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agonistic behaviour in the velvet swimming crab, *Necora puber* (L.). Animal Behaviour 47:885–894.

STAMPS, J. A., AND V. V. KRISHNAN. 1994. Territory acquisition in lizards: I. First encounters. Animal Behaviour 47:1375–1385.

TORRICELLI, P., M. LUGLI, S. PARMIGIANI, G. GANDOLFI, AND D. MAINARDI. 1990. Intermale aggression in the fresh-water goby *Padogobius martensi* (Pisces, Gobiidae): territorial defence during and outside the breeding period. Pp. 69–87. *In* P. F. Brain, S. Parmigiani, R. J. Blanchard, and D. Mainardi (Eds.), Fear and Defence. Harwood Academic, New York, New York, U.S.A.

TRAJONO, E. 1991. The agonistic behaviour of *Pimelodella kronei*, a troglobitic catfish from southeastern Brazil (Siluriformes, Pimelodidae). Behavioural Processes 23:113–124.

TERRITORIAL BEHAVIOR IN THE AUSTRALIAN SCINCID LIZARD *CTENOTUS FALLENS*

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ABSTRACT: Intraspecific aggression has not been reported for any of the 80+ species of the Australian scincid genus *Ctenotus*. During spring 1994, we made numerous observations of intraspecific aggression among captive and wild individuals of *Ctenotus fallens*, a species endemic to coastal Western Australia. Observed behaviors included aggressive displaying and biting. We subsequently conducted a laboratory and field study of social behavior between August 1995 and March 1996. Additional evidence for intraspecific aggression was obtained from staged encounters between neonates in outdoor enclosures. Observed aggression suggests that individual residents do not tolerate an intruder within the same enclosure. Results of a nearest neighbor analysis of adult male spatial patterns in the field revealed that males were regularly spaced, which is consistent with home range defense. A similar analysis on adult females also suggested regular spacing, but this result was not statistically supported. Incidence of fresh bite scars on individuals in the field depends upon reproductive status: 50% of sexually mature males and 50% of sexually mature females exhibited fresh bite scars whereas only 14% of juvenile lizards had fresh bite scars. Also evidenced by bite scars is that individuals of *C. fallens*, irrespective of cohort or sex, appeared to target the tail region for biting during intraspecific aggressive interactions. Tail autotomy from social interactions has potentially serious consequences, particularly for many Australian temperate-zone skinks, because the tail is the major lipid storage organ in species such as *C. fallens* that lack abdominal fat bodies. We therefore hypothesize that *C. fallens* may exploit an opponent's tail as an "Achilles' heel" during aggressive interactions, confounding interpretation of tail break frequencies as being primarily due to predation attempts.

Key words: Behavior; Bite scar; *Ctenotus fallens*; Lizards; Sauria; Tail autotomy

NEARLY all lizard species display some form of intraspecific aggression ranging from specific site defense (e.g., basking sites or burrows) to home range defense (Stamps, 1977). While most iguanians exhibit home range defense (Carpenter, 1967; Carpenter and Ferguson, 1977; Stamps, 1977, 1983), this appears to be rare in other lizard families (Stamps, 1977, 1983). For example, among scincids, only two species, *Scincella lateralis* and *Egernia striolata*, have been reported to show home range defense (reviewed by Stamps, 1977). The apparent lack of home range defense among non-iguanians could be partly an artifact of "choice of study organism," as the vast majority of lizard behavioral studies have been conducted on iguanian species. Iguanians are relatively easy to study in the field owing to their diurnality, conspicuousness, and ease of manipulation in mark-recapture studies whereas many other taxa of lizards tend to be nocturnal or crepuscular, secretive, and

are thus relatively difficult to study. Consequently, little is known about the social behavior of most non-iguanian taxa.

The Australian scincid lizard genus *Ctenotus* contains at least 80 species, which are distributed all over the continent (Cogger, 1992). Ecological studies of various temperate-zone species of *Ctenotus* suggest that these lizards are diurnal, terrestrial, and insectivorous (Davidge, 1979; James, 1989; Murray, 1980; Pianka, 1986; Taylor, 1984). Little is known about social behavior of *Ctenotus* (Greer, 1989), as only a single behavioral study of one species, *Ctenotus robustus* (formerly *C. lesueuri*), has been conducted (Done and Heatwole, 1977; Saylor, 1973). Although the investigators specifically looked for intraspecific aggression in *C. robustus* during the laboratory study, they did not observe it (Done and Heatwole, 1977; Saylor, 1973). On the other hand, Done and Heatwole (1977) observed aggressive behavior in two species of *Sphenomorphus*, which may be a sister group to *Ctenotus* (Storr, 1964). The species of *Sphenomorphus* referenced herein have been more recently placed in the genus *Eulamprus* (Cogger, 1992).

On several occasions during 1994, we observed captive adult males of *Ctenotus fallens* engage in aggressive interactions when temporarily placed together. These behavioral interactions included head bobbing, back and neck arching, face-offs, tail biting, and tail amputation. Additional evidence for intraspecific aggression came from field observations. For instance, on 4 November, while checking pit traps, the senior author found a live adult female and a recently killed juvenile that had apparently died from an attack by the other lizard while in the same pit trap. The juvenile had what appeared to be fresh bite scars on its body. Moreover, many other freshly caught individuals throughout spring 1994 exhibited what appeared to be bite scars on the head, body, and tail regions.

Ctenotus fallens is distributed along coastal Western Australia between Perth and Shark Bay (Cogger, 1992; Ehmann, 1992; Storr et al., 1981). They reach max-imum snout–vent lengths (SVL) of 90–96 mm (Cogger, 1992; Jennings, unpublished data; Storr et al., 1981) and appear to be ecologically similar to other species of *Ctenotus* (Ehmann, 1992; Jennings, unpublished data; Murray, 1980). In this paper, we report intraspecific aggression in *Ctenotus* for the first time and describe territorial behavior in *C. fallens*.

MATERIALS AND METHODS
Study Site

We carried out this study in the Lesueur National Park, Western Australia (30° 08' S, 115° 14' E) between August 1995 and March 1996. The local climate is Mediterranean with cool wet winters and hot dry summers. The habitat generally consists of dense 0.5–1.5 m tall "heath" overlying marine or colluvial sand deposits and lateritic rises with little topographic relief overall. Dominant plants, by aspect, on the study plot consisted of proteaceous and myrtaceous species including *Calothamnus quadrifidus*, *C. sanguineus*, *Dryandra armata*, *Isopogon* spp., *Conospermum stoechadis*, *Hibbertia hypericoides*, *Xanthorrhoea drummondii*, and several shrubby species of *Melaleuca*.

Laboratory Studies of Spacing Behavior

To observe and characterize aggressive behaviors in *C. fallens*, we conducted 12 staged encounters between "resident" and "intruder" neonates (40–45 mm SVL; sexes unknown) in outdoor enclosures. Five 1 × 1 m outdoor enclosures containing a sand substrate were constructed. Neonates were used instead of adults because the adult individuals were involved in an ongoing field study and because previous observations suggested that they exhibit the same aggressive behaviors as the adults, a phenomenon observed in another Australian skink, *Sphenomorphus tympanum* (Saylor, 1973).

A single resident was placed in each outdoor pen for an acclimation period of two days. Following the acclimation period, we placed a single intruder into a pen and observed behavioral interactions for 1 min. Five residents and five intruders were used. We conducted trials during the

morning and late afternoon hours, which are the periods of maximum activity for *C. fallens* in this region (Jennings, unpublished data).

Field Studies of Spacing Behavior

Mark and recapture sampling.—Because *C. fallens* inhabits dense vegetation, it was not practical to capture individuals by hand or noose. Instead, all lizards were live-trapped using pit fall trap arrays. Each array consisted of a 6–7-m aluminum fly screen drift fence located between two 20-1 buckets, which were sunk completely into the ground. We situated 18 arrays 2–4 m apart so as to form an approximately linear transect. A second, similar transect was located parallel to and approximately 150 m from the other transect. Data were collected from both transects during 31 August–15 March 1996. All traps were checked for freshly captured lizards once a day nearly every day of the study. The following data were recorded from each lizard: sex, mass, SVL, tail length, and numbers of fresh bite scars on tail, body, and head regions. We defined fresh bite scars as any unhealed lesion of the scales that appeared to be caused from a mechanical force such as biting. All lizards were individually marked by toe-clipping prior to immediate release. We defined three reproductive classes: adult males, adult females, and juveniles. The adult males and females were defined as individuals that were sexually mature during the spring breeding season (i.e., >80 mm SVL). Although males and females of *C. fallens* become sexually mature in 1 yr, they do not breed until their second spring (Bamford, 1986; Jennings, unpublished data). This growth pattern has also been documented for several other temperate-zone species of *Ctenotus* (James, 1991; Taylor, 1984). Juveniles were defined as all individuals that were not in breeding condition (55–80 mm SVL).

Spatial analysis.—According to Stamps (1977), acceptable evidence of home range defense includes "small to moderate home range overlaps and active defense of the home range." In the past, most investigators have had to decide subjectively whether a species defends "much" or "a small portion" of the home range (Stamps, 1977). On the other hand, statistical methods for detecting regular spacing of animals represent alternative methods for inferring home range defense particularly when data for home range overlap are unavailable, as in the present study. Indeed, regular or overdispersed spacing in populations of plants and animals implies that the individuals are competing with one another for a limiting resource (Pielou, 1977). Thus, spacing patterns of adult male and female lizards were analyzed using the nearest neighbor measure for a single dimension (Clark and Evans, 1979), which is a variation of the methodology developed by Clark and Evans (1954). The nearest neighbor statistic, R, can range from 0 (perfect aggregation) to 2.1491 (hexagonal regular spacing). A value of 1.0 indicates a random dispersion pattern. Statistical significance of differences in R from 1.0 was tested using the z transformation. Significance was accepted if $P < 0.05$. Nearest neighbor analyses were performed on individuals that were recaptured at least once (i.e., 19 adult males and 12 adult females). Several individuals captured once were found with another lizard (usually a recaptured one) in the same bucket at the same time so their independent co-occurrence is questionable, particularly on behavioral grounds. Recaptured individuals on the other hand can provide an idea of how sedentary individuals are over the spring activity period. We plotted the time since first capture (days) versus the linear distance traveled (m) from the original capture location for 19 males (25 captures total) and 12 females (23 captures total) to see how sedentary adult males and females are over a single activity season. Because numbers of recaptures for each lizard ranged from 1–3, we used average location of each lizard as the unit of analysis from which to derive nearest neighbor distances.

Scarring frequency analysis.—We have directly observed a tendency of individuals of *C. fallens* to inflict, via biting, minor lesions upon the scales of other individuals during aggressive interactions. We con-

TABLE 1.—Summary of stereotyped lizard behaviors commonly observed in captive individuals of *C. fallens*. Descriptions of behaviors from Carpenter and Ferguson (1977).

Behavior	Description
Head bob	Relatively rapid up-and-down movement of the head or head and neck region only, with no action in the front legs.
Arch back	Raises the back *dorsally*, producing an arch effect, higher in the center along the longitudinal axis. Associated with aggression and performed by the aggressor.
Face-off	Two individuals laterally presenting to one another, usually at close range and facing in opposite directions.
Chase	One individual rapidly persuing another individual.
Submissive behavior	Actions and postures assumed by a subordinate individual, usually in response to a dominant individual. Freeze.
Leg bite	A bite directed at a leg, usually not held for long.
Tail bite	A bite directed at the tail, usually not held for long.
Fight	Vigorously encounter another individual involving some contact.

ducted an analysis of scarring frequency on freshly-caught individuals to answer two questions. (1) Do differences in scarring frequencies exist among age-sex classes? (2) Are scars evenly distributed along the head, body, and tail? The first question was addressed by testing whether scarring frequencies, measured as the proportion of individuals with at least one fresh bite scar, was independent of reproductive status (R × C Test of Independence). Statistical tests were performed with Statview II software (Abacus Concepts, 1992) with α = 0.05. We addressed the second question by examining scar frequencies on the tail, body, and head regions of all three reproductive classes separately and combined.

RESULTS

Laboratory Studies of Spacing Behavior

Aggressive behavior was observed in all 12 trials, and the most consistently observed behaviors are listed in Table 1. In every trial, the resident, upon seeing the intruder, immediately moved towards the intruder and displayed with head bobs and arching of its neck and back to within 10 cm of the intruder. In 75% of trials, the intruder froze upon seeing the resident's displays and was subsequently attacked and chased by the resident. In the remainder of trials, a face-off occurred whereby both lizards head bobbed and oriented themselves anti-parallel (Fig. 1A). These face-offs lasted 5–30 s before the resident initiated an attack causing a brief fight

(Fig. 1B). Residents won 92% of time, chasing intruders around the pen. Finally, winners bit the tail or head of losers during fights and/or chases 42% of the time.

Field Studies of Spacing Behavior

The nearest neighbor analysis revealed that the 19 adult males of *C. fallens* were uniformly distributed along the transect (R = 1.4, P < 0.032; Table 2). A similar analysis of the 12 adult females failed to detect a non-random spatial pattern (R = 1.3, P = 0.15; Table 2). The distances dispersed by lizards from their initial capture locations suggests that adult males and adult females show considerable site fidelity throughout the activity season (Fig. 2A and B). Adult males traveled an average linear distance of 15 m regardless of whether the time interval was seven or 89 days (Fig. 2A). Similarly, the average distance traveled by adult females was only 7 m irrespective of time elapsed (Fig. 2B).

Scarring Frequency in a Natural Population

Frequency of fresh scars varied with reproductive status (G = 8.69, df = 2, P = 0.019). Only three of 21 juveniles exhibited fresh bite scars while 10 of 20 adult females and 15 of 30 adult males exhibited fresh bite scars. Most fresh scars were on the tail region (62%), followed by the body (26%), and the head had the fewest bite scars with 12% (Table 3).

A

B

TABLE 2.—Nearest neighbor analysis of adult males and females of *C. fallens*. Asterisk indicates statistical significance at $P < 0.05$ and n.s. represents not statistically significant.

	Males	Females
Number (n)	19	12
Length of transect 1 (m)	179	179
Length of transect 2 (m)	180	180
Combined length of transects, L (m)	359	359
Density, $\rho = n/L$ (individuals/m)	0.0529	0.0334
Observed distance to nearest neighbor, r_A (m)	13.5	19.5
Expected distance to nearest neighbor, $1/2\rho = r_E$ (m)	9.45	14.97
Standard error, SE r_E (m)	2.17	4.32
Significance test $(r_A - r_E)/$SE r_E	1.85	1.05
Normal probability	0.032*	0.15 n.s.
Ratio of observed to expected distance, $r_A/r_E = R$	1.4	1.3

DISCUSSION

Results of the laboratory experiment demonstrated that neonates of *C. fallens* exhibit aggression towards neonate conspecifics. Although neonates were used in staged encounters, the same aggressive behaviors were observed between different males, sexes, and cohorts suggesting that intraspecific aggression is an important social behavior of *C. fallens*. In all 12 staged encounters, the resident charged towards the intruder soon after an intruder was placed into the enclosure. At this point in the experiment, two different behavioral sequences unfolded: (1) the intruder froze while the resident displayed with head bobs and neck and back arching approximately 10 cm from the intruder, which was invariably followed by the resident attacking the intruder causing a chase around the entire enclosure; and (2) both lizards oriented themselves in a face-off whereby both lizards head bobbed in anti-parallel positions (Fig. 1A) until the resident attacked, causing a brief fight (Fig. 1B). The winner bit the intruder's tail or head 42% of the time holding on for up to 30 s during the fight and chase. Interestingly, residents won 92% of the contests and chased intruders around the entire enclosure until the intruder was removed. Although some of our results were biased by experimental conditions (e.g., only intruders were handled immediately before trials), similar observations have been reported in other studies (Jaeger et al., 1982; Saylor, 1973; Vitt and Cooper, 1985).

As to the nature of observed aggressive interactions, the experiment suggests that residents did not tolerate the presence of another individual anywhere inside the same enclosure. This observation complements our other finding that adult males appear to be regularly spaced under natural situations, as suggested by nearest neighbor analysis ($R = 1.4$, $P = 0.032$). The nearest neighbor analysis for adult females also suggested that individuals were uniformly distributed, but this result was not statistically supported ($R = 1.3$, $P = 0.15$). Our sample size of 12 females may have been too small to detect a non-random spatial distribution. Although our R values seem to be close to random expectation, comparisons to other studies suggest that this may not be so. For example, Clark and Evans (1954) used the nearest neighbor technique to analyze the spatial distributions of oak and hickory trees in a Michigan woodland. They obtained a statistically significant R value of 1.14, which was consistent with their hypothesis of re-

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FIG. 1.—Drawings made from original videotape of two neonates of *C. fallens* engaged in an aggressive interaction. (A) Face-off between two lizards. Note orientation of each lizard's tail with respect to their opponent. (B) Fight following face-off. Note lizard in foreground biting the anterior end of opponent's tail. (Illustration by Vincent Tran.)
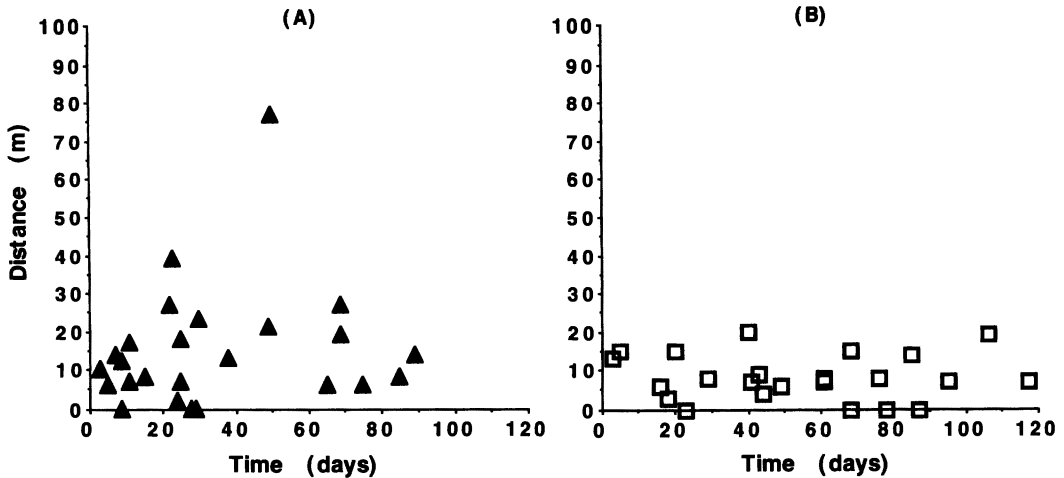
FIG. 2.—Scatterplots showing time elapsed (days) since time of first capture versus linear distances (m) traveled by *C. fallens* from initial capture locations: (A) 25 recapture records from 19 adult males (triangles), (B) 23 recapture records from 12 adult females (squares).

source competition among trees ($P <$ 0.00054; Clark and Evans, 1954). A second example comes from a spatial analysis of feeding sites for periodical cicadas by White et al. (1979). Feeding sites were found to be distributed more uniformly than random expectation ($R = 1.13$, $P < 0.01$ and $R = 1.12$, $P < 0.025$; White et al. 1979). Finally, Levings and Franks (1982) used the nearest neighbor analysis to evaluate the spatial distributions of 15 species of neotropical ground ants. All of their statistically significant tests ($n = 20$ tests) had R values between 1.1 and 1.6, but the majority of these values were near the lower end of this range (Levings and Franks, 1982). Why would significant R values tend to lie closer to random expectation rather than perfect hexagonal overdispersion? One explanation might be that perfect overdispersion, at least from a statistical point of view, may only apply to

certain sessile organisms (e.g., plants) whereas mobile organisms may, at best, be only imperfectly overdispersed. For example, territorial lizards probably spend much of their time patrolling the boundaries of their territories in order to detect and expel intruders. The presence of individuals at the edge of their territory would probably deflate R, especially for small sample sizes. We conclude, therefore, that our R value for adult males is a valid indicator of a uniform spatial distribution.

The bite scar frequency analysis of field-caught individuals provides additional evidence for intraspecific aggression. For instance, frequency of fresh bite scars on field-caught individuals varied with reproductive status, with both adult males and females exhibiting a three-fold higher incidence of fresh bite scars over juveniles. Interestingly, however, both adult males

TABLE 3.—Distribution of scars on tail, body, and head regions of a sample of *C. fallens* live-captured from the field.

Reproductive class	Body region			Number of individuals
	Tail	Body	Head	
Juveniles	13	5	0	21
Adult females	17	5	8	20
Adult males	34	17	4	30
Total	64	27	12	71

and females had the same frequency of fresh bite scars suggesting that both sexes engage in intraspecific aggression during the breeding season. The distribution of fresh bite scars on various body parts (Table 3) suggests that conspecific attacks are primarily directed at opponents' tails. Incidentally, we have previously observed an adult male break off the tail of another male in captivity. We discount the possibility that a significant proportion of these bite scars were the result of predation attempts on several grounds. First, these lesions are identical to those observed on captive individuals that were known to have been caused by intraspecific aggression. Secondly, mouth-shaped lesions on the anterior end of field-caught individuals' tails were observed several times. These lesions were caused by an animal with a 10–12-mm gape, which is the gape range of an adult *C. fallens*. Finally, on 25 November 1995, while searching for lizards on a 2-ha site that had burned a few hours earlier, we found an adult female of *C. pantherinus* (SVL = 89 mm) and an adult female of *C. fallens* (SVL = 96 mm) with its freshly amputated tail several centimeters away under a large rock near the middle of the burn zone. The amputated tail was not burned and could only have been bitten off by *C. pantherinus*. This observation coupled with our observations of captives suggest that individuals of *Ctenotus* can and do bite off conspecific and even congeneric tails during aggressive interactions. Finally, other studies have shown an association between bite scars and intraspecific aggression including such diverse organisms as skinks (Vitt and Cooper, 1985), the tuatara (Gillingham et al., 1995), and plethodontid salamanders (Jaeger, 1981; Staub, 1993).

Specificity in targeting certain body parts for attack by an individual has been documented in the plethodontid salamander *Plethodon cinereus* (Jaeger, 1981). In a classic study, Jaeger (1981) found that individuals of *P. cinereus* direct their biting at their opponent's snout in an attempt to "chemically blind" the opponent by damaging the nasolabial grooves. Why are conspecific attacks by *C. fallens* apparently directed at the tail? Studies of other Australian scincid lizards by Smyth (1974), Taylor (1984), and Wilson and Booth (1998) may provide the answer. Most scincids in the *Sphenomorphus* group (Greer, 1986) including *Hemiergis peronii* (Smyth, 1974), *Ctenotus taeniolatus* (Taylor, 1984), *Eulamprus quoyii* (Wilson and Booth, 1998), and *C. fallens* (Jennings, unpublished data) do not possess abdominal fat bodies. Moreover, the majority of the Australian species live in temperate regions (Cogger, 1992). Because the major fat reserves of at least *H. peronii*, *C. taeniolatus*, and *E. quoyii* are located in the tail and are drawn upon for overwintering and reproductive purposes (Smyth, 1974; Taylor, 1986; Wilson and Booth, 1998), the implications of tail autotomy caused by social interactions could be severe. Case in point, Smyth (1974) found that experimental removal of the tail of *H. peronii* caused a reduction in fecundity, with females producing up to 55% fewer eggs than normal. In another experimental study, Wilson and Booth (1998) determined that tailless females of *E. quoyii* experience a 75% reduction in clutch size. The tail could also be an important survival tool for individuals during droughts. Thus, tail autotomy, which probably arose as an adaptation to survive predation attempts, could be exploited as an "Achilles' heel" during aggressive social interactions. In this context, we have observed a tendency for individuals of *C. fallens* to appear "nervous" about having a conspecific in close proximity to its tail and will readily move its tail away from another individual. Moreover, during face-offs, each lizard invariably flares its tail away from its opponent (Fig. 1A). The possible widespread occurrence of such a "tail-attack strategy" during intra- and interspecific conflicts among lizards further highlights the questionable practice of equating natural tail loss frequency with predation intensity (Arnold, 1994).

Thus far, social behavior of Australian skinks has been mostly investigated through laboratory experiments (Done and Heatwole, 1977; Saylor, 1973; Torr and Shine, 1996; this study). Moreover, the results of these studies suggest that intraspe-

cific aggression is an important component of Australian scincid behavior. We have documented intraspecific aggression in the genus *Ctenotus* and have provided some indirect evidence that adult males of *C. fallens* defend home ranges. However, because cases of skinks defending home ranges are extremely rare (Stamps, 1977), additional studies should be carried out to determine more conclusively if *C. fallens* is truly territorial.

LITERATURE CITED

ABACUS CONCEPTS. 1992. Statview II. Abacus Concepts Inc., Berkeley, California, U.S.A.

ARNOLD, E. N. 1994. Caudal autotomy as a defense. Pp. 235–273. *In* C. Gans and R. B. Huey (Eds.), Biology of the Reptilia, Vol. 16: Ecology B. Branta Books, Ann Arbor, Michigan, U.S.A.

BAMFORD, M. J. 1986. The Dynamics of Small Vertebrates in Relation to Fire in Banksia Woodland near Perth, Western Australia. Ph.D. Thesis, Murdoch University, Western Australia, Australia.

CARPENTER, C. C. 1967. Aggression and social structure of iguanid lizards. Pp. 87–105. *In* W. W. Milstead (Ed.), Lizard Ecology. University of Missouri Press, Columbia, Missouri, U.S.A.

CARPENTER, C. C., AND G. W. FERGUSON. 1977. Stereotyped behavior in reptiles. Pp. 335–554. *In* C. Gans and D. W. Tinkle (Eds.), Biology of the Reptilia, Vol. 7. Academic Press, New York, New York, U.S.A.

CLARK, P. J., AND F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445–453.

———. 1979. Generalization of a nearest neighbor measure of dispersion for use in *K* dimensions. Ecology 60:316–317.

COGGER, H. G. 1992. Reptiles and Amphibians of Australia, 5th ed. Comstock Press, Ithaca, New York, U.S.A.

DAVIDGE, C. 1979. The Herpetofaunal Community of a Banksia Woodland near Perth, Western Australia. Ph.D. Thesis, Murdoch University, Western Australia, Australia.

DONE, B. S., AND H. HEATWOLE. 1977. Social behavior of some Australian skinks. Copeia 1977:419–430.

EHMANN, H. 1992. Encyclopedia of Australian Animals, Reptiles. Australian Museum, Sydney, Australia.

GILLINGHAM, J. C., C. CARMICHAEL, AND T. MILLER. 1995. Social behavior of the tuatara, *Sphenodon punctatus*. Herpetological Monographs 9:5–15.

GREER, A. E. 1986. On the absence of visceral fat bodies within a major lineage of scincid lizards. Journal of Herpetology 20:267–269.

———. 1989. The Biology and Evolution of Australian Lizards. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.

JAEGER, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. American Naturalist 117:962–974.

JAEGER, R. G., D. KALVARSKY, AND N. SHIMIZU. 1982. Territorial behaviour of the red-backed salamander: expulsion of intruders. Animal Behaviour 30:490–496.

JAMES, C. D. 1989. Comparative Ecology of Sympatric Scincid Lizards (*Ctenotus*) in Spinifex Grasslands of Central Australia. Ph.D. Thesis, University of Sydney, Sydney, Australia.

———. 1991. Growth rates and ages at maturity of sympatric scincid lizards (*Ctenotus*) in central Australia. Journal of Herpetology 25:284–295.

LEVINGS, S. C., AND N. FRANKS. 1982. Patterns of nest dispersion in a tropical ground ant community. Ecology 63:338–344.

MURRAY, P. J. 1980. The Small Vertebrate Community at Badgingarra, Western Australia. B.S. Honours Thesis, Murdoch University, Western Australia, Australia.

PIANKA, E. R. 1986. Ecology and Natural History of Desert Lizards. Princeton University Press, Princeton, New Jersey, U.S.A.

PIELOU, E. C. 1977. Mathematical Ecology. John Wiley and Sons, New York, New York, U.S.A.

SAYLOR, B. J. 1973. Comparative Social Behaviour in some Skinks and the Role of Hormones in Aggression. M.S. Thesis, University of New England, New South Wales, Australia.

SMYTH, M. 1974. Changes in the fat stores of the skinks *Morethia boulengeri* and *Hemiergis peronii* (Lacertilia). Australian Journal of Zoology 22:135–145.

STAMPS, J. A. 1977. Social behavior and spacing patterns in lizards. Pp. 265–334. *In* C. Gans and D. W. Tinkle (Eds.), Biology of the Reptilia, Vol. 7. Academic Press, New York, New York, U.S.A.

———. 1983. Sexual selection, sexual dimorphism, and territoriality. Pp. 169–204. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge, Massachusetts, U.S.A.

STAUB, N. L. 1993. Intraspecific agonistic behavior of the salamander *Aneides flavipunctatus* (Amphibia: Plethodontidae) with comparisons to other plethodontid species. Herpetologica 49:271–282.

STORR, G. M. 1964. *Ctenotus*, a new generic name for a group of Australian skinks. Western Australian Naturalist 9:84–85.

STORR, G. M., L. A. SMITH, AND R. E. JOHNSTONE. 1981. Lizards of Western Australia I. Skinks. West-

ern Australian Museum, Perth, Western Australia, Australia.

TAYLOR, J. A. 1984. Ecology of the Lizard, *Ctenotus taeniolatus*: Interaction of Life History, Energy Storage and Tail Autotomy. Ph.D. Thesis, University of New England, New South Wales, Australia.

———. 1986. Seasonal energy storage in the Australian lizard, *Ctenotus taeniolatus*. Copeia 1986:445–453.

TORR, G. A., AND R. SHINE. 1996. Patterns of dominance in the small scincid lizard *Lampropholis guichenoti*. Journal of Herpetology 30:230–237.

VITT, L. J., AND W. E. COOPER. 1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. Canadian Journal of Zoology 63:995–1002.

WHITE, J., M. LLOYD, AND J. ZAR. 1979. Faulty eclosion in crowded suburban periodical cicadas: populations out of control. Ecology 60:305–315.

WILSON, R. S., AND D. T. BOOTH. 1998. Effect of tail loss on reproductive output and its ecological significance in the skink *Eulamprus quoyii*. Journal of Herpetology 32:128–131.

LINGUALLY MEDIATED DISCRIMINATIONS AMONG PREY CHEMICALS AND CONTROL STIMULI IN CORDYLIFORM LIZARDS: PRESENCE IN A GERRHOSAURID AND ABSENCE IN TWO CORDYLIDS

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ABSTRACT: Insectivorous lizards that actively search for food, but not those that hunt by ambush, locate and identify prey chemicals by tongue-flicking, which gathers chemical samples for sensory analysis. However, only a tiny fraction of lizard species has been studied. One assumption of the comparative studies is that presence or absence of prey chemical discrimination is stable within most families because extensive data show that foraging mode is stable in most families. I present new experimental evidence on the relationship in cordyliform lizards, the families Cordylidae and Gerrhosauridae. The only previous data for the ambushing cordylids revealed no evidence of prey chemical discrimination in tests of *Cordylus cordylus* requiring lizards to tongue-flick cotton swabs held by an experimenter. In additional tests on *C. cordylus*, we presented chemical stimuli on ceramic tiles placed on the cage floors and observed responses through one-way glass. We conducted both swab tests and tile tests on the cordylid *Platysaurus pungweensis*. Neither cordylid species exhibited any sign of prey chemical discrimination, showing that experimenter's presence does not explain the absence of discrimination in the swab tests and extending the absence of prey chemical discrimination to another cordylid genus. Swab tests showed strong prey chemical discrimination in the actively foraging gerrhosaurid *Gerrhosaurus validus*, which tongue-flicked and bit swabs at higher rates in response to prey chemicals than to control stimuli. These findings are consistent with those for *G. nigrolineatus* and with the minimal foraging data available for Gerrhosauridae. All available data on cordyliform lizards support the relationship between foraging mode and chemosensory behavior and agree with the assumption of intrafamilial stability of prey chemical discrimination. Additional data needed on cordyliform foraging and prey chemical discrimination are noted.

Key words: Foraging behavior; Chemosensory behavior; Lacertilia; Cordyliformes; Cordylidae; Gerrhosauridae; *Cordylus cordylus*; *Platysaurus pungweensis*; *Gerrhosaurus validus*

MANY lizards can locate and identify prey using only chemical cues sampled by the tongue (Cooper, 1994a). Among carnivorous species, such lingually mediated prey chemical discrimination appears to be limited to active foragers, being absent in ambush (sit-and-wait) foragers (Cooper, 1994a,b). A tight evolutionary correlation strongly suggests that shifts in foraging mode induce changes in use of tongue-