ANIMAL BEHAVIOUR, 2003, **65**, 391–396
doi:10.1006/anbe.2003.2058, available online at http://www.sciencedirect.com

Adult male collared lizards, *Crotaphytus collaris*, increase aggression towards displaced neighbours

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*(Received 7 January 2002; initial acceptance 15 March 2002;
final acceptance 24 May 2002; MS. number: A9239)*

Differential responses to neighbours and strangers (the dear enemy phenomenon) and individual recognition presumably evolve to reduce costs of territorial defence. Territorial residents have been found to demonstrate reduced aggression towards neighbours wherever they are encountered along that resident's territory boundary except for when the neighbour is displaced to the boundary opposite the shared boundary. In this new location, the displaced neighbour represents a greater threat to the resident's territory ownership, and should be treated as equally aggressive as a stranger. Finding increased aggression towards displaced neighbours has been interpreted as individual recognition, but these results do not provide sufficient evidence to rule out the possibility that the resident sees the neighbour out of its normal context as just another stranger. We tested the hypothesis that territorial collard lizards can individually recognize neighbours and will increase aggression towards them as the threat to territorial ownership increases. Resident males treated neighbours that had been moved to the opposite boundary as equally aggressive as strangers. However, residents responded more aggressively towards strangers than towards neighbours on natural territories (the dear enemy phenomenon) and also in neutral arena encounters. Our results suggest that resident male collared lizards are able to recognize individuals regardless of context and respond to them according to the threat that they pose.

The relative threat of usurping a territory posed by an intruder has been suggested to explain the differential response of territory owners to neighours and strangers, where neighbours are treated less aggressively than strangers (i.e. the dear enemy phenomenon, Fisher 1954). The relative threat hypothesis argues that once territorial boundaries are established, neighbours do not represent a sufficient threat to territory ownership to warrant expenditure of time and energy that could be used for other aspects of that individual's time budget (Temeles 1994). However, the role of such threat and its assessment by territory owners in the evolution of the dear enemy phenomenon remains controversial. Another set of hypotheses emphasizes the degree of familiarity that a territorial resident has with the intruder (Ydenberg et al. 1988), using an asymmetric war of attrition model (Parker & Rubenstein 1981). Familiarity probably plays a role in how residents respond to neighbours and strangers, but other factors such as the relative threat posed by the intruder contribute more to the differential responses observed (Temeles 1994).

Theory predicts, and experimental evidence has shown, that escalation will not occur during neighbour interactions as long as the neighbours do not cross established territory boundaries (Ydenberg et al. 1988), with the exception of when neighbours are encountered at the boundary opposite the shared boundary, in which case the displaced neighbour is treated as equally aggressive as a stranger (Trivers 1985; Bradbury & Vehrencamp 1998). One explanation for the observed increase in aggression towards the displaced neighbour is that the resident recognizes the individual as being displaced and assesses that neighbour as more of a threat to territorial ownership. In this case, a displaced neighbour represents at least the same threat as a stranger, and an escalated encounter is expected. Another possibility, neglected in the literature, is that the resident can no longer identify the individual out of its usual place and must reassess the individual as a presumed stranger before reacting. Appropriate methodology is critical to determine which explanation is appropriate for the system under investigation.

Differential response to neighbours and strangers in previous studies using neutral arena encounters with lizards (Glinski & Krekorian 1985; Olsson 1994; López & Martín 2001) suggest individual recognition, but say little

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0003–3472/02/$30.00/0

about the costs and benefits that must be assessed in naturally established territories. Realizing this, recent workers have addressed dear enemy questions with laboratory-defined territories (Qualls & Jaeger 1991) or naturally defined territories (Fox & Baird 1992; Whiting 1999). Previous studies displacing neighbours to the opposite boundary have claimed to provide evidence for individual recognition in many taxa (Falls & Brooks 1975; Wiley & Wiley 1977; Falls 1978; Myrberg & Riggio 1985; McGregor & Westby 1992), suggesting that residents can recognize a neighbour despite location, but these studies failed to consider the possibility that environmental context is necessary for recognition. The purpose of our investigation was to determine whether collared lizards, a territorial species whose behaviour has been well studied (Fitch 1956; Baird et al. 1996) and in which dear enemy recognition has been documented (Fox & Baird 1992), would increase aggression towards a displaced neighbour, and, if so, whether they can recognize the neighbour outside of its environmental context. We used field manipulations and neutral arena encounters to test the hypothesis that territorial residents can recognize a displaced neighbour and respond to the increased threat they pose to their territorial ownership.

METHODS

General Methods

The study site was located on Sooner Lake dam in north-central Oklahoma on a substrate consisting of concrete-covered rip-rap boulders. In May–June 1999 and 2000, we captured lizards and measured each lizard to the nearest 0.5 mm for snout–vent length. For visual identification at a distance, we marked each lizard with a unique pattern of coloured beads sewn through the base of the tail using a short length of monofilament fishing line (after Fisher & Muth 1989). The base of the tail was cooled with ice before surgery to reduce discomfort as much as possible. Since beads are not completely permanent, we also toe-clipped lizards according to guidelines jointly published by the three North American herpetological societies (*Guidelines for Use of Live Amphibians and Reptiles in Field Research*: Applied Ecology Research Group 1987). We observed no adverse effects of toe clipping on the survival or behaviour of lizards, in agreement with the majority of other studies that have addressed this issue (e.g. Dodd 1993; Paulissen & Meyer 2000).

We surveyed the study area and generated scale maps that we used to determine home ranges. The maps were scale representations of the study area with points on the maps designating numbered flags on the actual site. The flags were in close enough proximity so that several could be seen from any given location, and accurate locations could be determined for each lizard sighting by triangulation. We walked the site daily, observed lizards with binoculars, and mapped their locations so that territories could be defined by the minimum convex polygon procedure (Rose 1982), using at least 20 sightings per lizard. Data were collected for all sightings and intrusions (see below) when the substrate temperature was 30–40 °C, the optimal temperature range for collared lizards in central Oklahoma (Uzee 1990).

Field Experiments

Once territory boundaries were defined, we conducted the following trials with 22 resident subjects, each against: (1) a neighbour male at a familiar boundary (neighbour), (2) a neighbour male at an opposite, unfamiliar boundary (displaced neighbour) and (3) a stranger male at a familiar boundary (stranger). Thus, 66 trials were conducted. We conducted intrusions so that the order of type of intrusion (e.g. neighbour, displaced neighbour, or stranger) was random and no lizard was used in more than one trial on a given day. Intrusions were spaced as far apart temporally as possible to eliminate any effects of order on the response of the lizards. The mean number of days between successive intrusions for a given resident lizard was 7 days. We conducted all intrusions during June 1999 and 2000 after territories had been established and while aggression was at its peak in central Oklahoma (Fox & Baird 1992; Baird et al. 2001). We captured strangers from areas at least 2 km away from the study site to ensure that subject residents were not familiar with intruders. Neighbour or stranger adult males were introduced at the boundary of the territories of adult males by tethering them around the waist, with approximately 8 cm of monofilament fishing line, to the end of a 4.5-m pole and placing them at the desired location on a large rock draped with a neutral-coloured piece of carpet to avoid flight into otherwise accessible cracks and crevices. We conducted 10-min focal observations to quantify the behaviour of each target resident during the encounter. Agonistic behaviour was quantified by determining the frequency of aggressive and submissive displays during encounters and the latency to the first aggressive act. All trials were size-matched such that strangers matched, within 1 mm snout–vent length (SVL), the size of the neighbour that was normally encountered at that boundary. All intruders were returned to the exact location of capture with no subsequent effects on behaviour or survival (i.e. they were sited/recaptured at least 2 years following their participation in the present study, which is the typical life span for adult collard lizards).

Comparisons were made for the following measures of aggression as defined in Fox & Baird (1992) and Baird et al. (1997): (1) latency to first aggressive act, (2) maximum aggression (scaled responses: 5=fight then display; 4=display then fight; 3=display but not fight; 2=display then flee; 1=no response; 0=flee), (3) total aggressive acts and (4) graded agonism score (sum of frequencies of behaviour patterns weighted by level of escalation: following Fox & Baird 1992). During some of the intrusions (15 of 66) the level of aggression by the subject was so intense that the interaction was stopped before 10 min had elapsed to prevent serious injury to the intruder. The time at which each of these interactions was stopped was noted and total aggressive acts and graded agonism scores were adjusted to be comparable to the 10-min interactions.

Neutral Arena Trials

To determine whether these lizards were capable of individually recognizing neighbours when they were taken out of their normal environmental context, we conducted trials in a neutral arena with 13 adult males. We placed an adult resident male and its male neighbour, or a stranger size-matched to that neighbour (within 1 mm SVL), into an arena (2.5 × 1.25 × 0.75 m) at the study site with an opaque divider separating them. We allowed 5 min for the lizards to acclimate before removing the divider and allowing them to interact. We then conducted a 10-min focal observation on both lizards, with behaviour patterns recorded as discussed above. Arena interactions were conducted at the study site in areas not part of any of the lizards' territories, thus avoiding any potential bias due to familiarity with the environment. We conducted trials so that the order of the type of interaction was random and no lizard was used in more than one trial on a given day. The mean number of days between successive trials for a given resident lizard was 1.5 days.

Analysis

All tests were conducted using SYSTAT (SPSS 1998), and a sequential Bonferonni adjustment was used for four related tests (Rice 1989). Results from 1999 and 2000 were not significantly different (Kolmogorov–Smirnov two-sample tests: $P>0.25$ for all measures of aggression), so data were combined from both years for all analyses. To avoid potential problems of intercorrelation among our measures of aggression, we analysed the relationship between them using a correlation matrix, discarding redundant variables (those highly correlated to retained variables). Then, to determine whether there were significant differences between the resident's responses to neighbours and strangers, neighbours and displaced neighbours, and displaced neighbours and strangers, we conducted pairwise comparisons using Wilcoxon matched-pairs signed-ranks tests (Conover 1999). For neutral arena encounters, we analysed the relationship between the variables using a correlation matrix, and then used one-tailed Wilcoxon matched-pairs signed-ranks tests to compare the response of a lizard to a neighbour and a stranger for the retained measures of aggression as described above. One-tailed tests were used because we predicted a priori that focal lizards would respond more aggressively towards strangers than towards neighbours. We report actual P values for independent tests; all P values reported as significant individually retained significance when adjusted for Bonferroni probabilities.

RESULTS

Since the three types of intrusions for a given resident were conducted randomly and not varied systematically across the 22 residents, we tested for order effects with a Friedman's test for each measure of aggression, using order (i.e. first, second, or third) as the factor and the responses of residents as the dependent variable. We tested for pairwise order effects in the neutral arena trials with a Wilcoxon matched-pairs signed-ranks test for each measure of aggression in the same manner as for the field experiments. We detected no order effects on agonistic response for field experiments or neutral arena trials ($P>0.25$ for all measures of aggression). That is, for a given measure of aggression, there was no consistent difference in response among the first, second and third intrusions in the field trials, or between the first and second intrusions in the neutral arena trials.

For the field experiments, there was significant correlation between total aggressive acts and graded agonism score (pairwise $r>0.93$ for neighbours, displaced neighbours and strangers). We analysed the graded agonism score instead of the total aggressive acts because, as a weighted count of escalation, we felt it better summarized the agonistic behaviour of the lizards. Pairwise comparisons with Wilcoxon signed-ranks tests revealed significant differences between residents' responses towards neighbours and strangers, and neighbours and displaced neighbours, but not towards displaced neighbours and strangers (Fig. 1). Residents waited longer to respond to neighbours than strangers ($T=-3.07$, $N=22$, $P=0.002$) and displaced neighbours ($T=-2.81$, $N=22$, $P=0.005$), but there was no significant difference in latency to respond to displaced neighbours and strangers ($T=-0.21$, $N=22$, $P>0.50$). Residents had a lower maximum aggression score and had a lower graded agonism score towards neighbours than strangers (maximum aggression: $T=2.84$, $N=22$, $P=0.005$; graded agonism: $T=3.36$, $N=22$, $P=0.001$) and towards neighbours than displaced neighbours (maximum aggression: $T=3.24$, $N=22$, $P=0.001$; graded agonism: $T=3.77$, $N=22$, $P<0.001$), but there was no significant difference between displaced neighbours and strangers (maximum aggression: $T=-1.60$, $N=22$, $P=0.109$; graded agonism: $T=-1.61$, $N=22$, $P=0.108$). Displaced neighbours were treated slightly more aggressively than strangers (Fig. 1), but this difference was not significant.

For neutral arena interactions, there was significant correlation among maximum aggression, total aggressive acts and graded agonism (pairwise $r>0.64$ for responses towards both neighbours and strangers). We again chose to present the results for the graded agonism score instead of the other two for the reasons described above. Wilcoxon matched-pairs signed-ranks tests showed a significant difference between responses to neighbours and strangers in a neutral arena (Table 1). Individuals waited longer to respond to neighbours than strangers ($T=-2.62$, $N=13$, $P<0.01$) and had a higher graded agonism score towards strangers ($T=3.18$, $N=13$, $P<0.001$).

DISCUSSION

Our results confirm the dear enemy phenomenon in male collared lizards in the field and suggest that residents are able to individually recognize neighbours and their normal locations. Territorial individuals have mutually

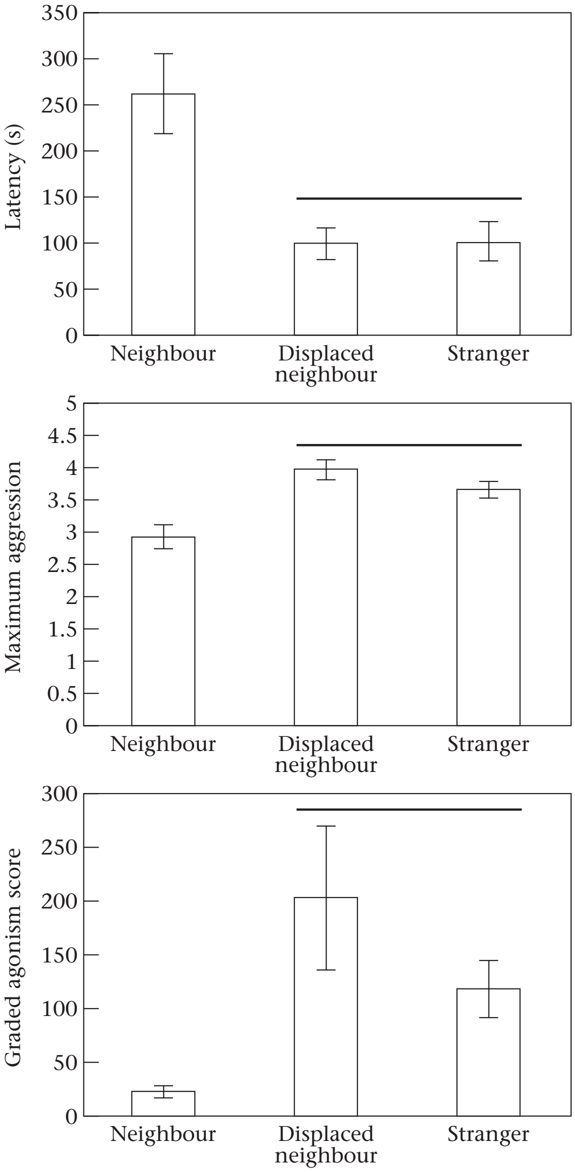

Figure 1. Mean responses (±SE) for three measures of aggression by resident adult male collared lizards (N=22) during staged encounters in the field between neighbours, displaced neighbours and strangers. Lines above bars indicate no significant difference in the residents' responses.

Table 1. Mean (±SE) aggressive responses by adult male collared lizards (N=13) towards neighbours and strangers in a neutral arena

	Neighbours	Strangers	P*
Latency (s)	42.9±8.1	24.8±1.9	<0.01
Graded agonism	10.8±0.9	30.7±3.7	<0.001

Latency: latency to first aggressive act; graded agonism: sum of frequencies of behaviour patterns weighted by the level of escalation (see text for details).
*Wilcoxon matched-pairs signed-ranks test.

respected boundaries to avoid potentially costly escalated encounters (Jaeger 1981), but they will increase aggression towards neighbours if there is a heightened threat of territory loss. Male collared lizards do not seem to misidentify neighbours when neighbours are displaced from their normal environmental context as shown by the observation that they recognized their neighbours in a neutral arena, away from their normal environmental context and free of other environmental cues. This study represents the first to integrate field manipulations with neutral arena encounters to test alternative hypotheses explaining increased aggression towards displaced neighbours, as well as the first study with a reptilian species to demonstrate increased aggression towards a neighbour placed at an unfamiliar (opposite) territory boundary.

Previous studies showing increased aggression towards neighbours on an opposite boundary have concluded that territorial residents are capable of individual recognition (e.g. Falls & Brooks 1975; Wiley & Wiley 1977; Falls 1978; Myrberg & Riggio 1985; McGregor & Westby 1992). We disagree. The above findings may suggest individual recognition, but the possibility of just the opposite conclusion, that they cannot recognize individuals, cannot be discarded. These previous studies did not provide sufficient evidence that residents were capable of individual recognition because residents were not allowed to interact with neighbours outside their normal environmental context when their presence did not pose an increased threat. If environmental context or location is required to recognize an individual, then a displaced neighbour may be viewed as a stranger and treated as such. In this case, one would also expect elevated aggression towards a displaced neighbour compared with a neighbour in his right place. Surprisingly, this alternative interpretation has received little attention in the literature. There must be corroborating evidence, ideally with the same individuals, showing that residents are capable of individual recognition without environmental cues to put the neighbour into context. Otherwise, conclusions about individual recognition become circular.

Theory predicts that contests should escalate when the payoff of winning is larger than the costs of losing, including costs of injury (Maynard Smith & Parker 1976). For a contest between neighbours, both of whom have a territory, the payoff of winning is small compared with the possible costs of losing a valuable territory. Costs are further augmented in those species where the contestants are capable of inflicting serious injuries to one another, such as in *C. collaris*, thus potentially reducing their future fitness (Jaeger 1981). When a resident encounters a displaced neighbour, the neighbour must be reassessed in terms of his relative threat to the territory holder. A displaced neighbour may have lost his territory, or may be trying to expand his current territory, and thus, his very presence at an unfamiliar location poses an increased threat to the resident (Ydenberg et al. 1988). There is presumably strong selective pressure for residents to increase aggression towards displaced neighbours because those that do not potentially lose fitness in terms of lost territory area and/or mates.

The results of this study stress the importance of the relative threat of an intruder in determining how territorial residents respond to that intruder, but this study also reveals the importance of familiarity as evidenced by the results of the neutral arena encounters. Neighbours have established sociospatial relationships over time and repeated exposure to each other. In a neutral arena, where there is no valuable resource, neither a neighbour nor a stranger represents much of a threat to the future fitness of a given resident, and there is no established sociospatial relationship. Territorial neighbours have, however, over the course of time, developed dyadic social relationships concerning both territory ownership and relative dominance based on previously assessed and recognized asymmetries in resource holding potential (e.g. Stamps & Krishnan 1994 and references therein). Strangers have no prior experience with each other, and no such relationships. Like other territorial social animals, collared lizards tend to work out dyadic dominance relationships when placed in a neutral arena (e.g. Fox & Rostker 1982; Baird et al. 1997); hence, the difference in residents' aggressive responses towards neighbours and strangers in a neutral arena suggests individual recognition.

The observation that residents increased aggression towards displaced neighbours suggests that, despite the familiarity of that neighbour, there is still an increased threat (i.e. the dear enemy phenomenon is context specific). Our results combining field manipulations and neutral arena encounters reject the hypothesis that resident male collared lizards are misidentifying displaced neighbours and suggest that they are capable of recognizing individuals regardless of environmental context and responding to them according to their threat.

Acknowledgments

We thank E. N. Ackland and D. Riedle for help in the field, OG&E Electric Services for access to the study site, T. A. Baird for valuable discussions about the study, D. Duvall, C. C. Peterson, J. A. Stamps and two anonymous referees for comments on the manuscript, and the Rob & Bessie Welder Wildlife Foundation for partially funding the research. This manuscript is Welder Contribution No. 575. This research was evaluated and approved by the Animal Behavior Society's Animal Care Committee on 30 June 2002.

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