, S243–5.
- Cogger H. G. (1975) Sea snakes of Australia and New Guinea. In: *The Biology of Sea Snakes* (ed. W. A. Dunson) pp. 59–140. University Park Press, Baltimore.
- Comendant T., Sinervo B., Svensson E. I. & Wingfield J. (2003) Social competition, corticosterone and survival in female lizard morphs. *J. Evol. Biol.* **16**, 948–55.
- Conradt L. (1998) Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proc. Roy. Soc. Lond. Ser. B* **265**, 1359–63.
- Fitzgerald M., Shine R. & Lemckert F. (2002) Spatial ecology of arboreal snakes (*Hoplocephalus stephensii*, Elapidae) in an eastern Australian forest. *Aust. Ecol.* **27**, 537–45.
- Graves B. M. & Duvall D. (1995) Aggregation of squamate reptiles associated with gestation, oviposition, and parturition. *Herpetol. Monogr.* **9**, 102–19.
- Gregory P. T. (1982) Reptilian hibernation. In: *Biology of the Reptilia, Volume 13* (eds C. Gans & F. H. Pough) pp. 53–154. Academic Press, London.
- Gregory P. T. (2004) Analysis of patterns of aggregation under cover objects in an assemblage of six species of snakes. *Herpetologica* **60**, 178–86.
- Ineich I. & Laboute P. (2002) *Sea Snakes of New Caledonia*. IRD Editions, Paris.
- King M. B. & Duvall D. (1990) Prairie rattlesnake seasonal migrations: episodes of movement, vernal foraging and sex differences. *Anim. Behav.* **39**, 924–35.
- Lanham E. J. & Bull. C. M. (2004) Enhanced vigilance in groups in *Egernia stokesii*, a lizard with stable social aggregations. *J. Zool. (Lond.)* **263**, 95–9.

- LeMaster M. P. & Mason R. T. (2002) Variation in a female sexual attractiveness pheromone controls male mate choice in garter snakes. *J. Chem. Ecol.* **28**, 1269–85.
- LeMaster M. P. & Mason R. T. (2003) Pheromonally-mediated sexual isolation among denning populations of red-sided garter snakes, *Thamnophis sirtalis parietalis*. *J. Chem. Ecol.* **29**, 1027–43.
- LeMaster M. P., Moore I. T. & Mason R. T. (2001) Conspecific trailing behaviour of red-sided garter snakes, *Thamnophis sirtalis parietalis*, in the natural environment. *Anim. Behav.* **61**, 827–33.
- Lever C. (2001) *The Cane Toad. The History and Ecology of a Successful Colonist*. Westbury, Otley.
- Luiselli L. (1996) Individual success in mating balls of the grass snake, *Natrix natrix*: size is important. *J. Zool. (Lond.)* **239**, 731–40.
- Mantyniemi S. & Romakkaniemi A. (2002) Bayesian mark-recapture estimation with an application to a salmonid smolt population. *Can. J. Fish. Aquat. Sci.* **59**, 1748–58.
- O'Connor D. & Shine R. (2003) Lizards in 'nuclear families': a novel reptilian social system in *Egernia saxatilis* (Scincidae). *Mol. Ecol.* **12**, 743–52.
- O'Connor D. E. & Shine R. (2004) Parental care protects against infanticide in the lizard *Egernia saxatilis* (Scincidae). *Anim. Behav.* **68**, 1361–9.
- O'Donnell R. P., Ford N. B., Shine R. & Mason R. T. (2004) Male red-sided garter snakes, *Thamnophis sirtalis parietalis*, determine female mating status from pheromone trails. *Anim. Behav.* **68**, 677–83.
- Osterwalder K., Klingensböck A. & Shine R. (2004) Field studies on a social lizard: home range and social organization in an Australian skink, *Egernia major*. *Aust. Ecol.* **29**, 241–9.
- Plummer M. V. (1981) Communal nesting of *Opheodrys aestivus* in the laboratory. *Copeia* **1981**, 243–6.
- Prosser M. R., Weatherhead P. J., Gibbs H. L. & Brown G. P. (2002) Genetic analysis of the mating system and opportunity for sexual selection in northern water snakes (*Nerodia sipedon*). *Behav. Ecol.* **13**, 800–7.
- Ruckstuhl K. E. (1999) To synchronise or not to synchronise: a dilemma for young bighorn males? *Behaviour* **136**, 805–18.
- SAS Institute (1998) *Statview 5*. SAS Institute, Cary.
- Seigel R. A. (1993) Summary: future research on snakes, or how to combat 'lizard envy'. In: *Snakes: Ecology and Behavior* (eds R. A. Seigel & J. T. Collins) pp. 395–402. McGraw-Hill, New York.
- Shine R. (1979) Activity patterns in Australian elapid snakes (Squamata: Serpentes: Elapidae). *Herpetologica* **35**, 1–11.
- Shine R. (2005) All at sea: aquatic life modifies mate-recognition modalities in sea snakes (*Emydocephalus annulatus*, Hydrophiidae). *Behav. Ecol. Sociobiol.* **57**, 591–98.
- Shine R. & Bonnet X. (2000) Snakes: a new 'model organism' in ecological research? *Trends Ecol. Evol.* **15**, 221–2.
- Shine R. & Shetty S. (2001) Moving in two worlds: aquatic and terrestrial locomotion in sea snakes (*Laticauda colubrina*, Laticaudidae). *J. Evol. Biol.* **14**, 338–46.
- Shine R., Cogger H. G., Reed R. N., Shetty S. & Bonnet X. (2002) Aquatic and terrestrial locomotor speeds of amphibious sea-snakes (Serpentes, Laticaudidae). *J. Zool. (Lond.)* **259**, 261–8.
- Shine R., Bonnet X., Elphick M. J. & Barrott E. G. (2003a) A novel foraging mode in snakes: browsing by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae). *Funct. Ecol.* **18**, 16–24.
- Shine R., Shine T. & Shine B. G. (2003b) Intraspecific habitat partitioning by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae): the effects of sex, body size, and colour pattern. *Biol. J. Linn. Soc.* **80**, 1–10.
- Shine R., O'Donnell R. P., Langkilde T., Wall M. D. & Mason R. T. (2005) Snakes in search of sex: the relationship between mate-locating ability and mating success in male garter snakes. *Anim. Behav.* **69**, 1251–58.
- Sokal R. R. & Rohlf F. J. (1981) *Biometry*, 2nd edn. Freeman, New York.
- Stevens R. A. (1973) A report on the lowland viper, *Atheris superciliaris* (Peters), from the Lake Chilwa floodplain of Malawi. *Arnoldia* **22**, 1–22.
- Stow A. J. & Sunnucks P. (2004) High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Mol. Ecol.* **13**, 419–30.
- Sun L., Shine R., Zhao D. & Tang Z. (2000) Biotic and abiotic influences on activity patterns of insular pit-vipers (*Gloydius shedaoensis*, Viperidae) from north-eastern China. *Biol. Conserv.* **97**, 387–98.
- Voris H. K. (1966) Fish eggs as the apparent sole food item for a genus of sea snake, *Emydocephalus* (Krefft). *Ecology* **47**, 152–4.
- Webb J. K. & Shine R. (1997) A field study of spatial ecology and movements of a threatened snake species, *Hoplocephalus bungaroides*. *Biol. Conserv.* **82**, 203–17.
- Whitaker P. B. & Shine R. (2003) A radiotelemetric study of movements and shelter-site selection by free-ranging brown snakes (*Pseudonaja textilis*, Elapidae). *Herpetol. Monogr.* **17**, 130–44.