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Original article

Interspecific aggression in flat lizards suggests poor species recognition

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Abstract.—Mistaken identity and competitive exclusion are two alternative hypotheses proposed to explain interspecific aggression between males. We examined agonistic behaviour in males of two lizard species: *Platysaurus minor* and *P. monotropis*. In each of nine outdoor field enclosures, we maintained a male and a female of both species (i.e., four total) and observed the dominance relationship between the males. Interspecific aggression was intense and *P. monotropis* was dominant in eight of nine enclosures. Furthermore, *P. minor* males received significantly more bite marks than *P. monotropis* males during the course of the experiment. To distinguish among the two hypotheses for interspecific aggression (mistaken identity and competitive exclusion), we presented *P. minor* males from sympatry and allopatry with model lizards of both taxa and measured aggressive responses. All trials with models were conducted in field enclosures where males were kept alone for the duration of the experiment. The model experiment revealed that compared to *P. minor* from sympatry, allopatric *P. minor* males were no less aggressive towards the heterospecific model than the conspecific model, a finding that supports the mistaken identity hypothesis. Finally, in the same experiment, we included a supernormal stimulus (pink *Platysaurus* model) to test if males were simply responding to a brightly coloured male lizard. Males showed some aggression towards the supernormal model, but significantly less than towards the two models (*P. minor* and *P. monotropis*) combined.

Key words.—*Platysaurus,* flat lizards, interspecific aggression, species recognition, mistaken identity, competitive exclusion.

Animal signals have a diversity of functions (reviewed in Dawkins and Krebs 1978; Ryan 1990; Maynard Smith & Harper 1995; Johnstone 1997) that include recognition of mates and rivals (Ryan & Rand 1993). Such signals are the product of natural selection acting on signal structure and receiver sensory systems (Johnstone 1997). In addition, how a signal is perceived by a receiver is strongly influenced by microhabitat and environmental conditions (Endler 1992, 1993), resulting in coevolution of signals, sensory systems, and microhabitat choice (Endler 1992). In the case of male rival recognition, agonistic responses are generally most intense among conspecifics (Cooper & Vitt 1987a; Hess & Losos 1991), but may be just as intense among heterospecifics (Oritz & Jenssen 1982).

Interspecific aggression has been explained as mistaken identity (i.e., misdirected intraspecific behaviour) resulting from a lack of discriminatory ability (Murray 1971; Kohda 1981; Nishikawa 1987), or as competitive exclusion by interference competition (Myrberg & Thresher 1974; Jenssen *et al*. 1984; Nishikawa 1987). Competitive exclusion may be regarded as an adaptive response to the presence of a competing species, while mistaken identity, if beneficial, would be exaptive (Gould & Vrba 1982; Nishikawa 1987). A possible consequence of interspecific aggression, depending on the dominance relationship, may be the exclusion of one of the two species from part of its habitat (Jaeger 1971; Reed 1982; Jenssen *et al*. 1984). For example, Jamaican *Anolis opalinus* are forced to perch much higher than preferable, when in the presence of a competitor (*A. l. lineatopus*) (Jenssen 1973).

To distinguish among the two alternative causes of interspecific territoriality, Hess & Losos (1991) measured aggressive behaviour of *A. cristatellus* towards *A. gundlachi* in an area of sympatry and allopatry. They argued that if interspecific territoriality towards a competing species is adaptive, aggression would be stronger in sympatry than in allopatry; in alloptary, there would be no opportunity for the origin of interspecific aggression. Conversely, if interspecific aggression were misdirected intraspecific behaviour, males from sympatry and allopatry would show the same level of aggression towards heterospecific males. A similar approach was used for salamanders and showed evidence of mistaken identity and competitive exclusion (Nishikawa 1985, 1987).

Interspecific aggression among males has previously been observed between the two cordylid lizards *Platysaurus minor* and *P. monotropis* (MJW *pers. obs.*). The aim of this study was to verify experimentally interspecific aggression and to elucidate any dominance relationship between *P. minor* and *P. monotropis*. Furthermore, an experiment using a conspecific and a heterospecific model was designed to address the cause of interspecific aggression (competitive exclusion *vs*. mistaken identity). Finally, a supernormal (pink) model was used to test if males were merely responding to brightly coloured male lizards with a *Platysaurus*-like morphology.

MATERIALS AND METHODS

*Study area.—*Lizards were collected from two study areas in the Northern Province of South Africa: (1) the foothills of the Blouberg Mountains (23°11'S, 28°50'E); and (2) Warmbad (24°15'S, 28°18'E). In the Blouberg Mountains, *P. minor* (‘*P. minor* (s)’ for sympatry hereafter) and *P. monotropis* are sympatric. They inhabit isolated rocky outcrops that were fragmented by Kalahari sands about 10 000 years ago (Broadley 1978). The outcrops range in size from < 30 m to > 500 m long and many of the outcrops are separated by < 50 m. In Warmbad, only *P. minor* (‘*P. minor* (a)’ for allopatry hereafter) is present, occurring on the rock faces of hills. The two study areas are separated by 200 km. A number of isolated *P. minor* populations occur between the two sites, but *P. monotropis* is only known from the foothills of the Blouberg Mountains (Branch 1998). Therefore, due to the very specialised habitat requirements of *Platysaurus*, it is reasonable to assume that *P. minor* (a) (i.e., from Warmbad) has not been in recent contact with *P. monotropis*.

Study animals.—Platysaurus minor and *P. monotropis* occur in a very restricted area in north-western South Africa (Branch 1998). *Platysaurus minor* males have a grey-black back, a blue or yellow-green throat, orange sides and a light-red tail while the females are grey-black with three pale dorsal stripes (Branch 1998; Broadley 1978). Male *P. monotropis* have a bright orange throat, a blue-green dorsum and an orange-red tail. Female *P. monotropis* differ from other *Platysaurus* females by having some orange on the labials, throat, and belly (*pers. obs*). Males of the two species therefore differ considerably in colour, while females are similar dorsally.

Most of the discrete outcrops in sympatric areas were occupied by one of the two species, and dispersal between the outcrops may be very limited (Broadley 1978; Jacobsen 1994). However, both species have recently been found together on one outcrop (L. Verburgt, *pers. comm.*). Also, small outcrops containing *Platysaurus* were frequently separated by marginal distances (50 m in one case). Such populations may be very small (< 20 adults, *pers. obs.*) and it seems extremely unlikely that they had been isolated for thousands of years without immigration. Therefore, we expect that there is at least periodic dispersal between the outcrops and contact between the two taxa.

A total of 109 lizards were collected, of which 73 males were measured soon after capture. We measured snout-vent length (SVL) to the nearest mm with a ruler. Two head variables were measured to the nearest 0.01 mm with digital callipers: head length (HL), from the anterior tip of the tympanum to the tip of the snout, and head width (HW), the distance between the two widest points on the occiput. Body mass was measured to the nearest 0.1 g with an electronic balance. All lizards were returned to their site of capture upon completion of the study.

Field enclosures.—We maintained lizards in field enclosures at the Experimental Farm of the University of Pretoria. The field enclosures measured 1.8 x 1.8 x 0.8 m. The floor of each enclosure was rough concrete, while the walls consisted of Nutec® ceiling boards. Each enclosure contained two discrete refuges, 340 - 360 mm apart. Each refuge consisted of four concrete building blocks (390 x 190 x 140 mm) forming a crevice for shelter. All enclosures were of equal size and design. Lizards were fed a continuous supply of termites and provided with water *ad libitum*. All observations were conducted during the morning activity period, from behind blinds.

Experiment 1: mixed enclosures.—We investigated interspecific aggression and dominance between males in field enclosures containing one male and one female each of *P. minor* (s) and *P. monotropis* ('mixed enclosures'). Males were approximately size-matched. Females were included because we expected their presence to increase male territorial/aggressive behaviour. Five-min focal observations during peak activity (08:00 - 10:30) were recorded on a dictaphone. Each mixed enclosure was observed one to three times in a morning, depending upon weather conditions. At least one hour elapsed between successive observations on the same field enclosure, and the field enclosures were observed in a different order each day.

At the beginning of each 5-min observation period, we noted the position of each of the two males (on top of a refuge; looking out of a crevice; on the concrete floor). During focal sampling, we recorded which male initiated a contest and which male won (defined as the male which did not move away). We also recorded bite marks on all male lizards at the beginning and at the end of the experiment. We maintained nine mixed enclosures during November - December (i.e., during the breeding season) 1998 and conducted a total of 22 observation periods on each enclosure.

Experiment 2: lizard models.—We tested whether interspecific aggression was due to competitive exclusion or mistaken identity using lizard models presented to *P. minor* from sympatry and allopatry. Models were cast from dead lizards, creating exact replicas made from a silicon-plastic mix. They were painted by a professional artist to closely resemble living lizards. Three models were used: a *P. minor* male (SVL = 71, HL = 15.8, HW = 12.7 mm, mass = 6.7 g), a *P. monotropis* male (SVL = 71, HL = 16.7, HW = 13.3 mm, mass = 6.8 g), and a supernormal model (SVL = 71, HL = 16.2, HW = 13.69 mm, mass = 7.9 g) painted brown on the dorsum, and pink on the labials, sides, and venter. The purpose of the supernormal stimulus was to test if males respond to any brightly coloured *Platysaurus*. We chose pink because it does not occur in any *Platysaurus* taxon. The pink model was made from another *Platysaurus*, *P. orientalis*, in order not to match its shape with one of the two tested species. Models were presented to male *P. minor* (s) and *P. minor* (a) kept alone in field enclosures. Before tests began, we waited at least four days, thereby allowing the males to establish a territory. Each male was tested with all three models in a counterbalanced sequence (repeated measures design) with a minimum interval of 24 h between trials. Trials were conducted during December 1998 and January 1999.

All experiments with models were conducted using the same procedure. The model was placed on a building block between the two refuges such that it was level with and about 150 mm from each crevice. When placing the model into an enclosure, the resident disappeared into one of the crevices. Resident males were observed for 5-min, starting when the male re-emerged from his shelter (usually after 2 - 5 min). The sequence of aggressive behaviours (Table 1) was recorded on a dictaphone. The highest level of aggression shown by the tested male was used as the aggression index (AI) for this trial.

If the resident male did not emerge from his crevice after 10 min, the trial was terminated and the model removed. Such males were retested with the same model on another day and were only dropped from the study if they failed to emerge from their crevice for three consecutive trials. Ten male *P. minor* (a) and eight male *P. minor* (s) responded to all three models.

Data analysis.—Statistical analysis followed Conover (1980) and Zar (1996). Nonparametric analyses were performed where the assumptions of normality or homoscedacity were not met. We used the software package SYSTAT, and set a = 0.05; all tests were two-sided.

RESULTS

Body size.—Body measurements for all collected animals are reported in Table 2. Compared with *P. minor* (s), *P. monotropis* males were significantly larger in all body variables measured (Mann-Whitney test, SVL: $U = 269.5$, $P = 0.008$; HL: $U = 16$, $P < 0.001$; HW: $U = 32$, $P < 0.001$; mass: $U = 246$, $P = 0.003$). To further examine differences in proportions, we regressed the log (base 10) of HL and HW and the log of the cube root of mass on the log of SVL, for *P. monotropis* and *P. minor* (s) combined. The residuals were then compared between *P. monotropis* and *P. minor* (s). This procedure removes the effect of size (Vitt 1993). The difference of the residuals was highly significant for HL ($U = 13$, $P < 0.001$) and HW ($U = 45$, $P < 0.001$) but not significant for mass ($U = 332.5$, $P = 0.084$). The comparison of the measurements between *P. monotropis* and *P. minor* (s) shows that *P. monotropis is* not only about 3 % longer, but also is a bulkier lizard with a proportionally larger head. *Platysaurus minor* (s) males were significantly larger than *P. minor* (a) males in all four body variables measured (SVL, HL, HW, and mass, all $U < 4.2$, all $P < 0.001$).

Table 1. Types of aggressive behaviour used in the model experiment. The numbers are the scores given to each behaviour. For each trial, the highest score reached was used as its aggression index (AI).

1	Head bobbing: the head is rapidly moved up and down for ca. 0.5 s
2	Throat display: the lizard stands high on its forelegs, head held up, facing the model
3	Lateral display: the lizard stands sideways to the model
4	Ventral display: as for lateral display, but includes lifting the side facing the model such that the belly is exposed towards the model
5	Lateral approach: usually in the position of ventral display, the lizard rapidly approaches the model, running sideways like a crab, stopping only a few cm from the model
6	Back arch: as for ventral display, but showing the dorsum to the model
7	Tail trembling: the terminal half of the tail trembles rapidly
8	Bite
9	Tail trembling and bite shown simultaneously

Experiment 1: mixed enclosures.—Aggressive interactions between males occurred in all nine mixed enclosures and were generally of very short duration. The subordinate male almost always ran away immediately upon sighting the other male and chases were brief. Only five of 26 contests (19 %) lasted longer than 5 s, and only one physical fight with jaw locking and wrestling was observed. *Platysaurus monotropis* won more contests in eight field enclosures, *P. minor* in one ($\chi^2_8 = 5.44$, $P = 0.02$). In three field enclosures, the *P. minor* males were found dead, probably due to the stress inflicted by the *P. monotropis* male. These deaths occurred very early during the experiment and were not anticipated. Subsequently, in one field enclosure (data not included in the analysis) the males were separated when the *P. minor* male first appeared stressed. In the six enclosures without deaths, the dominant male won 89 - 100 % of the contests (Table 3). Fourteen contests resulted from chance encounters between the two males, i.e., a contest started immediately upon visual contact between the males and no clear initiator could be defined. The other 12 encounters were all initiated by the dominant male. The only dominant male which was never observed initiating a contest was *P. minor* from Field Enclosure 2 (Table 3), the only field enclosure where *P. minor* was dominant. The subordinate or dead males had significantly more additional bite marks at the end of the

Table 2. Body measurements (mm) of male *Platysaurus*. *Platysaurus minor* from sympatry (s) and allopatry (a) are shown separately. Means ± SD and ranges (in parentheses) are given for snout-vent length (SVL), head length (HL), head width (HW) and mass (g).

	P. monotropis	*P. minor* (s)	*P. minor* (a)
N	29	31	13
SVL	72.21 ± 2.92 (66 - 77)	70.39 ± 2.04 (66 - 75)	66.31 ± 2.56 (62 - 70)
HL	16.88 ± 0.73 (15.36 - 18.27)	15.19 ± 0.39 (14.24 - 15.84)	14.61 ± 0.47 (13.87 - 15.47)
HW	13.68 ± 0.71 (12.40 - 15.11)	12.22 ± 0.45 (11.07 - 12.97)	11.55 ± 0.55 (10.81 - 12.45)
mass	7.54 ± 1.33 (4.7 - 9.5)	6.57 ± 0.91 (4.4 - 8.6)	5.18 ± 0.58 (4.3 - 6.0)

experiment than the winning males (Wilcoxon matched-pairs test, $T = 0$, $N = 9$, $P = 0.008$, Table 3). The SVL of the winners was not significantly different (Wilcoxon matched-pairs test, $T = 17.5$, $N = 9$, $P = 0.94$) from that of losers (Table 3). There was also no difference in mass ($T = 16$, $N = 9$, $P = 0.44$). However, winners had significantly longer ($T = 5$, $N = 9$, $P = 0.038$, Table 3), and a trend towards wider heads ($T = 7.5$, $N = 9$, $P = 0.076$).

The position of the males at the beginning of each focal observation was analysed for only the six field enclosures where the *P. minor* male survived. The winner sat exposed significantly more often than the loser (Wilcoxon matched-pairs test, $T = 1$, $N = 6$, $P = 0.046$, Table 3). In the only field enclosure where this was not the case, the difference between winner and loser was small (11 *vs*. 13), while in the other cases, the difference was always marked.

Experiment 2: lizard models.—There was no relationship between order of presentation of the models and level of aggression (Friedman's ANOVA with the factors 'first', 'second', and 'third presentation' for *P. minor* (s) and *P. minor* (a) combined (18 cases): $\chi^2 = 0.194$, $P = 0.91$). In fact, on average, the model presented last scored highest, the second model lowest. Therefore, lizards did not become habituated to the models.

Figure 1 shows the means of the aggression index (AI) for both populations of *P. minor* towards the three models. For each lizard, we divided its score towards the heterospecific model by the average score towards the conspecific model, for both populations separately, in order to remove possible population specific differences in baseline aggressiveness (Nishikawa 1987). We then compared the values for *P. minor* (a) and *P. minor* (s). *Platysaurus minor* from allopatry were no less aggressive towards the heterospecific *P. monotropis* model than the *P. minor* from sympatry (Mann-Whitney test, $U = 35$, $P = 0.65$).

Table 3. Male body measurements (mm) and results of male-male agonistic interactions in the mixed enclosures (groups of one male and one female of *P. minor* (s) and *P. monotropis*). In Field Enclosure 2, *P. minor* was the winner, in all others, *P. monotropis*. Statistical tests comparing winner *vs*. loser are given in the text. f.e. = field enclosure, SVL = snout-vent length, HL = head length, *P. mo* = *P. monotropis*, *P. mi* = *P. minor* (s).

f.e.	Body measures (mm) SVL / HL		Contest wins		Additional bite marks		Sitting exposed[1]	
	P. mo	*P. mi*	*P. mo*	*P. mi*	*P. mo*	*P. mi*	*P. mo*	*P. mi*
1	75 / 18.3	73 / 15.5	2	0	0	10	13	7
2	72 / 16.6	70 / 15.2	0	2	2	1	1	16
3	67 / 16.0	70 / 15.7	win	died	0	4	—	—
4	66 / 15.4	68 / 15.3	3	0	1	8	11	4
5	75 / 17.1	71 / 14.8	8	1	4	8	11	13
6	67 / 15.5	71 / 15.0	win	died	0	5	—	—
7	69 / 16.2	70 / 14.4	7	0	0	2	16	8
8	72 / 16.9	72 / 15.7	3	0	1	7	10	1
9	77 / 18.1	72 / 15.2	win	died	0	7	—	—

[1] From all the focal observations, number of times the male was seen sitting exposed at the beginning of the observations.

Aggression towards the supernormal model was on average lower, although the difference between the response towards the three different models was not significant (Friedman's ANOVA, *P. minor* (s):$\chi^2_7 = 0.25$, $P = 0.88$; *P. minor* (a): $\chi^2_9 = 1.25$, $P = 0.54$). We combined the AIs towards the conspecific and heterospecific model by taking their average and compared this measure with the supernormal model using a Wilcoxon matched-pairs test. For *P. minor* (s) and *P. minor* (a) combined, the AIs towards the supernormal model were significantly lower ($Z = -1.15$, $N = 18$, $P = 0.013$).

DISCUSSION

Our results confirm that male *P. monotropis* and *P. minor* are interspecifically aggressive. The mixed enclosures revealed that *P. monotropis* is the stronger lizard. *Platysaurus minor* died in three field enclosures, probably due to the presence of the *P. monotropis*. In the six field enclosures where *P. minor* survived, *P. monotropis* won more contests in five of them, *P. minor* in one. One male usually won all contests, except for one field enclosure where *P. monotropis* won eight and *P. minor* one contest (Field Enclosure 4 in Table 3). Dominant males (contest winners) spent more time in an exposed position, initiated more contests, and had less bite marks. This consistency shows that the variables 'winning/initiating contests', 'additional bite marks', and 'sitting exposed' are valid measures of dominance in this lizard species, at least under our experimental conditions.

A comparison of body size between the winner and the loser of each field enclosure suggested that SVL was not an important factor determining dominance. Head size was a better predictor of contest success, although our study did not specifically address the role of head size in determining dominance. Nevertheless, it is likely that larger heads offer an advantage during male-male contests (Cooper & Vitt 1987b), especially in *Platysaurus*, where escalated contests often include biting.

We found that *P. minor* (a) showed high levels of aggression towards a model of *P. monotropis*. This result suggests that the interspecific aggression performed by *P. minor* (s) is not a specific adaptation to the presence of *P. monotropis*. Rather, it seems that *P. minor* mistake *P. monotropis* for a competing conspecific male. Note that our findings do not say anything about potential benefits from interspecific aggression. By definition, if the trait is beneficial but has not specifically evolved for its present purpose it is called an exaptation (Gould & Vrba 1982). Therefore, if our conclusion of mistaken identity is true and the aggressive behaviour confers a benefit to *P. minor*, it would be called exaptive. On the other hand, the dominance of *P. monotropis* over *P. minor* observed in the enclosures may imply that being aggressive is not beneficial to *P. minor*, and that *P. minor* might eventually be displaced by the larger *P. monotropis*. However, field observations suggest possible microhabitat partitioning through subtle differences in rock type (PK, MJW *pers. obs.*), supporting the idea that each of the two species may be the better competitor in its own microhabitat. If so, coexistence may be stable, at least at present.

If, contrary to our conclusion, the aggression in sympatry has evolved as a response to the presence of the congeneric species, then interspe-

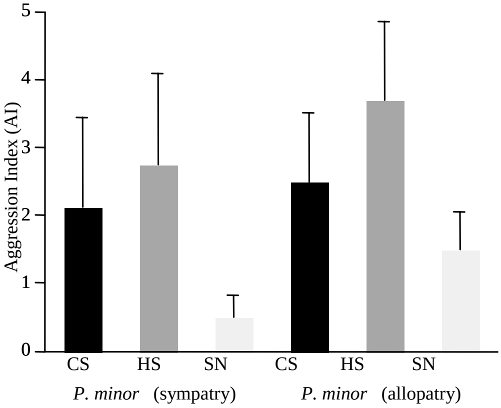

Figure 1. Mean (±SE) aggression index (AI) for *Platysaurus minor* (sympatric) and *P. minor* (allopatric) for the model experiment in which lizards were presented with a conspecific (CS), heterospecific (HS: *P. monotropis*) and supernormal (SN) model in a repeated measures design. $N_{\text{sympatry}} = 8$, $N_{\text{allopatry}} = 10$.

cific aggression found in the allopatric *P. minor* population needs explanation. Gene flow between the area of sympatry, where interspecific aggression might be selected for, and the area of allopatry (200 km distant), is likely to be nonexistent or extremely low due to the very specialised habitat requirements of *Platysaurus*. Also, the observed differences in the body variables between *P. minor* (s) and *P. minor* (a) is consistent with the assumption of low gene flow. In the study area in allopatry, no other *Platysaurus* were present. It is therefore impossible that *P. minor* (a) confused the *P. monotropis* model for a similar and competing species to which *P. minor* (a) could have adapted by evolving interspecific aggression. The observation that test lizards responded with reduced aggression towards the supernormal model shows that the males were not indiscriminant in their aggressive response towards any lizard-type stimulus that appeared in their territory. Such an indifference might be a consequence of the experimental situation (Hess & Losos 1991), but this was clearly not the case here. It must be stressed that we only investigated mistaken identity *vs.* competitive exclusion in *P. minor*, and not *P. monotropis*. Also, we were only able to work with one sympatric and one allopatric population. This fact has to be kept in mind when interpreting the data, although we see no obvious reasons to believe that the two populations were not representative. Finally, if competitive exclusion was operating, we would have expected aggression between heterospecific females and even between heterospecific males and females. No such aggression was ever observed.

Models are purely visual stimuli. Other cues are almost certainly involved in the process of species recognition. Behavioural patterns and chemicals are known to be important signals in certain lizard species (Echelle *et al.* 1971; Cooper & Vitt 1985; Cooper & Garstka 1987; Cooper and Greenberg 1992). Also, we do not know how exactly the lizards perceived the colours of our models. On the other hand, the use of models has the advantage of reducing the experimentally induced variance between trials (Macedonia & Stamps 1994). *Platysaurus monotropis* and *P. minor* are interspecifically aggressive even when they have the full range of signals available, as demonstrated in the mixed enclosures. The model experiments suggest that the lizards at least visually mistake one another.

This study was initiated on the finding that *P. monotropis* and *P. minor* are interspecifically aggressive. Our data support the mistaken identity hypothesis for male-male aggression and show that *P. monotropis* is dominant over *P. minor*. Although these results were obtained under semi-natural conditions, they may provide insight into historically natural processes. The two *Platysaurus* are not sister taxa (Jacobsen & Newbery 1989). It is therefore unlikely that the two species lack discriminatory ability due to a recent ancestral split. However, given that very few *Platysaurus* are sympatric, let alone syntopic (Broadley 1978), there may be an evolutionary lag resulting in taxa that respond to other *Platysaurus* species.

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LITERATURE CITED

Branch, W.R. 1998. Field Guide to the Snakes and Other Reptiles of Southern Africa, 3rd ed. Struik Publishers, Cape Town.

Broadley, D.G. 1978. A revision of the genus *Platysaurus* A. Smith (Sauria: Cordylidae). Occas. pap. Natl. Mus. Rhod. 4: 129-185.

Conover, W.J. 1980. Practical Nonparametric Statistics, 2nd ed. John Wiley & Sons, New York.

Cooper, W.E., Jr. & W.R. Garstka. 1987. Discrimination of male conspecific from male heterospecific odours by male scinicid lizards (*Eumeces laticeps*). J. Exp. Zool. 241: 253-256.

Cooper, W.E., Jr. & N. Greenberg. 1992. Reptilian coloration and behavior. Pp. 298-422. *In* C. Gans and D. Crews (Eds.), Biology of the Reptilia. Vol. 18. Brain, Hormones, and Behavior. University of Chicago, Chicago.

Cooper, W.E., Jr. & L.J. Vitt. 1985. Interspecific odour discrimination among syntopic congeners in scincid lizards (genus *Eumeces*). Behaviour 97: 1-9.

Cooper, W.E., Jr. & L.J. Vitt. 1987a. Intraspecific and interspecific aggression in lizards of the scincid genus *Eumeces*: chemical detection of conspecific sexual competitors. Herpetologica 43: 7-14.

Cooper, W.E., Jr. & L.J. Vitt. 1987b. Deferred agonistic behavior in a long-lived scincid lizard *Eumeces laticeps*. Oecologia 72: 321-326.

Dawkins R., & J.R. Krebs. 1978. Animal signals: information or manipulation? Pp. 282-309. *In* J.R. Krebs & N.B. Davies (Eds.), Behavioural Ecology: an Evolutionary Approach, 1st ed. Blackwell Scientific Publications, Oxford.

Endler, J.A. 1992. Signals, signal conditions, and the direction of evolution. Am. Nat. 139: S125-S153.

Endler, J.A. 1993. Some general comments on the evolution and design of animal communication systems. Phil. Trans. R. Soc. Lond. B 340: 215-225.

Echelle, A.A., A.F. Echelle & H.S. Fitch. 1971. A comparative analysis of aggressive display in nine species of Costa Rican *Anolis*. Herpetologica 27: 271-288.

Gould, S.J. & E.S. Vrba. 1982. Exaptation - a missing term in the science of form. Paleobiology 8: 4-15.

Hess, N.E. & J.B. Losos. 1991. Interspecific aggression between *Anolis cristatellus* and *A. gundlachi*: comparison of sympatric and allopatric populations. J. Herpetol. 25: 256-259.

Jacobsen, N.H.G. & R.E. Newbery. 1989. The genus *Platysaurus* A. Smith, 1844 in the Transvaal. J. Herpet. Ass. Afr. 36: 51-63.

Jacobsen, N.H.G. 1994. The *Platysaurus intermedius* complex (Sauria: Cordylidae) in the Transvaal, South Africa, with descriptions of three new taxa. South Afr. J. Zool. 29: 132-143.

Jaeger, R.G. 1971. Competitive exclusion as a factor influencing the distributions of two species of terrestrial salamanders. Ecology 52: 632-637.

Jenssen, T.A. 1973. Shift in the structural habitat of *Anolis opalinus* due to congeneric competition. Ecology 54: 863-869.

Jenssen, T.A., D.L. Marcellini, C.A. Pague, & T.A. Jenssen. 1984. Competitive interference between the Puerto Rican lizards *Anolis cooki* and *A. cristatellus*. Copeia 1984: 853-862.

Johnstone, R.A. 1997. The evolution of animal signals. Pp. 155-178. *In* J.R. Krebs & N.B. Davies (Eds.), Behavioural Ecology: an Evolutionary Approach, 4th edition. Blackwell Scientific Publications, Oxford.

Kohda, M. 1981. Interspecific territoriality and agonistic behavior of a temperate pomacentrid fish, *Eupomacentrus altus*. Z. Tierpsychol. 56: 205-216.

Macedonia, J.M. & J.A. Stamps. 1994. Species recognition in *Anolis grahami* (Sauria, Iguanidae): evidence from responses to video playbacks of conspecific and heterospecific displays. Ethology 98: 246-264.

Maynard Smith, J. & D.G. Harper. 1995. Animal signals: models and terminology. J. theor. Biol. 177: 305-311.

Murray, B.G. 1971. The ecological consequences of interspecific territorial behavior in birds. Ecology 52: 414-423.

Myrberg, A.A. & R.E. Thresher. 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fishes. Am. Zool. 14: 81-96.

Nishikawa, K.C. 1985. Competition and the evolution of aggressive behavior in two species of terrestrial salamanders. Evolution 39: 1282-1294.

Nishikawa, K.C. 1987. Interspecific aggressive behaviour in salamanders: species-specific interference or misidentification? Anim. Behav. 35: 263-270.

Ortiz, P.R., & T.A. Jenssen. Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. Z. Tierpsychol. 60: 227-238.

Reed, T.M. 1982. Interspecific territoriality in the Chaffinch and Great Tit on islands and the mainland of Scotland: playback and removal experiments. Anim. Behav. 30: 171-181.

Ryan, M.J. 1990. Sexual selection, sensory systems and sensory exploitation. Oxford Surv. Evol. Biol. 7: 157-195.

Ryan, M.J. & A.S. Rand. 1993. Species recognition and sexual selection as a unitary problem in animal communication. Evolution 47: 647-657.

Vitt, L.J. 1993. Ecology of isolated open-formation *Tropidurus* (Reptilia: Tropiduridae) in Amazonian lowland rain forest. Can. J. Zool. 71: 2370-2390.

Zar, J.H. 1996. Biostatistical Analysis, 3rd ed. Prentice Hall International, New Jersey.

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