

## The dear enemy phenomenon in the collared lizard, *Crotaphytus collaris*, with a cautionary note on experimental methodology

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Territoriality evolves when the benefits gained from exclusive access to limited resources exceed the costs of defence (Brown 1964). One mechanism by which individuals may minimize defence costs is to reduce aggression towards familiar occupants of neighbouring territories; the dear enemy phenomenon (Krebs 1982; Ydenberg et al. 1988). Early experimental field studies on birds clearly demonstrated differential responses by residents to the recorded songs of strangers and neighbours played back at the territorial borders of residents (Falls 1969). Subsequent field studies have implicated the importance of an intruder's location with respect to territory geometry. Usually, heightened responses to strangers are especially evident when intrusions are simulated at territory centres compared with boundaries (Falls & Brooks 1975; Giraldeau & Ydenberg 1987). In one case, however, resident responses were stronger towards strangers than towards neighbours at territory boundaries, but equal at territory centres (Wunderle 1978). Furthermore, acoustic stimuli of neighbours broadcast as opposite sides of residents' territories elicit aggression as strong as that towards sounds of strangers (Falls & Brooks 1975; Myrberg & Riggio 1985).

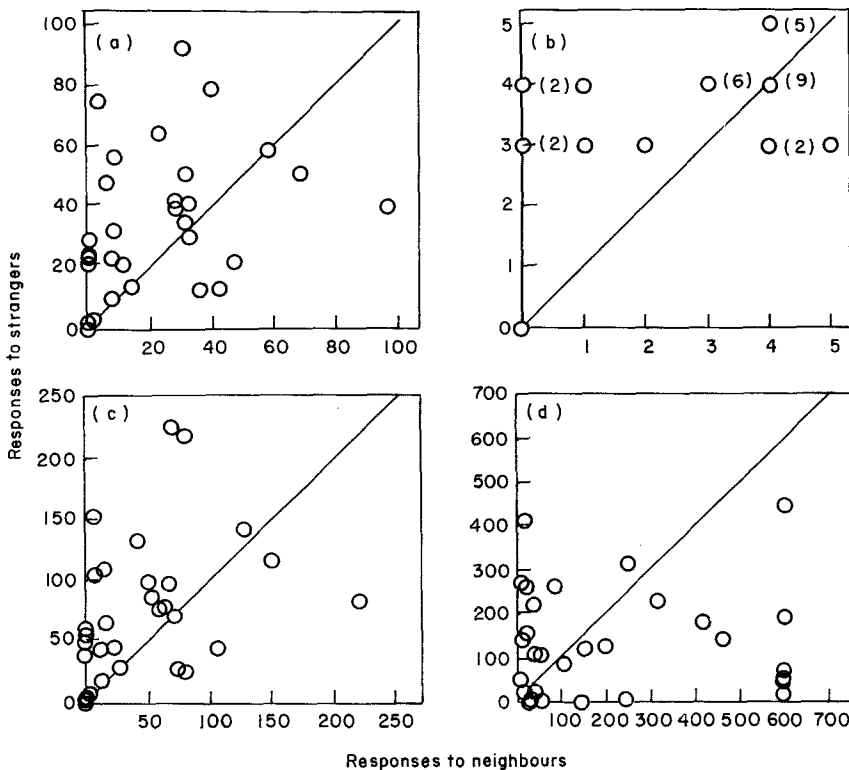
Although evidence of reduced aggression towards neighbours has been reported in a wide variety of species (Ydenberg et al. 1988), field studies conducted on naturally established territories are largely restricted to birds. No field studies on naturally established territories have been conducted in reptiles. We performed a field test of the dear enemy phenomenon in male collared lizards, *Crotaphytus collaris*.

We tethered size-matched neighbours and strangers (within 1 cm snout–vent length) at the natural territory borders of residents. Experiments were conducted during June–July 1984, 1985 and 1990 at the Wichita National Wildlife Refuge near

Cache, Oklahoma, and during June–July 1990 at Arcadia Lake near Edmond, Oklahoma. We captured 31 territorial adult males by noose and marked them by toe-clips and dorsal spots of acrylic paint. We defined territories using convex polygons encircling locations of resightings over 2–5 weeks (sightings per individual: 6–24,  $\bar{X}$  = 12.1). Strangers were captured at least 5 km distant and were unknown to the residents, while neighbours occupied adjacent territories.

On separate days and in randomly alternating order, we presented a stranger or neighbour at the edge of each resident male's territory. We positioned both intruders at the border shared between the resident and its test neighbour. There were no statistically detected differences in time of day or air temperatures for trials with neighbours and strangers (Wilcoxon matched-pairs signed-ranks test:  $Z = 0.26$  and  $Z = 0.45$ ,  $N = 31$  pairs,  $P > 0.50$ ). To stage intrusions, we placed a tripod near the resident, 2–4 m inside the territory. The intruder was tethered to the lower end of the centrepost of the tripod, with sufficient line to allow free movement beneath the tripod. Each 10-min encounter began as soon as we withdrew and the resident had a clear view of the intruder. We tallied the behaviour of the resident, noting the time at which behaviour directed towards the intruder first occurred.

Pairwise comparisons of resident responses to strangers and neighbours (one-tailed Wilcoxon matched-pairs signed-ranks test; Bonferroni adjustment for four related tests,  $P < 0.0125$ ) showed that responses to neighbours were significantly weaker than responses to strangers in three of four analyses (Fig. 1a–c). An unweighted count of approach, display, pushup, circle, bite, and gape behaviour (see Carpenter 1978 for descriptions) revealed that neighbours elicited fewer total aggressive acts ( $Z = 2.45$ ,  $N = 29$  untied pairs,  $P < 0.01$ ) than did



**Figure 1.** Response to strangers (ordinate) and to neighbours (abscissa) by 31 territorial residents. (a) Total aggressive acts/10 min trial; (b) maximum aggression; (c) graded aggression; (d) latency to first aggression (s). Diagonal lines represent the null hypothesis of equal responses to strangers and neighbours. Each data point represents a single individual's response to a stranger and a neighbour; in (b) parenthetical numbers to the right of data points indicate the number of superimposed values.

strangers (Fig. 1a). Neighbours also elicited less intense aggression. Maximum aggression (scaled trials: 5 = fight then display; 4 = display then fight; 3 = display but no fight; 2 = display then flee; 1 = no response; 0 = flee) was reduced towards neighbours (Fig. 1b:  $Z = 3.06$ ,  $N = 21$  untied pairs,  $P < 0.001$ ), as was graded aggression (weighted counts of aggressive acts: 3 = bite; 2 = display, pushup, circle, or gape; 1 = approach; 0 = no response; -1 = retreat or flee; Fig. 1c:  $Z = 2.64$ ,  $N = 31$ ,  $P < 0.01$ ). Residents also tended to wait longer before attacking neighbours (Fig. 1d:  $Z = 1.18$ ,  $N = 30$  untied pairs,  $P = 0.12$ ), but this difference was not statistically significant.

Ours are the first data from field experiments to document the dear enemy phenomenon in the defence of territories by reptiles. Adult male collared lizards defend territories with little spatial overlap, and intense aggressive interactions sometimes result in injury (unpublished observations).

Decreased aggression towards neighbours, therefore, may reduce the temporal and energetic costs of defence as well as the risk of injury. Qualls & Jaeger (1991) recently documented the dear enemy phenomenon in green anole males, *Anolis carolinensis*, that were allowed to establish territories in enclosures. To date, the only other investigation addressing the dear enemy phenomenon in reptiles was conducted on the desert iguana, *Dipsosaurus dorsalis*, in neutral arenas in which territories were not established (Gliński & Krekorian 1985).

From neutral arena studies, the dear enemy phenomenon has been generalized to include differential responses towards familiar versus unfamiliar conspecifics, divorced from territorial defence ('dear enemy recognition'). Staged interactions under these conditions have shown that non-neighbours elicit more intense aggression than do neighbours in some species (e.g. Barash 1974;

Glinski & Krekorian 1985; Randall 1989), but not in others where it was expected (Vestal & Hellack 1978). We urge caution in drawing conclusions from neutral arena studies. The dear enemy hypothesis is founded on the ratio of benefits to costs of territoriality. Benefits derive directly from resources (and familiarity with them) in the territory. Costs are time, energy and risk of injury associated with territorial defence. Costs to residents of challenges by strangers exceed those of routine encounters with territorial neighbours (Krebs 1982). Because neutral arenas do not replicate the cost-benefit relationship that favours territory defence, this design does not adequately test for the dear enemy phenomenon. In our view, future work should employ tests performed in the field or at least under conditions that closely reflect the field because these are the conditions under which territoriality is adaptive.

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