AN ETHOGRAM FOR ADULT MALE RAINBOW SKINKS, CARLIA JARNOLDAE

TRACY LANGKILDE, LIN SCHWARZKOPF AND ROSS ALFORD

School of Tropical Biology, James Cook University, Townsville, Queensland, 4811, Australia

An ethogram for male rainbow skinks, Carlia jarnoldae (mean snout-to-vent length 44 mm), was derived from observations of captive individuals in large, semi-natural field enclosures during the summer. Males were observed in one of four treatments: solitary, socially with a male conspecific, socially with a female conspecific, or with a model of an avian predator. We identified 32 different types of behaviour, including postures and simple movements. Six of the behaviours (dorsolateral orientation, head bob, letisimulation, slow motion, throat flash and tail wave) are of particular interest because their functions are either controversial or unknown. We describe them in detail, and infer their functional significance from the contexts in which they occurred. Dorsolateral orientation and slow motion behaviours appear to function primarily in courtship; throat flashes may provide information to conspecifics; and letisimulation may function as an antipredator behaviour. The function of head bobs remains unresolved, and tail waves appear to signal residency, but need further investigation. Although the behaviours exhibited by C. jarnoldae males were generally similar to those reported in other skinks, two of the behaviours we observed (letisimulation and throat flash) have not previously been recorded in a skink. Carlia jarnoldae males were outside refugia for most of our observation periods, and appeared to defend areas of the enclosures from conspecific males. Both visual signals (dorsolateral orientations, slow-motion behaviour and throat flashes) and chemical cues were used to communicate with conspecifics.

Key words: behaviour, lizard, social interactions, visual signals

INTRODUCTION

Lizards provide an excellent model system for studying signal evolution. However, the scientific literature on lizard social behaviour displays a strong taxonomic bias, with disproportionate attention to certain lineages, such as iguanids (Carpenter & Ferguson, 1977; Stamps, 1977; Ord et al., 2001). Although the family Scincidae is one of the largest and most diverse lizard lineages (ecologically, geographically and morphologically), the social behaviour of scincids has received far less attention than many other groups. Small skinks are thought to lack obvious social displays (Done & Heatwole, 1977; Stamps, 1977), but recent research has revealed that skinks exhibit complex social characteristics, including stable social aggregations (Greer, 1989; Gardner et al., 2001), kin recognition (Bull, 2000; Bull et al., 2000, 2001), female mate choice (Cooper & Vitt, 1993), mate guarding (Olsson & Shine, 1998), and aggressive territory defence (Jennings & Thompson, 1999).

Skinks occur virtually worldwide, but are most diverse in Australia (>300 species: Cogger, 2000). Nevertheless, we have been able to locate in the literature comprehensive descriptions of behavioural repertoires (ethograms) for only three species of Australian skink (*Carlia rostralis*: Whittier & Martin, 1992; Whittier, 1994; *Lampropholis guichenoti*: Torr & Shine, 1994; *Ctenotus fallens*: Jennings & Thompson, 1999), as well as for one North American species (*Eumeces inexpectatus*: Perrill, 1980). Before we can

understand and interpret the evolution of behavioural traits in lizards, we need to document patterns in a large number of phylogenetically divergent lineages. Ethograms for a range of species are necessary before we can undertake comparative studies.

This study aims to provide a thorough account of the behaviours displayed by males of an Australian skink, *Carlia jarnoldae*, under a range of circumstances, and to explore their probable function. We observed males in naturalistic outdoor enclosures in one of four treatments: while alone, with a female conspecific, with a male conspecific, or in the presence of a "predator". We describe the behaviours observed during these trials, and discuss the functional significance of various behaviours by examining the degree to which they are performed in the different treatments.

METHODS

Carlia jarnoldae is a diurnal skink found throughout north-eastern Queensland (Cogger, 2000). It is locally abundant in the Townsville region, inhabiting rocky areas in dry sclerophyll forest and tropical woodlands. It is a small skink – adult males average 44 mm snout-vent length (SVL), 68 mm tail length and weigh 2.4 g; adult females average 43 mm SVL, 64 mm tail length and weigh 1.9 g. Adults show striking sexual dimorphism; males are heavier, but not longer, and much more colourful than are females (Cogger, 2000).

The behaviour of males was observed over two summers (January to March), in 1999 and 2001. This season falls within the normal mating period of this species, which is from October to June (pers. obs.). We collected 66 individuals (11 females and 55 males) from Campus

Correspondence: T. Langkilde, School of Biological Sciences, Heydon-Laurence Building A08, University of Sydney, NSW 2006, Australia. *E-mail*: langkild@bio.usyd.edu.au

Creek, James Cook University, Townsville, Australia (19º 16'S, 146º 48'E). These skinks are capable of tail autotomy and - because tail loss may alter an animal's behaviour - we used only animals with complete tails. We randomly designated individual males as either focal (n=44) or stimulus (n=11) animals, while females were all used as stimulus animals (n=11). Focal males were observed and their behaviour was recorded during observation periods, and stimulus animals were introduced into the enclosures of focal males during social observations. Both focal and stimulus individuals were marked on the top of the snout with a small $(2 \times 2 \text{ mm})$ spot of coloured nail polish to facilitate visual identification from a distance. Focal and stimulus individuals were marked with different colours, which were assigned randomly. This mark did not influence the lizards' behaviour (Langkilde, 1999), as marks were relatively inconspicuous, and skink displays involving colour are generally oriented laterally (pers. obs.; Carpenter & Ferguson, 1977; Whittier, 1994).

For observations, skinks were housed separately in one of eight oval, plastic enclosures $(200 \times 100 \times 50)$ cm, $L \times W \times D$). These enclosures were located outdoors at JCU campus. The enclosures received direct natural sunlight from approximately 0700 hrs to 1830 hrs each day. Each enclosure was partially covered with shade cloth (patches of cloth shading 50% or 80% of incoming solar radiation were used), providing skinks with sunny and shady areas, similar to the wild, to allow natural basking behaviour (pers. obs.). Animals were visible for most of our observation periods. Water was available ad libitum, and individuals were able to feed on insects that frequently entered the open enclosures. There was no significant change in mass of skinks from the day of capture to the day of release (paired samples *t*-test: *t*= 0.459, df=24, *P*=0.65, 4-15 days; average 10.6 days) indicating that food supply was sufficient. Each enclosure contained sand and leaf litter as substrate, and two wooden boards (300 \times 200 mm, L \times W) that were slightly raised above the substrate at one end provided shelters, basking sites, and display areas. We randomly assigned skinks to the enclosures 24-48 hrs prior to behavioural observations.

The behaviour of male C. jarnoldae was observed in one of four treatments: focal animal alone ("solitary" observations; n=11), focal animal with a male conspecific ("social + male" observations; n=11), focal animal with a female conspecific ("social + female" observations; n=11), and focal animal exposed to a predator ("predator" observations; n=11). All observations were made from behind an opaque screen to minimize observer effects. During solitary observation periods we simply observed the focal animal. During social observation periods, a conspecific male or female was placed in the vicinity of the focal male. The observer then withdrew behind the blind, and waited 5 minutes before commencing observations. The introduced non-focal animal was removed 20 minutes later. No injuries resulted during aggressive interactions. During predator observation periods, we placed a taxidermic mount of a laughing kookaburra (*Dacelo novaeguineae*) on the rim of the enclosures. Kookaburras are visual predators of small lizards (Barker & Vestjens, 1989), and spend much of their time perched in trees watching for prey (Simpson *et al.*, 1996). Therefore, the model was arranged in a natural pose on the edge of the enclosure, providing a stimulus similar to that of a real bird. We observed the focal male for 20 minutes (commencing 5 minutes after withdrawing behind the blind), and then removed the kookaburra.

All observations were made between 0700 and 1100 hrs, corresponding to the period of maximum activity in the wild (pers. obs.). On each observation day, we determined the order in which individual focal males were to be observed with a random numbers table. Observation periods were always 20 minutes, commencing 5 minutes after withdrawing behind the blind. Within 5 minutes of withdrawing behind the blind, skinks had usually emerged from under the shelters to which they fled when approached. Observations were made using a customwritten event-recording program on an HP 200LX palmtop computer. At the completion of testing, visual identification marks were removed, all animals were individually marked by toe clipping to avoid recapture and they were released at the point of capture.

DATA ANALYSIS

Only animals that were fully visible (i.e. not hidden under the shelters) for at least five minutes of the observation period were used in the analyses, as it is not possible to observe and record all behaviours exhibited by partly emerged animals, and shorter periods of exposure were too brief to provide a reasonable sample of possible behaviours. Kruskal-Wallis tests were used to analyse the number of males that performed each behaviour. Analyses of the number of times each male performed each behaviour during the 20 minute observation period yielded quantitatively similar results.

RESULTS AND INTERPRETATION OF BEHAVIOURS

Thirty-two behaviours were observed in male *C. jarnoldae* (Table 1). Females were also observed during the "social + female" trials, but their behaviour was not recorded as it was impossible to record the behaviour of two individuals simultaneously. Thus, although we were unable to quantify female behaviours and determine their functional significance, we were able to verify that females displayed similar behaviours. Females were observed performing 23 of the 32 behaviours recorded. The only behaviours we did not observe in females were those associated with mating, fighting or displays in males, such as copulations and flank bites, fighting, and dorsolateral orientations. We also did not observe females gaping.

ETHOGRAM FOR RAINBOW SKINKS

TABLE 1. The following behaviours were recognized in captive male *C. jarnoldae*. These behaviours have been assigned to functional categories, based on the results of this and previous studies on lizard behaviour (Carpenter *et al.*, 1970; Done & Heatwole, 1977; Whittier & Martin, 1992; Torr & Shine, 1994; Whittier, 1994). For behaviours that were previously unknown, or for which the function was previously unresolved, we have justified the classification in more detail later (these are indicated with an *). There are five behaviours which remain unresolved, as they are either rarely observed, or occur in all contexts.

Functional category	Behaviour	Description
Courtship	Dorsolateral orientation*	Slight dorsoventral compression of the body and postural adjustment so that the body is tilted and dorsolaterally presented to a stimulus
	Slow motion*	All movements occur in short, rapid jerks, appearing as if under a strobe light.
MATING	Cloaca drag	Pulling the body forward with the forelimbs while keeping the cloacal region in contact with the substrate.
	Copulation	Insertion of hemipenis and pelvic thrusting while cloacae are in opposition.
	Flank bite	Mouth grip by the male on the skin of the neck or side of the female, maintained during copulation.
	Pelvic thrust	Forward thrusting movements of the pelvic region and the base of the tail by the male during copulation.
Aggressive	Bite	One skink grasps another in its jaws.
	Fight	Vigorously encountering another individual, usually involving some
		contact and biting.
Social	Throat flash*	An exaggerated mouth scrape, resulting in complete exposure of the gular colouration in the direction of a stimulus.
Maintenance	Adpress	One or more limbs raised off the substrate and held against the side of the body.
	Bask flat	A conspicuous dorsoventral flattening of the body against the
	Deels bish	substrate (occurs both in the sun and in the shade).
	Bask nign	(occurs in both sun and shade).
	Bask raised	Head raised but forebody resting against the substrate (occurs in both sun and shade).
	Defecate	The tail is raised and the body moved forward as faeces are passed.
	Drink	The snout is placed in water or against dew and the tongue slowly protruded and returned to the mouth.
	Eat	A food item is grasped in the jaws and consumed.
	Forage	Movement through vegetation and under ground debris such as leaf
	Leg lift	Lift legs onto back while lying with ventral surface against substrate. Reduces contact with hot substrate
	Mouth scrape	The side of the mouth is scraped on a hard substrate.
Movement	Crawl	A slow, forward movement with the body in contact with the substrate.
	Jump Run	Leap into the air such that all four feet leave the substrate. A fast, forward movement with the body raised off the substrate.
Exploratory	Tongue flick	The rapid movement of the tongue in and out of the mouth.
	Turn head	Movement of the head while the body remains motionless. (Looking around).
Escape	Flee Patrol	One skink moves quickly away from another skink or a predator. Running or crawling along the perimeter of the enclosure.

Antipredator	Letisimulation*	Actions taken by an individual that convey the impression that the individual is dead. "Playing dead".
Unresolved	Arc tail	Raise the tail in an arc, with the distal portion brought forward over the back.
	Gape	A wide opening of the jaws.
	Head bob	Relatively rapid movement of the head up and down from the neck.
	Tail undulate*	A sinusoidal movement of the entire tail while the tail is held horizon- tally just above the substrate.
	Tail wave*	Movement of the tail in a waving motion, occurring at different levels of intensity.

TABLE 1. (continued...)

Males exhibited a wide range of social behaviours, and interacted socially with most individuals they encountered, although these interactions were generally brief (approximately 3-5 minutes). During "social + male" encounters, males were observed attacking other males, chasing them around the enclosures and occasionally biting them, and chasing them out from under the shelters. In one trial, we observed males fighting, and in five trials we observed males chasing each other. None of these behaviours were observed in any other treatment. Generally, the active period (lasting approximately 45 min) was spent basking (mean percentage time ±SE: 72.19±4.04 secs), interspersed with periods of inactivity during which refuge was sought (mean percentage time ±SE: 24.10±16.32 secs), and occasional periods of foraging behaviour (mean percentage time ±SE: 1.78;±0.61 secs).

The behaviour of individuals in enclosures was similar to that observed in the wild (Langkilde, 1999).The majority of the behaviours we observed were similar to those reported for other skinks (Carpenter & Ferguson, 1977; Torr & Shine, 1994; Whittier, 1994); however, a few have not been previously described, or their function is unclear because they have not been systematically observed under different controlled circumstances. Of these behaviours, we give a more detailed description of those that were commonly observed, and infer their probable significance from the contexts in which they are performed. The other unresolved behaviours (arc tail, gape and tail undulate) were observed too rarely to infer their function from our data.

DORSOLATERAL ORIENTATIONS

Dorsolateral orientations were performed by significantly more males (H=6.6, df=3, P<0.001) when a conspecific female was present (6/11 males) than in any other treatment (1/11 males in predator trial, and none in any other treatment). This behaviour was performed for an average of 10.6 (±2.93 SE) seconds.

Dorsolateral orientations are performed by dorsoventrally compressing the body and positioning it in such a way that it is dorsolaterally presented to a stimulus individual. This posture exaggerates the male's body size and profile, and exposes the dorsal series of black and white stripes, the lateral band of blue spots on a black background, and the bright orange lateral coloration of male *C. jarnoldae*.

Both lateral presenting and lateral tilting postures have been described as separate aggressive behaviours in many lizards, including skinks (Mount, 1963; Perrill, 1980; Cooper & Vitt, 1988; Torr & Shine, 1994; Jennings & Thompson, 1999), agamids (Carpenter et al., 1970; Brattstrom, 1971) and iguanids (Greenberg, 1977a, b), but their simultaneous use has only been described in one lizard species, the skink, C. rostralis (Whittier, 1994). C. rostralis males use this behaviour primarily in dominance/subordination interactions with other males (Whittier, 1994). The function of this behaviour may be similar in the two species: to make the animal appear larger and more colourful. C. rostralis appear to perform dorsolateral orientations to seem larger and more threatening to a rival male (Whittier, 1994), whereas C. jarnoldae may perform this display to "impress" females with their size and colour, or as a general signal of fitness to females (and possibly predators: Rohwer, 1982; Cooper & Greenberg, 1992).

HEAD BOB

Almost all males (41/44) were observed performing head bobs, and the proportion of males that performed this behaviour did not significantly differ between treatments (H=0.73, df=3, P=0.28). This behaviour lasts for an average of 1.48 (±0.32 SE) seconds.

Head bob behaviours have been observed in many lizards, including skinks (Done & Heatwole, 1977; Torr & Shine, 1994; Whittier, 1994), iguanids (Phillips, 1995; Jenssen *et al.*, 2000) and agamids (LeBas & Marshall, 2000; Znari & Benfaida, 2001). Head bobs performed by iguanids and agamids are complex and highly ritualized (Carpenter *et al.*, 1970; Lovern *et al.*, 1999; Jenssen *et al.*, 2000). *C. jarnoldae* performed headbobs at varying amplitudes and frequencies, but as each bob was extremely rapid it was not possible to record these variations. In other species (iguanids and agamids), this behaviour is a submissive social signal associated with territorial fighting and courtship, and

functions as a threat or challenge signal (Brattstrom, 1971; Greenberg, 1977*a*; Phillips, 1995). It may also increase visual acuity, possibly enhancing depth of field (e.g. as in *Chamaelinorops barbouri*: Jenssen & Feely, 1991, and possibly *Lampropholis guichenoti*: Torr & Shine, 1994).

C. jarnoldae perform head bobs in all contexts, even when solitary, thus they may have multiple functions. It would be interesting to determine whether head bobs are used to different extents by resident and non-resident animals.

LETISIMULATION

This is the first record of death-feigning behaviour in a skink. Both males (n=5) and females (n=7) exhibited letisimulation behaviour, but only in response to being captured by a human. Upon capture, the skink would convulse and its body and legs would become rigid. This would last until the skink was replaced on the ground or otherwise stimulated to move (e.g. by blowing on it), though if a letisimulating individual were gently placed upside down on a rock it would remain in this pose until stimulated to move. The skink would then quickly right itself and flee. Some individuals would repeat this behaviour each time they were captured, and flee each time they were released. Letisimulation behaviour may reduce predation risk, as movement is a cue used by predators to facilitate prey detection (Gluesing, 1983), so remaining motionless may cause predators to release prey or abandon pursuit.

SLOW MOTION

Slow motion behaviour was performed by significantly more males when a female was present (5/11 males; H=7.13, df =3, P=0.005), but was occasionally observed during "social + male" (2/11 males) and "predator" trials (1/11 males). This behaviour lasts for an average of 9.29 (±2.92 SE) seconds.

When performing slow motion, all movements appear short and jerky, as if being viewed under a strobe light. Slow motion has only been reported in a few species of lizard, and is thought to function as a courtship display in some (*Anguis fragilis*: Palmer, 1937; *Crotaphytus collaris*: Greenberg, 1945), and have an antipredator function in others (*Lacerta vivipara*: Thoen *et al.*, 1986; Van Damme *et al.*, 1990; and *Oedura lesueurii*: Downes & Adams, 2001). Torr & Shine (1994) suggested that slow motion in *Lampropholis guichenoti* may be an assertion display in agonistic interactions, and provided circumstantial evidence that a pheromone may be associated with this behaviour.

Slow motion is performed by male *C. jarnoldae* primarily in the presence of females and may play a part in courtship. It is difficult to say how it would function in courtship, but it is possible that it may appease the female, allowing the male to approach. Alternately it may act as an "honest" signal of strength and endurance, or control and co-ordination, as it is a vigorous behaviour that involves the use of many muscles in opposition to each other, and may be energetically costly. Slow motion behaviours are also directed at conspecific males, possibly as a threat display, and may act as an "honest" signal of superior escape ability in the presence of a predator (Leal & Rodriguez-Robles, 1995; Leal & Rodriguez-Robles, 1997*a*,*b*; Leal, 1999).

THROAT FLASH

The proportion of males that performed this behaviour differed significantly between treatments (H=9.33, df =3, P=0.005). Males mostly performed this behaviour during social trials (8/11 males for "social + female"trials, and 6/11 males for "social + male" trials), some during "predator" trials (4/11 males) and none during solitary trials. This behaviour lasts an average of 2.93 (\pm 0.39 SE) seconds.

The gular coloration of adult C. jarnoldae males is pale bluish-white, which becomes brilliant blue during the reproductive season, whereas that of females and juveniles is white to grey. C. jarnoldae males display this gular coloration by turning the head laterally until the throat is facing the stimulus individual, and angling the head towards the substrate before sweeping the head back into its original position. This behaviour appears to be an exaggerated and ritualized form of the mouth scrape behaviour, which is apparently used to remove food from the sides of the mouth after eating. Throat flashes start from a higher position than do mouth scrapes, and with the head turned more and therefore displaying more of the throat. During a throat flash the head is moved in a horizontal arc rather than being scraped along the substrate, with the jaw barely touching the latter.

The gular region is displayed in behaviours performed by many lizards, such as dewlap extensions in iguanids (Zucker, 1994; Carpenter, 1995; Zucker & Murray, 1996; Tokarz, 2002), throat displays in agamids (Brattstrom, 1971; LeBas & Marshall, 2000) and varanids (Bels *et al.*, 1995), and the "head raised" posture in the skink *Carlia rostralis* (Whittier, 1994), but this is the first record of the throat being displayed when the head is turned to the side.

Gular coloration provides information about age and sex that can be assessed from a distance (Whittier, 1994; Carpenter, 1995), and can be used to signal dominant status and exhibit territorial behaviour (Zucker, 1994; Bels *et al.*, 1995; Tokarz, 2002). This display probably provides similar information in this species, as the throat coloration of C. *jarnoldae* is different in males, females and juveniles and becomes exaggerated during the mating season, and throat flash behaviour is performed mostly during social trials. This behaviour is also performed when a predator is present, indicating that it may also function as a signal to predators, though the intended message is unclear.

TAIL WAVES

Tail waves occurred at three intensities that appeared to be part of a continuum of waves with similar functions: at the lowest intensity, skinks waved the distal third of the tail from side to side; next they moved the whole tail from side to side, and at the highest intensity they vigorously lashed the whole tail along the side of the body and over the back. Tail waves were very commonly performed by males of this species, but were performed by significantly fewer males when alone (4/ 11 males) than in any other treatment (9/11 males for 'social + female' trials; 9/11 males for 'social + male' trials, 11/11 males for 'predator' trials), and were performed primarily by resident males. Tail waves last an average of 2.11 (±0.09 SE) seconds. These behaviours will need to be further explored to determine their function.

DISCUSSION

Skinks are thought to lack social displays, and many species are less territorial and more fossorial than are other lizards (Stamps, 1977). However, *C. jarnoldae* used visual signals such as dorsolateral orientations, slow motion behaviour and throat flashes to communicate with conspecifics. We also observed males fighting, and chasing each other around the enclosures and out from under the shelters. Tongue flicks were also used, maybe to detect chemicals on, or left by, conspecifics (Alberts & Werner, 1993; Cooper, 1996; Cooper *et al.*, 1999). *Carlia jarnoldae* is a highly interactive, surfaceactive species that uses a wide array of visual and chemical signals to communicate with both conspecifics and predators.

Many of the behaviours performed by C. jarnoldae were similar to those described for other skinks (Carpenter & Ferguson, 1977; Torr & Shine, 1994; Whittier, 1994), but leg waves, which have been observed in other skinks (Carpenter & Ferguson, 1977; Whittier, 1994), were not observed in C. jarnoldae. We observed throat flash and letisimulation behaviours that have not been described in skinks before. Letisimulation was observed only in response to being captured, suggesting that it has an antipredator function. Throat flash behaviour displays the males' gular coloration, which may provide information about age, sex and reproductive status, or may act as a signal of aggression. C. jarnoldae appears less likely to engage in physical contact during aggressive interactions than are other skinks (e.g. Sphenomorphus kosciuskoi Done & Heatwole, 1977), but instead rely more on challenge or threat displays and chasing opponents rather than on physical combat to settle disputes.

ACKNOWLEDGMENTS

We thank R. Shine, F. Seebacher, R. Brooks, B. Congdon, and A. Krockenberger, for providing valuable comments on the manuscript, and Nicola Peterson for collecting some of the data presented here. The research

presented here adhered to the Guide for Appropriate Treatment of Amphibians and Reptiles in Field Research (ASIH and HL), the legal requirements of Australia, and the ethics guidelines for James Cook University, Townsville. Ethics approval was obtained in January, 1998, certificate number A515. Animal collection was covered by a Scientific Purposes Permit number NO/001257 /96/SAA, issued in June, 1998.

REFERENCES

- Alberts, A. C. & Werner, D. I. (1993). Chemical recognition of unfamiliar conspecifics by green iguanas: functional significance of different signal components. Animal Behaviour 46, 197-199.
- Barker, R. D. & Vestjens, W. J. M. (1989). The food of Australian birds. Volume 1: Non-Passerines. ACT Australia: CSIRO.
- Bels, V. L., Gasc, J. P., Goosse, V., Renous, S. & Vernet, R. P. (1995). Functional analysis of the throat display in the sand goanna Varanus griseus (Reptilia, Squamata, Varanidae). Journal of Zoology 236, 95-116.
- Brattstrom, B. H. (1971). Social and thermoregulatory behavior of the bearded dragon, *Amphibolurus* barbatus. Copeia 1971, 484-497.
- Bull, M. C. (2000). Monogamy in lizards. Behavioural Processes 51, 1-3.
- Bull, C. M., Griffin, C. L., Bonnett, M., Gardner, M. G. & Cooper, J. B. (2001). Discrimination between related and unrelated individuals in the Australian lizard Egernia striolata. Behavioral Ecology and Sociobiology 50, 173-179.
- Bull, M. C., Griffin, C. L., Lanham, E. J. & Johnston, G. R. (2000). Recognition of pheromones from group members in a gregarious lizard, *Egernia stokesii*. *Journal of Herpetology* 34, 92-99.
- Carpenter, G. C. (1995). The ontogeny of a variable social badge - throat color development in tree lizards (Urosaurus ornatus). Journal of Herpetology 29, 7-13.
- Carpenter, C. C., Badham, J. A. & Kimble, B. (1970). Behavior patterns of three species of *Amphibolurus* (Agamidae). *Copeia* **1970**, 497-505.
- Carpenter, C. C. & Ferguson, G. W. (1977). Variation and evolution of stereotyped behaviour in reptiles. In: *Biology of the Reptilia, Vol.* 7, 335-554. Gans, C. & Tinkle, D. W. (Eds). London: Academic Press Inc.
- Cogger, H. G. (2000). Reptiles and amphibians of Australia. New Holland: Reed Books.
- Cooper, W. E. Jr. (1996). Chemosensory recognition of familiar and unfamiliar conspecifics by the scincid lizard *Eumeces laticeps*. *Ethology* **102**, 454-464.
- Cooper, W. E. & Greenberg, N. (1992). Reptilian colouration and behaviour. In: Biology of the Reptilia, Vol. 18. Physiology B., 298-422. Gans, C. & Crews, D. D. (Eds). Chicago: University of Chicago Press.
- Cooper, W. E., Jr., Van Wyk, J. H., Le, P. & Mouton, F. N. (1999). Discrimination between self-produced pheromones and those produced by individuals of the

same sex in the lizard Cordylus cordylus. Journal of Chemical Ecology 25, 197-208.

- Cooper, W. E. Jr. & Vitt, L. J. (1988). Orange head coloration of the male broad-headed skink (*Eumeces laticeps*), a sexually selected social cue. Copeia 1988, 1-6.
- Cooper, W. E., Jr. & Vitt, L. J. (1993). Female mate choice of large male broad-headed skinks. *Animal Behaviour* 45, 683-693.
- Done, B. S. & Heatwole, H. (1977). Effects of hormones on the aggressive behaviour and social organization of the scincid lizard, Sphenomorphus kosciuskoi. Zeitschrift für Tierpsychologie 44, 1-12.
- Downes, S. J. & Adams, M. (2001). Geographic variation in antisnake tactics: the evolution of scent-mediated behavior in a lizard. *Evolution* 55, 605-615.
- Gardner, M. G., Bull, C. M., Cooper, S. J. B. & Duffield, G. A. (2001). Genetic evidence for a family structure in stable social aggregations of the Australian lizard Egernia stokesii. Molecular Ecology 10, 175-183.
- Gluesing, E. A. (1983). Collared lizard predation: the effects of conspicuous morphology and movement. *Copeia* 1983, 835-837.
- Greenberg, N. (1945). Notes on the social behavior of the collared lizard. *Copeia* 1945, 225-230.
- Greenberg, N. (1977a). An ethogram of the blue spinylizard, Sceloporus cyanogenys (Reptilia, Lacertilia, lguanidae). Journal of Herpetology 11, 177-195.
- Greenberg, N. (1977b). A neuroethological study of display behavior in the lizard Anolis carolinensis (Reptilia, Lacertilia, Iguanidae). American Zoologist 17, 191-201.
- Greer, A. E. (1989). The biology and evolution of Australian lizards. NSW: Surrey Beatty and Sons Pty Ltd.
- Jennings, B. W. & Thompson, G. G. (1999). Territorial behavior in the Australian scincid lizard *Ctenotus* fallens. Herpetologica 55, 352-361.
- Jenssen, T. A. & Feely, P. C. (1991). Social behaviour of the male anoline lizard *Chamaelinorops barbouri*, with a comparison to *Anolis*. Journal of Herpetology 25, 454-462.
- Jenssen, T. A., Orrell, K. S. & Lovern, M. B. (2000). Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. *Copeia* 1, 140-149.
- Langkilde, T. (1999). Tails as a signalling system in skinks: their function and the consequences of their loss. Honours Thesis, James Cook University, Townsville, Australia.
- Leal, M. (1999). Honest signalling during prey-predator interactions in the lizard Anolis cristatellus. Animal Behaviour 58, 521-526.
- Leal, M. & Rodríguez-Robles, J. A. (1995). Antipredator responses of Anolis cristatellus (Sauria: Polychrotidae). Copeia 1995, 155-161.
- Leal, M. & Rodríguez-Robles, J. A. (1997a). Antipredator responses of the Puerto Rican Giant Anole, Anolis cuvieri (Squamata: Polychrotidae). Biotropica 29, 372-375.

- Leal, M. & Rodríguez-Robles, J. A. (1997b). Signalling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. *Animal Behaviour* 54, 1147-1154.
- LeBas, N. R. & Marshall, N. J. (2000). The role of colour in signalling and mate choice in the agamid lizard Ctenophorus ornatus. Proceedings of the Royal Society Biological Sciences Series B. 267, 445-452.
- Lovern, M. B., Jenssen, T. A., Orrell, K. S. & Tuchak, T.
 (1999). Comparisons of temporal display structure across contexts and populations in male *Anolis carolinensis*: Signal stability or lability? *Herpetologica* 55, 222-234.
- Mount, R. H. (1963). The natural history of the red-tailed skink Eumeces egregius. American Midland Naturalist 70, 356-385.
- Olsson, M. & Shine, R. (1998). Chemosensory mate recognition may facilitate prolonged mate guarding by male snow skinks, *Niveoscincus microlepidotus*. *Behavioral Ecology and Sociobiology* 43, 359-363.
- Ord, T. J., Blumstein, D. T. & Evans, C. S. (2001). Intrasexual selection predicts the evolution of signal complexity in lizards. *Proceedings of the Royal Society of London, Series B* 268, 737-744.
- Palmer, M. G. (1937). Notes on the breeding habits of the slow worm (Anguis fragilis). American Naturalist 1937, 222.
- Perrill, S. A. (1980). Social communcation in *Eumeces* inexpectatus. Journal of Herpetology 14, 12-135.
- Phillips, J. A. (1995). Does cadence of Iguana iguana displays facilitate individual recognition? Behavioral Ecology and Sociobiology 37, 337-342.
- Rohwer, S. (1982). The evolution of reliable and unreliable badges of fighting ability. *American Zoologist* 22, 531-546.
- Simpson, K., Day, N. & Trusler, P. (1996). Field guide to the birds of Australia. 5th edn. Australia: Viking.
- Stamps, J. A. (1977). Social behavior and spacing patterns in lizards. In: Biology of the Reptilia, Volume 7, Ecology and Behavior A, 264-334. Gans, C. & Tinkle, D. W. (Eds). New York: Academic Press.
- Thoen, C., Bauwens, D. & Verheyen, R. F. (1986). Chemoreception and behavioural responses of the common lizard *Lacerta vivipara* to snake chemical deposits. *Animal Behaviour* **34**, 1805-1813.
- Tokarz, R. R. (2002). An experimental test of the importance of the dewlap in male mating success in the lizard *Anolis sagrei*. *Herpetologica* **58**, 87-94.
- Torr, G. A. & Shine, R. (1994). An ethogram for the small scincid lizard Lampropholis guichenoti. Amphibia-Reptilia 15, 21-34.
- Van Damme, R., Bauwens, D., Vanderstighelen, D. & Verheyen, R. F. (1990). Responses of the lizard Lacerta vivipara to predator chemical cues: the effects of temperature. Animal Behaviour 40, 298-305.
- Whittier, J. (1994). Behavioural repertoire of Carlia rostralis (Scincidae) in the wet tropics of Queensland, Australia. In: Herpetology in Australia: a diverse discipline, 305-310. Lunney, D. & Ayers, D. (Eds). NSW, Australia: Royal Zoological Society, NSW.

- Whittier, J. & Martin, J. (1992). Aspects of social behaviour and dominance in male rainbow skinks, *Carlia rostralis. Australian Journal of Zoology* **40**, 73-79.
- Znari, M. & Benfaida, H. (2001). Socio-sexual behaviour and spacing organization of Agama impalearis. Revue d'Ecologie – La Terre et la Vie 56, 321-338.
- Zucker, N. (1994). Social influence on the use of a modifiable status signal. *Animal Behaviour* 48, 1317-1324.
- Zucker, N. & Murray, L. (1996). Determinants of dominance in the tree lizard Urosaurus ornatus - the relative importance of mass, previous experience and coloration. *Ethology* 102, 812-825.

Accepted: 27.1.03

.

2.