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When to be neighbourly: differential agonistic responses in the lizard *Platysaurus broadleyi*

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Abstract Differential treatment of neighbours and strangers (the dear enemy phenomenon) can reduce the costly effects of territory defence. Individual recognition, and by extension the dear enemy phenomenon, was examined in the cordylid lizard *Platysaurus broadleyi.* I had no knowledge of familiarity between individuals and therefore classed intruders as neighbours or non-neighbours and tested for differences in agonistic response consistent with the dear enemy phenomenon. In the dear enemy phenomenon, levels of aggression are inversely related to degree of familiarity such that residents are more tolerant of immediate neighbours than distant territory holders. A manipulative field experiment in conjunction with field observations of known territory holders revealed that resident males allowed neighbours to approach more closely than non-neighbours before challenging them, residents were more aggressive towards non-neighbours than neighbours, contests between neighbours were significantly longer than between neighbours and non-neighbours and contests between residents and non-neighbours were likely to result in a win for the resident, while neighbours frequently drew contests. These results suggest a level of recognition consistent with the dear enemy phenomenon. I also manipulated front leg colour to test the hypothesis that it alone could serve as a cue for individual recognition. I found no support for this hypothesis and suggest that multiple cues operate in individual recognition.

Key words *Platysaurus broadleyi* · Territoriality · Dear enemy phenomenon · Rival recognition

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Introduction

Individual recognition both between and within sexes is a widespread phenomenon in many animals (Ydenberg et al. 1988; Temeles 1994), and may be mediated acoustically (Wunderle 1978; Myrberg and Riggio 1985; Randall 1994), chemically (Randall 1991) or visually (Fox and Baird 1992). The advantages and consequences are numerous, and include incest avoidance by kin recognition (Krebs and Davies 1993), spatial patterns that increase reproductive success (Randall 1989), pair bond maintenance (Wunderle 1978), mate recognition and differential treatment of familiar and unfamiliar potential mates (Cooper 1985); and reduced aggression towards familiar conspecifics (Fox and Baird 1992; Olsson 1994a; Temeles 1994).

In the context of male-male competition, recognition of rivals can reduce the costs of contests with predictable outcomes (Olsson 1994b). In territorial species, mutual respect of boundaries and reduced aggression may reduce the costs of territory maintenance (dear enemy phenomenon; Fisher 1954). Specifically, reduced aggression between neighbours may decrease the energetic costs of territory defence and the risk of injury from escalated contests (Ydenberg et al. 1988). Results from previous studies on lizards suggest that differential aggression towards familiar versus unfamiliar rivals constitutes individual recognition and provides evidence of the dear enemy phenomenon (Glinski and O'Neil Krekorian 1985; Qualls and Jaeger 1991; Fox and Baird 1992).

The Augrabies flat lizard, *Platysaurus broadleyi* [formerly *P. capensis*; Branch and Whiting (1997)] is a sexually dichromatic cordylid lizard restricted to rocky outcrops in the Gordonia-Kenhardt districts of Northern Cape Province, South Africa. Males are territorial and aggressively exclude intruding males from their territories by flashing a ventrally concealed status-signalling badge or by chasing them (unpublished data). Resident males defend portions of rock in full view of rivals and also patrol their territories. In high-density areas, territories are smaller and closer together. In such areas, territories are at a premium such that many males adopt a satellite ('floater') strategy (unpublished data). Because resident males return to the same territory every day and are readily visible, neighbours can be readily distinguished from non-neighbours. Encounters between non-neighbours are generally the result of a male travelling between his territory and a prey patch or sleeping crevice.

Preliminary field observations suggested that males are not equally agonistic towards other males. If males are familiar to one another, and dominance has been established, residents may avoid costly aggressive behaviour by reducing aggression towards neighbours. The 'war of attrition' (hereafter WOA) model (Ydenberg et al. 1988) has been invoked to explain this phenomenon. Under WOA, the degree of contest escalation depends on the familiarity of the contestants such that initial contests are the fiercest or longest. Ydenberg et al. (1988) suggest that the likelihood of a role mistake (one individual incorrectly assuming the winner or loser's role) is directly related to familiarity. Familiar individuals (e.g. neighbours) have had more contact in the past and are therefore less likely to make a role mistake than less familiar individuals (strangers/non-neighbours). Therefore, in the context of WOA, aggression and degree of familiarity are inversely related such that aggression is highest between complete strangers and lowest between neighbours. In *P. broadleyi* at Augrabies, it was not always clear if an intruder was a complete stranger to a resident. If males were completely unfamiliar with one another (true strangers), encounters should be very rare. Therefore, for the purpose of this paper, two types of intruder exist to a resident male: neighbours and non-neighbours. Although residents may have had prior contact with both classes of individual, they can reasonably be expected to be more familiar with neighbours. Under the WOA, residents should be less aggressive towards neighbours than non-neighbours.

Male *P. broadleyi* have forelegs that are polymorphic for colour. Legs may be yellow, orange, or a combination of the two, often with one colour dominating. Colours on other parts of the body are less variable, suggesting that one function of foreleg colour might be individual recognition. In the event that lizards are capable of individual recognition, they might use multiple cues that may or may not include foreleg colour, and altering foreleg colour may be insufficient to nullify the remaining cues.

I tested the hypothesis that male *P. broadleyi* are capable of individual recognition. Individual recognition among rival males is defined as a differential agonistic response based upon physical features, not upon behaviour. I also examined the extent to which rival recognition influences agonistic behaviour (dear enemy phenomenon), and then tested the hypothesis that foreleg colour alone may function in individual recognition.

Methods

Study area

Field work was conducted during August to early November 1995–1997, at Augrabies Falls National Park (hereafter Augrabies; 28°35′S, 20°20′E), Northern Cape Province, South Africa. The study area is xeric, but aridity is ameliorated by the Orange River. The banks of the river are rocky, and this is where *P. broadleyi* congregates in the presence of its primary prey, the black fly (*Simulium* spp.). More detailed descriptions of the study area are available in Whiting and Greeff (1997) and Branch and Whiting (1997).

Dear enemy phenomenon: experimentally induced encounters

Prior to experimental manipulation, males were observed in the field to establish if and where a male was resident, and to determine which individuals were immediate neighbours. Individuals were identified using features of body coloration or by painting a temporary white enamel number on the dorsum.

Experiments were conducted on individuals habituated to humans, allowing close approach. These individuals also responded to thrown food. I threw bread crumbs to decrease the distance between individuals and thereby initiate agonistic interactions between neighbours and intruders. Interactions between the resident and the intruder were orchestrated by attracting the intruder from about 5–50 m distant with the reward of food, thereby guiding the intruder towards the resident's territory by strategically throwing bread. During 10-min trials, I recorded (1) the distance to which a resident allowed an intruder to approach before challenging (cm), (2) the duration of the interaction (s), (3) the type of agonistic display (Table 1), (4) in the case of a chase, the distance of the chase (cm), and (5) whether an intruder was a neighbour or non-neighbour. Trials were conducted for 12 resident males. A matched-pairs design was used in which a specific condition was presented first in alternate trials. Interactions only between the focal animal and a single neighbour and non-neighbour were quantified. Wilcoxon signed-rank (matched-pairs) tests were used to assess significance of differences between neighbours and non-neighbours in approach distance, chase distance and duration of interactions. In four trials, the resident did not challenge his neighbour although the potential for interaction existed (they were visible to the resident and within 1 m). For three of these (resident-neighbour

Table 1 Scores for graded aggressive responses used during male contests. A ventral display occurred when a male elevated one side of his body to flash an abdominal status-signalling badge at a rival. A ventral display approach occurred if a male maintained the ventral display position while approaching an intruder. A chase sometimes occurred in conjunction with a ventral display. A back arch often preceded a fight and occurred when two males were in close proximity (<15 cm). It consisted of a challenger elevating one side of his body and thereby presenting its dorsum to a rival. A lunge occurred when a male appeared to bite a rival but kept his mouth close

Score	Behaviour
0	No response
1	Approach
2	Ventral display
3	Ventral display approach
4	Chase
5	Ventral display-chase (in either sequence)
6	Back arch
7	Lunge
8	Bite

context), the closest approach distance was recorded and used instead of the distance when aggression was initiated. In the fourth case, I failed to record approach distance. In cases where a resident did not chase a neighbour or intruder, but the potential existed, chase distance was scored as zero. Agonistic displays in *P. broadleyi* are graded, and were scored on a scale of 1–8 (Table 1). The possibility exists that a resident would base an agonistic response on the behaviour of an intruder rather than who he is (neighbour vs non-neighbour). To reduce this possibility, I scored only the initial response of a resident towards an intruder, thus reducing the time available for a resident to evaluate an intruder and the potential for an intruder's behaviour to influence the resident. Significance of differences in agonistic behaviour by residents to neighbours and non-neighbours was tested using a Wilcoxon test. Based on the prediction that residents would be more aggressive to non-neighbours than neighbours, tests evaluating graded aggressive responses were one-tailed. The significance of differences in contest outcome was evaluated using sign tests in which an outcome was scored as zero (draw) or +1 (win) for contests initiated by the resident (there were no defeats). The significance of differences in the mean number of contests drawn was also evaluated using sign tests.

Dear enemy phenomenon: natural encounters

Observations of known (marked) territorial males and their neighbours were made on an unmanipulated natural population. Territories were therefore mapped such that I could easily distinguish neighbours and non-neighbours. Data were obtained either from scan sampling or 15-min focal animal samples (Martin and Bateson 1993). The data collected were used to independently examine (1) the duration of contests, (2) graded aggressive responses and (3) outcome of naturally occurring contests. As in the field experiment, only the first reaction of the resident towards the intruder was used. From preliminary field observations, I hypothesised that there would be no difference in levels of aggression between the two data sets but that contest duration between neighbours would be longer than between non-neighbours for natural encounters. In the experiment in which encounters were induced by throwing bread crumbs, males were confronted with an abnormally high number of intruders attracted by food. This could reduce contest duration because the resident was constantly presented with different males to challenge. Therefore, I used only natural field observations of unmanipulated contests to examine the difference in contest duration between neighbours and non-neighbours. Although the presence of males other than the desired male could have a confounding effect, I saw no evidence that the presence of other males changed the resident's behaviour other than in contest duration. Also, all males experienced similar conditions.

Statistical analysis was as for the field experiment. A matched-pairs design was used in which a specific condition was presented first in alternate trials. Equal numbers of encounters between a resident and a single neighbour and a single non-neighbour were used.

Foreleg colour as a cue for individual recognition

To test whether foreleg colour alone is a cue for individual recognition by males, I painted their front legs to alter the dominant colour. For example, in males with orange-dominated forelegs, I used yellow, and vice versa. I caught known individuals and used tethering to present them to free-ranging males with neighbouring territories. The tethered individual was therefore familiar to the free-ranging male. Tethering consisted of tying a male around the waist and attaching him to a fishing rod by 1 m of dental floss. The tethered lizard was slowly lowered to the ground so as not to startle the resident, and manoeuvred to about 3 m from the resident. A matched-pairs design was used in which free-ranging males were presented a male with no alteration to foreleg colour (sham painted with water), and the same male with painted forelegs. Free-ranging and tethered males were used only once, and the order of presentation (painted versus control) was altered such that the painted individual was presented first for 7 of the 13 trials. Leg paint was easily removed by rubbing. The number and types (Table 1) of aggressive behaviours and their duration were recorded for 26 trials (two trials per free-ranging lizard). An interaction began when the free-ranging male performed one of the behaviours listed in Table 1, and was terminated if no behaviour occurred after a 5-s lapse. The significance of differences between treatments in the number of aggressive behaviours performed was assessed using a Wilcoxon signed-ranks (matched-pairs) test. A Wilcoxon test was also used to assess differences in graded aggressive responses (Table 1). I predicted that residents would be more aggressive and perform more aggressive behaviours towards painted ('unfamiliar') individuals; therefore, both tests were one-tailed. The significance of differences in contest duration among treatment groups was assessed using a Wilcoxon test (two-tailed).

Unless otherwise stated, I made no assumptions about contest outcome, therefore all tests were two-tailed. The normal approximation with continuity correction was applied for all Wilcoxon tests (Analytical Software 1996). Means ± 1 SE are reported. Significance levels were set at alpha = 0.05.

Results

Dear enemy phenomenon: experimentally induced encounters

Residents allowed neighbours to approach significantly closer ($Z = 2.61$, $n = 10$, $P = 0.009$) than non-neighbours before aggressively challenging them (Table 2). Residents chased non-neighbours significantly farther ($Z = 2.45$, $n = 10$, $P = 0.014$) than neighbours (Table 2). Contest duration between neighbours and non-neighbours was not significantly different ($Z = 0.09$, $n = 9$, $P = 0.93$; Table 2). Residents were

Table 2 Descriptive statistics (mean ± 1 SE, range in parentheses) of behavioural variables measured during encounters between neighbours and non-neighbours

	Neighbour/ non-neighbour	Approach distance (cm)	Chase distance (cm)	Contest duration (s)	Graded response
Staged encounters	Neighbour	23.0 ± 6.84 (10–80)	2.5 ± 1.31 (0–10)	5.33 ± 2.61 (0.5–19)	2.17 ± 0.49 (0–4)
	Non-neighbour	123.0 ± 19.09 (50–250)	150.83 ± 45.17 (0–400)	2.83 ± 0.47 (1–5.5)	3.92 ± 0.23 (3–5)
Natural encounters	Neighbour	–	–	23.4 ± 13.62 (1–141)	2.2 ± 0.13 (2–3)
	Non-neighbour	–	–	3.0 ± 0.63 (1–8)	3.1 ± 0.38 (2–5)
Individual recognition (foreleg colour)	Unpainted			36 ± 7.2 (0–92)	4.46 ± 0.62 (0–8)
	Painted			42.69 ± 6.5 (1–90)	5.35 ± 0.61 (2–8)

significantly more aggressive ($Z = 2.61$, $n = 12$, $P = 0.0045$; one-tailed) towards non-neighbours than neighbours (Table 2) and won significantly more contests (sign test, $n = 12$, $P = 0.004$) with non-neighbours (100% of encounters) than neighbours (25% of encounters). The likelihood of a contest ending in a draw between neighbours (25% of encounters) and between non-neighbours (zero draws) was not significantly different, but a significant relationship was likely precluded by small sample size. Residents ignored neighbours in four trials, but always challenged non-neighbours. Contests with no outcome (draws and ignored combined) occurred significantly more often (sign test, $P = 0.0078$) between neighbours (75% of encounters) than between non-neighbours (all trials had an outcome).

Dear enemy phenomenon: natural encounters

Resident males were engaged in contests significantly longer ($Z = 2.5$, $n = 10$, $P = 0.006$; one-tailed) with neighbours than non-neighbours (Table 2), were significantly more aggressive ($Z = 1.78$, $n = 10$, $P = 0.031$; one-tailed) towards non-neighbours than neighbours (Table 2) and won significantly more contests (sign test, $n = 10$, $P = 0.016$) with non-neighbours (80% of encounters) than neighbours (10% of encounters). Contests were also more likely (sign test, $n = 10$, $P = 0.031$) to result in a draw between neighbours (60% of encounters) than between non-neighbours (zero draws). Of ten trials, residents ignored non-neighbours in two and neighbours in three. Contests with no outcome (draws and ignored combined) occurred significantly more often (sign test, $n = 10$, $P = 0.016$) between neighbours (90% of encounters) than between a resident and a non-neighbour (20% of encounters).

Foreleg colour as a cue for individual recognition

The number of agonistic behaviours performed by free-ranging males towards painted (mean = 3.08 ± 0.59, range: 1–8) and unpainted (mean = 3.46 ± 0.61, range: 0–7) males was not significantly different ($Z = 0.58$, $n = 13$, $P = 0.28$). In addition, aggression by resident males towards painted and unpainted males was not significantly different ($Z = 1.56$, $n = 13$, $P = 0.06$; Table 2). Finally, the duration of agonistic encounters between free-ranging males and painted and unpainted males was not significantly different ($Z = 1.73$, $n = 11$, $P = 0.08$; Table 2).

Discussion

Several findings collectively suggest a level of individual recognition and familiarity among individuals. Compared to non-neighbours, residents allowed neighbours to approach more closely before challenging them, residents were less aggressive towards neighbours than non-neighbours, contests between neighbours were significantly longer than those between non-neighbours and contests between non-neighbours were more likely to result in a win for the resident (initiator), while neighbours frequently drew contests. The results also provide support for the dear enemy phenomenon (Fisher 1954), particularly because significant differences in graded aggressive responses (Fox and Baird 1992) between neighbour-neighbour and neighbour-non-neighbour contests existed during both staged and natural encounters.

It is probable that in many cases male *P. broadleyi* were to some degree familiar with intruders. The WOA model (Ydenberg et al. 1988; also see Temeles 1994) predicts that aggression and familiarity are inversely related, such that more distant territory holders are treated more aggressively by residents. I did not quantify the relationship between levels of aggression and territory distance, but at a categorical level (neighbours versus non-neighbours) the results of this study support the WOA model.

Mutual respect of territorial boundaries between neighbours should have energetic advantages. By reducing energetic expenditure during territorial defence with neighbours, more energy can be devoted to excluding non-familiar intruders (Krebs 1982; Temeles 1994) or feeding and courtship. Also, less aggressive interactions between neighbours reduce the risk of injury from fighting and may also reduce predation risk.

In contrast to the field experiment, unmanipulated individuals engaged in longer contests with neighbours than non-neighbours, and contests were also more likely to end in a draw. Longer interactions may function to reinforce territorial boundaries between neighbours, particularly since they generally ended in a draw. Although interactions between neighbours were longer, they were less aggressive and generally consisted of non-contact ventral displays. Compared to the experimental males, unmanipulated males rarely chased intruders, possibly contributing to contests of longer duration. In the experiment, the focal male was faced with several intruders, and this likely contributed to contests of shorter duration. Intruders were after food, whereas residents were defending a territory (non-resource based) and may have been more motivated than their opponent.

At Augrabies, lizards are locally dense. High-quality territories are at a premium and many males adopt a ‘sneaker’ strategy (unpublished data). (The highest-quality territories are near the river, where black flies are most abundant.) An immediate consequence of this high density is an increase in the number of agonistic interactions and territorial disputes. The frequency of agonistic encounters is further increased when males travel from communal sleeping crevices to territories or discrete food patches. Differential treatment of neighbours versus non-neighbours therefore provides an effective means of reducing the costly effects imposed by agonistic encounters.

It is possible that the observed behavioural differences were due to factors other than individual recognition. For example, size differences may have influenced the outcome of encounters. I assumed that any size biases should affect both groups (neighbours and non-neighbours) equally. I also did not detect any noticeable differences in size between the two groups, although lizards were not measured. Most importantly, *P. broadleyi* are equally aggressive on their own territories, regardless of an intruder's size (unpublished data).

In summary, *P. broadleyi* territorial behaviour best fits the dear enemy phenomenon in which aggression is tightly linked to degree of familiarity. Contests between non-neighbours were significantly more aggressive and more likely to escalate to combat. Although I could not positively identify complete strangers and had no information on previous contest experience between individuals, I could distinguish immediate neighbours from distant-territory holders. Within the dear enemy phenomenon, two functional hypotheses have been proposed: (1) discrimination allows contestants to minimise the energy they expend on aggressive acts and (2) discrimination may prevent injury from contests that escalate to fights (Ydenberg et al. 1988). The immediate advantage of the dear enemy phenomenon in *P. broadleyi* is a reduction in costly interactions (energy expenditure, injury) with a predictable outcome. Although the mechanisms of individual recognition in *P. broadleyi* remain elusive, it is likely that several traits collectively cue individual discrimination.

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