

NEIGHBOR ASSESSMENT AND THE DEAR ENEMY
PHENOMENON IN COLLARED LIZARDS,
CROTAPHYTUS COLLARIS

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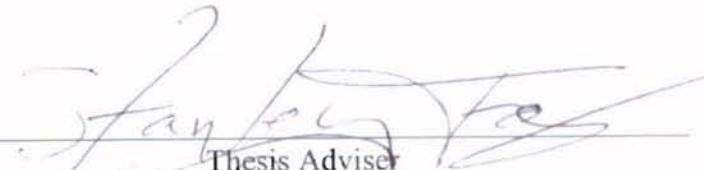
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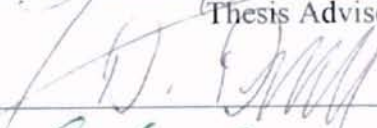
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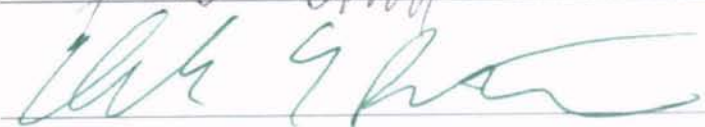
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INTRODUCTION

This project was designed to test several hypotheses concerning the dear enemy phenomenon, neighbor assessment, and individual recognition among territorial individuals of the lizard *Crotaphytus collaris*. Male and female collared lizards were used to test hypotheses regarding the role of threat and familiarity in the evolution of neighbor assessment. This research, with the exception of chapter 2, is presented as a series of papers in correct format for submission to an appropriate scientific journal. For stylistic completeness Chapter 2 is in correct format for *Herpetologica*. Chapter 3 is in correct format for submission to *Animal Behaviour* and chapter 4 for *Herpetologica*.

LITERATURE REVIEW

The eastern collared lizard (*Crotaphytus collaris*) is a large, diurnal lizard that has a broad distribution in the southwestern United States, ranging from western Arizona and eastern Utah, across Kansas to southern Missouri and northern Arkansas, then southwest into the Mexican states of eastern Durango, northern Zacatecas, and San Luis Potosí (McGuire, 1996). Collared lizards inhabit arid to semi-arid habitats, usually associated with rock outcroppings, ledges, or boulders (Conant and Collins, 1991; Smith, 1946). The species has also been successful at colonizing man-made habitat such as rip-rap boulder dams and quarries. The southeastern border of the species' distribution in the U.S. and Mexico abuts that of the much more geographically restricted congener, *C. reticulatus*. The western border abuts the distributions of *C. bicinctores* in the U.S. and *C. nebrius* in southern Arizona and northwestern Sonora, Mexico (McGuire, 1996).

The taxonomic status of the species has remained controversial (see McGuire, 1996 and references therein), but current taxonomic arrangements place *Crotaphytus collaris* as a species in a genus with eight others, including *C. antiquus*, *C. bicinctores*, *C. dickersonae*, *C. grismeri*, *C. insularis*, *C. nebrius*, *C. reticulatus*, and *C. vestigium*. There are five subspecies of *C. collaris* (*C. c. auriceps*, *C. c. baileyi*, *C. c. collaris*, *C. c. fuscus*, and *C. c. melanomaculatus*), but McGuire (1996) synonymized all of them as *C. collaris*, stating that there is insufficient evidence that the taxa represent independent lineages or that they are even useful as color pattern classes for identification. Frost and Etheridge (1989) placed *C. collaris*, its congeners, and the genus *Gambelia* in the monophyletic family Crotaphytidae, but there has been recent controversy over the taxonomic arrangement of this and other iguanian groups in relation to the Iguanidae (Macey et al., 1997; Pough et al., 2001; Schulte et al., 1998).

Throughout the range of the species, there is great variation in color pattern. Adults have been shown to be variably and significantly sexually dichromatic (McCoy et al., 1997), with males being more brightly colored. Both sexes have two characteristic collars posterior to the head and a pattern of white spots on the dorsum. Adult males range in dorsal coloration from green, turquoise, or olive to brown or grayish. Head coloration is typically on a continuum of yellow, ranging from “pale to fluorescent” (McGuire, 1996). The bright coloration of adult males has been suggested to serve in sex recognition (Greenberg, 1945), female choice, and as a signal of resource holding potential during male-male interactions (Baird et al., 1997). Females are more subdued in coloration and are typically brown to tan in coloration, although some populations maintain a green component (McGuire, 1996). When gravid, adult females display a series of bright orange to crimson spots or bars (Fitch, 1956) that cycle with reproductive condition (Ferguson, 1976) and the hormones associated with that cycle, particularly progesterone (Cooper and Ferguson, 1972, 1973). The function of female orange bars remains unclear (Cooper and Greenberg, 1992). Juveniles are not as sexually dimorphic in coloration. Both sexes resemble adult females in coloration, but juvenile males often display orange bars similar to that of gravid adult females (Fitch, 1956; Rand, 1983). The functional significance, if any, of the orange bars to the juvenile males is uncertain (Cooper and Greenberg, 1992). Sexual dimorphism in body dimensions is also exhibited, with significant variation existing among populations. Males are larger in head size, front and hind limb length, tail length, snout-vent length (SVL) and body mass (McCoy et al., 1994). Sexual size dimorphism is absent in juveniles (Husak, unpublished data) until the approximate size of sexual maturity (see below).

Reproduction has been studied extensively for the species and throughout its

geographical range. Within its distribution, *C. collaris* shows variation in its reproductive cycle, but it appears that generally two clutches are laid per season from May to mid-July, with the exception of a single clutch occurring in the northern edge of its range (Ballinger and Hipp, 1985; Fitch, 1956). Yearling females delay reproduction and lay only one clutch (Ballinger and Hipp, 1985; Fitch, 1956). There is no information to believe that there is significant geographic variation in average adult clutch size (7-8 eggs per clutch), but clutch size does vary with body size (Ballinger and Hipp, 1985). Male *C. collaris* typically mature in their first year of life at about 72-76 mm SVL (Baird and Timanus, 1998; Ballinger and Hipp, 1985; Trauth, 1979), and females in their first year at about 70-75 mm SVL (Baird et al., 1996; Ballinger and Hipp, 1985; Fitch, 1956; Trauth, 1978).

The general feeding ecology of this species has been thoroughly described, and dietary habits have been studied throughout its range, including Utah (Knowlton, 1938), Oklahoma (Blair and Blair, 1941), Kansas (Fitch, 1956), Colorado (Johnson, 1966), Arkansas and Missouri (McAllister, 1985), New Mexico (Best and Pfaffenberger, 1987), and Texas (Husak and McCoy, 2000). It is considered a “sit-and-wait” forager (McAllister, 1985; Pianka, 1966), remaining relatively motionless until a prey item comes close enough to run at and catch. It is an opportunistic predator, consuming mainly arthropods but also such things as birds (Best and Pfaffenberger, 1987), mammals (McAllister and Trauth., 1982), other lizards (Best and Pfaffenberger, 1987; Fitch, 1956; McAllister, 1985; McGuire, 1996), snakes (Baird, 2000; Best and Pfaffenberger, 1987; Husak and Ackland, 2000), and plant tissue (Best and Pfaffenberger, 1987; Husak and McCoy, 2000; McAllister, 1985). Selection of prey is in most cases due to availability (Best and Pfaffenberger, 1987; McAllister, 1985) and/or conspicuousness (Gluesing,

1983). There seems to be little ontogenetic shift in diet. Juveniles tend to have a less variable diet and eat smaller prey items than adults, but the types of prey consumed among age classes is similar (Best and Pfaffenberger, 1987; McAllister, 1985). Sexual differences in diet seem to have played little to no role in the evolution of sexual dimorphism for this species (Best and Pfaffenberger, 1987; Husak and McCoy, 2000 ; McAllister, 1985).

The thermal ecology of *C. collaris* is well documented, but primarily from laboratory investigations. Dawson and Templeton (1963) examined the effects of temperature on oxygen consumption, heart rate, breathing rate, and evaporative water loss. Thermoregulatory behavior, and how it is affected by environmental parameters, has also been examined in the laboratory (Sievert, 1989; Sievert and Hutchison, 1989, 1991). Adults and juveniles seem to prefer a temperature range between 30-40° C (Uzee, 1990), and maintain an internal body temperature of approximately 38° C by thermoregulating with behavior patterns such as basking, stretching and compressing the body, and panting (Fitch, 1956; Sievert and Hutchison, 1991).

A great deal of work has been done concerning the behavior of this species (e.g., Baird and Timanus, 1998; Baird et al., 1996, 1997; Bontrager, 1980; Cooper et al., 1996; Fitch, 1956; Fox and Baird, 1992; Greenberg, 1945; Mosley, 1963; Rostker, 1983; Sloan and Baird, 1999 Sugerman and Hacker, 1980; Yedlin and Ferguson, 1973). Collared lizards are a typical polygynous, territorial, iguanian species, and many of the details of their social organization are well known. Typically, adult males (2+ yrs) acquire and defend an all-purpose territory against other adult males with displays or occasional fighting (Baird et al., 1996; Fitch, 1956; Yedlin and Ferguson, 1973). They also exhibit the dear enemy phenomenon, presumably to reduce costs of territoriality (Fox and Baird,

1992). Females have smaller home ranges that overlap male territories and the home ranges of other females (Baird et al., 1996). Female social behavior is less clear than that of males. Females have been reported as “territorial” (Rostker, 1983), nest site defenders (Yedlin and Ferguson, 1973), mildly aggressive (Baird et al., 1996), and aggressive after oviposition (Sloan and Baird, 1999). Juvenile males adopt subordinate tactics, such as having low rates of display and movement, so that they are less conspicuous to adult males until they get an opportunity to acquire their own territory during the subsequent year (Baird and Timanus, 1998).

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RESPONSE OF ADULT MALE COLLARED LIZARDS, *CROTAPHYTUS COLLARIS*,
TO INCREASED THREAT BY A NEIGHBOUR

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Abstract. In many taxa, territory residents respond less aggressively to neighbours than they do toward strangers (the dear enemy phenomenon), presumably because the neighbour represents less of a threat than a stranger. It has been hypothesized and shown empirically that residents will demonstrate reduced aggression towards neighbours wherever they are encountered along that resident's territorial boundary except for when they are on the boundary opposite the shared boundary, where they represent a greater threat. Finding increased aggression toward displaced neighbours has been interpreted as individual recognition, but it does not provide sufficient evidence to rule out the possibility that the resident sees the neighbour out of normal context as literally just another stranger. My objective was to test the hypothesis that a territorial lizard species (*Crotaphytus collaris*) can individually recognize neighbours and increase aggression toward them as threat increases. Resident males responded more aggressively to strangers than neighbours in neutral arena encounters and exhibited the dear enemy phenomenon in field experiments. Additionally, residents treated neighbours on the opposite boundary equally aggressively as strangers and although not significant, tended to respond even more aggressively to displaced neighbours than to strangers. My 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.

Research examining how threat determines the behaviour of interacting individuals has focused primarily on encounters between territorial neighbours where neighbours are treated less aggressively than strangers, presumably because the neighbour represents less of a threat than a stranger (i.e., the dear enemy phenomenon, Fisher 1954), but knowledge concerning how threat influences assessment and subsequent behaviour is restricted to very few experimental tests (Jaeger 1981; Ydenberg et al. 1988; Temeles 1994). Changing the threat imposed by a neighbour should greatly influence the way an individual interacts with that neighbour (Getty 1987; Ydenberg et al. 1988).

The relative threat posed by an intruder has been suggested to explain the dear enemy phenomenon (Jaeger 1981; Getty 1987; Temeles 1994), and the relative threat hypothesis argues that once territorial boundaries are established, neighbours do not represent a sufficient threat to warrant expenditure of time and energy that could be used for other aspects of that individual's time budget. However, the role of threat and its assessment in the evolution of the dear enemy phenomenon remains controversial. Another set of hypotheses emphasizes the degree of familiarity a territory resident has with the intruder (Ydenberg et al. 1988), using an asymmetric war of attrition model (Parker & Rubenstein 1981). Getty (1989) proposed another hypothesis based on familiarity, stating that individuals fight to learn about one another. Temeles (1994) suggested that familiarity 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.

Theory predicts, and experimental evidence has shown, that escalation will not occur during contests between neighbours as long as the neighbours do not cross established territory boundaries (Ydenberg et al. 1988), with the exception of when

neighbours are positioned at the boundary opposite the shared boundary (Figure 1) where the displaced neighbour is treated equally aggressively as a stranger (Trivers 1985; Bradbury & Vehrencamp 1998). One possible explanation for the observed increase in aggression toward the displaced neighbour is that the resident recognizes the individual as being displaced and assesses that neighbour as more of a threat because the potential losses are now greater. 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 place and must reassess the individual as a true stranger before reacting. Appropriate methodology is critical to determine which explanation is appropriate for the system under investigation (Molles & Vehrencamp 2001).

Lizards are ideal organisms to study neighbour relationships. Previous neutral arena encounters with lizards (Glinski & Krekorian 1985) suggest individual recognition, but say little about the costs imposed by an intruder that they must assess in their naturally established territories (Fox & Baird 1992). 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 side of a territory have claimed to provide evidence for individual recognition in other 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 take into account the possibility that environmental context is necessary for recognition.

The collared lizard (*Crotaphytus collaris*) is a broadly distributed species of lizard in the southwestern United States. It is an archetypal territorial, polygynous, iguanian

lizard easily observed and manipulated in the field, and its behaviour and social organization have been well studied (Fitch 1956; Yedlin & Ferguson 1973; Baird et al. 1996). Dear enemy recognition has been documented in this species as well (Fox & Baird 1992), making it an ideal species for further tests of neighbour relationships and individual recognition. The purpose of this investigation was to determine if collared lizards increase aggression toward a displaced neighbour, and, if so, if they can recognize the neighbour outside of his normal environmental context. Integrating field manipulations and neutral arena encounters will test the hypothesis that territorial residents can recognize a displaced neighbour and respond to its increased threat.

METHODS

General Methods

The study site was located on Sooner Lake dam in north-central Oklahoma on a substrate consisting of rip-rap boulders sprayed with a concrete slurry at the time the dam was constructed. In May-June of 1999 and 2000, lizards were captured by noosing and permanently marked with toe-clips and a unique pattern of colored beads attached with a short length of monofilament fishing line sewn through the base of the tail for visual identification at a distance (after Fisher & Muth 1989). The base of the tail was cooled with ice before surgery to reduce discomfort as much as possible. When first captured, each lizard was weighed to the nearest 0.5 g and measured to the nearest 0.5 mm for total length and snout-vent-length.

The study area was surveyed and scale maps were generated and 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. The site was walked daily, lizards were observed with binoculars, and their locations were mapped 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) only when the substrate temperature was between 30-40° C, the optimal temperature range for collared lizards in central Oklahoma (Uzee 1990).

Field Experiments

Once territory boundaries were defined, staged intrusions were conducted so that the order of type of intrusion (e.g., resident or neighbour) was random and no lizard was used in more than one trial on a given day. The following trials were conducted with 22 resident subjects against: 1) neighbour male at familiar boundary (Familiar Side, FS), 2) neighbour male at opposite boundary (Opposite Side, OS), and 3) stranger male at FS boundary (Stranger, ST). All intrusions were conducted during June of 1999 and 2000 after territories had been established and aggression was at its peak in central Oklahoma (Fox & Baird 1992; Baird et al. 2001). Strangers were captured from areas 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, with approximately 8 cm of monofilament fishing line, to a modified 4.5-m golfball retriever and placing them at the desired location on a neutral-colored piece of carpet to avoid flight into otherwise accessible cracks and crevices. Ten-minute focal observations were conducted to quantify the behaviour of each target resident during the encounter. Agonistic behaviour was quantified by determining the frequency of aggressive and submissive displays (defined in Table 1) during encounters and the latency to the first aggressive act. All trials were size-matched such that strangers

matched, within 1 mm SVL, the size of the neighbour that was normally encountered at that boundary.

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 (sum of frequencies of behaviour patterns weighted by level of escalation: Table 2, modified from Fox & Baird 1992). During some of the intrusions the level of aggression by the subject was so intense that the interaction was stopped before ten minutes 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 ten-minute interactions.

Neutral Arena Trials

To determine if these lizards were capable of recognizing neighbours when they were taken out of environmental context, I conducted trials in a neutral arena on 13 adult males. An adult resident male and its male neighbour, or a stranger size-matched to that neighbour (within 1 mm SVL), were placed into a 2.5 m x 1.25 m x 0.75 m arena at the study site with an opaque divider separating them. They were allowed five minutes to acclimate before the divider was removed and the animals were allowed to interact. A 10-minute focal observation was then conducted on both lizards, with all behaviour recorded (Table 1). 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.

Analysis

All tests were conducted using SYSTAT (SPSS, Inc. 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 2-sample tests, $p > 0.25$ for all measures of aggression), so data were combined from both years for all analyses. A Friedman test was performed to determine overall differences among the responses to ST, FS, and OS. Friedman tests found to be significant were further analyzed with pairwise comparisons using Wilcoxon signed-ranks tests (Conover 1999) to determine if there were significant differences between FS and ST, between FS and OS, and between OS and ST. For neutral arena encounters, one-tailed Wilcoxon signed-ranks tests were used to compare the response of a lizard to a neighbour and a stranger for the four measures of aggression described above. I report actual p-values for independent tests; all p-values reported as significant individually retain significance when adjusted for Bonferroni probabilities.

RESULTS

Friedman tests revealed an overall significant difference among the responses by residents toward ST, FS, and OS for all four measures of aggression (Latency: $N = 22$, $F = 10.182$, $p < 0.005$; Maximum aggression: $N = 22$, $F = 10.636$, $p < 0.005$; Total aggressive acts: $N = 22$, $F = 16.159$, $p < 0.001$; Graded agonism: $N = 22$, $F = 22.932$, $p < 0.001$). Pairwise comparisons with Wilcoxon signed-ranks tests revealed significant differences between responses toward FS and ST, FS and OS, but not between OS and ST (Figure 2). Residents waited longer to respond to FS than ST ($T = -3.068$, $p = 0.002$) and OS ($T = -2.808$, $p = 0.005$), but there was no significant difference in latency between OS and ST ($T = -0.211$, $p > 0.50$). Residents had a lower maximum aggression score, displayed fewer total aggressive acts, and had a lower graded agonism score toward FS

than ST (Maximum aggression: $T = 2.839$, $p = 0.005$; Total aggressive acts: $T = 3.099$, $p = 0.002$; Graded agonism: $T = 3.360$, $p = 0.001$) and toward FS than OS (Maximum aggression: $T = 3.241$, $p = 0.001$; Total aggressive acts: $T = 3.523$, $p < 0.001$; Graded agonism: $T = 3.771$, $p < 0.001$), but there was no significant difference between OS and ST (Maximum aggression: $T = -1.604$, $p = 0.109$; Total aggressive acts: $T = -1.616$, $p = 0.106$; Graded agonism: $T = -1.607$, $p = 0.108$). Displaced neighbours were actually treated slightly more aggressively than strangers (Figure 2), but this difference was not significant.

A Wilcoxon signed-ranks test showed a significant difference between responses to neighbours and strangers in a neutral arena (Table 3). Individuals waited longer to respond to neighbours than strangers ($T = -2.622$, $N = 13$, $p < 0.01$), had a lower maximum aggression score toward strangers during the encounter ($T = 2.00$, $N = 13$, $p < 0.05$), displayed more total aggressive acts toward strangers ($T = 3.184$, $N = 13$, $p < 0.001$), and had a higher graded agonism score toward strangers ($T = 3.182$, $N = 13$, $p < 0.001$).

DISCUSSION

Previous studies of lizards have shown the dear enemy phenomenon to be present in nature (Fox & Baird 1992; Whiting 1999) and in the laboratory (Qualls & Jaeger 1991), and individual recognition to be present in neutral arenas (Glinski & Krekorian 1985; Olsson 1994; Lopez & Martin 2001). My study confirms the dear enemy phenomenon in male collared lizards in the field and suggests that residents are able to individually recognize neighbours and their normal location and respond to them according to their threat. Territorial individuals have mutually respected boundaries to avoid costly escalated encounters, but they will increase aggression toward neighbours if

there is sufficient threat. Male collared lizards do not seem to be misidentifying neighbours when they are placed on the opposite side of where they are normally encountered as shown by the fact that they can still recognize 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 the effects of familiarity and threat on neighbour relations, as well as the first reptile study to demonstrate increased aggression toward a neighbour placed on the opposite boundary.

The exact cue, or suite of cues, for individual recognition in lizards is not known (Glinski & Krekorian 1985). Iguanian lizards perform stereotyped displays (Carpenter 1967), but there is a certain amount of variation among individuals in their “signature” display (see Stamps & Barlow 1973; Bels 1986; Martins 1991). Color pattern has also been suggested to be involved in individual recognition (Olsson 1994; but see Whiting 1999). *Crotaphytus collaris* displays great variation in color pattern (McCoy et al. 1997), but it is unknown whether or not it plays a role in individual recognition. There is probably a suite of morphological and behavioural cues (Whiting 1999) that individuals use to recognize each other. Staged interactions in neutral arenas have shown that residents can distinguish neighbours from strangers away from their natural environment (Glinski & Krekorian 1985; this study), but the mechanism for identification has not been discerned and more empirical evidence is needed. Individual recognition among lizard species is most likely a species-specific phenomenon and broad generalizations about mechanisms of individual recognition, especially of species that may depend on visual and olfactory cues, should be made with caution.

Previous studies that have shown increased aggression toward neighbours on the

opposite boundary have used that result to conclude that territorial residents are capable of individual recognition. I disagree. This finding 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 prove that residents were capable of individual recognition because they were not given a chance to recognize a neighbour both out of environmental context *and* when it was not a potentially increased threat. If environmental context or location is required to recognize an individual (Molles & Vehrencamp 2001), then the displaced neighbor may be literally viewed as a stranger and treated as such. One would expect in this case elevated aggression toward a displaced neighbour compared to a neighbor in his right place. 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.

Once territorial boundaries are defined, a neighbour poses little threat to a territorial resident in terms of usurping mates or portions of his territory, and aggressive acts toward that neighbour would be an unnecessary expenditure of energy that could be used for other aspects of the resident's time budget such as foraging and reproduction (Jaeger 1981). Escalation of contests occurs 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 to the possible costs of losing (i.e., 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 neighbour is encountered on the opposite side of where he is

normally encountered at a resident's territory boundary, he must be reassessed in terms of his relative threat to the territory holder. His very presence is a threat to the resident because the displaced neighbour is now viewed as having more to gain (i.e., the resident's territory and mates) or else he would not be there (Ydenberg et al. 1988). In the eyes of the resident, a displaced neighbour (who is capable of defending a territory because he previously did) no longer has a territory or is trying to "add on" to his territory (because he is off of it) and threatens to usurp the resident's territory. There is strong selective pressure for males to increase aggression toward displaced neighbours because those that do not potentially lose fitness in terms of lost territory area or mates.

The relative threat of the intruder and the familiarity of the intruder (an asymmetric war of attrition model) have been proposed to explain reduced aggression toward neighbours relative to strangers. Explanations based solely on familiarity have been criticized for inappropriately using a war of attrition model (Getty 1989), dependency on the behaviour of intruders rather than residents ("fighting to learn" hypothesis; Getty 1989; Ydenberg et al. 1989), and the fact that they ignore possible differences in the costs and benefits of defending their territory against different intruders (Bradbury & Vehrencamp 1998). Recently, Temeles (1994) suggested that the relative threat of the intruder is more important to how a neighbour responds at a territorial boundary, but familiarity may play some role. This is supported by the cases of where Northern Harrier (*Circus cyaneus*) residents on feeding territories (Temeles 1989; 1990), the ant *Pogonomyrmex barbatus* (Gordon 1989), and the termite *Nasutitermes corniger* (Dunn & Messier 1999) increased aggression toward neighbours rather than strangers because the neighbours in these cases represented more of a threat to residents than strangers. Such results do not support the asymmetric war of attrition model. The war of

attrition model predicts that escalation should occur more frequently in situations where role mistakes during an interaction are more likely. In the three examples above, increased aggression is not directed toward the type of intruder where role mistakes are more likely -- strangers.

When a neighbour is displaced to the opposite boundary, the threat of that individual increases and escalation is expected. The war of attrition model also explains this phenomenon, but without including the idea of increased threat. In this model, the displaced neighbour is now "less familiar" because his fitness payoff, V , has changed (presumably increased or else he would not be in that new location), resulting in escalation due to role mistakes drawn from faulty comparisons of benefit-cost ratios of the two opponents (Ydenberg et al. 1988). The ratio of fitness payoff to resource holding potential (V/K) of the neighbour presumably increases when he is on the opposite boundary since his resource holding potential, K , has not changed, but his fitness payoff, V , has increased. According to game theory, the V/K ratio of a stranger should always involve the most role mistakes because neither V nor K are known, but for a displaced neighbour, at least K is known. Role mistakes, then, are more likely during interactions between strangers than between neighbours. The model predicts escalation to be more likely as role mistakes increase in frequency, so most escalation should be directed toward strangers, then displaced neighbours, and then neighbours at the correct boundary because that is the order in which the frequency of role mistakes should decrease. I obtained results contradictory to this, so the war of attrition model is not supported in this case. The "fight to learn" hypothesis (Getty 1989) can also be rejected because the residents know their neighbours regardless of context, and conditions have not changed in their territories. The only logical conclusion to be drawn from my data is that the resident

recognizes a displaced neighbour and perceives him as an increased threat, and so responds by escalating aggression.

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 socio-spatial relationships over time and repeated exposure to each other. When a neighbour is displaced, the agreement between them is broken, so escalation occurs. In a neutral arena, there is no valuable resource, neither a neighbour or a stranger represent much of a threat to the future fitness of a given resident, and there is no established socio-spatial relationship. Territorial neighbours have, however, over the course of time, developed dyadic social relationships concerning both territory ownership and relative dominance. Because neighbours have encountered and assessed each other over considerable time, they each know the other has the advantage in his own territory, but outside of those territories they know that one of them will be dominant over the other due to other previously assessed and recognized asymmetries in RHP. Strangers have no prior experience with each other, and no such relationships. Since collared lizards are social animals, they will naturally work out a dyadic dominance relationship when placed in a neutral arena. Again, that relationship has already been resolved between neighbours, but with a stranger, no; hence the difference in aggressive response toward neighbours and strangers in a neutral arena. Familiarity is important when deciding how to respond to an intruder, but, in this case, not in the sense of how “familiarity” is used in the war of attrition model.

Resident collared lizards, on average, waited a shorter amount of time to respond to displaced neighbours than strangers, and responded more intensely, although these

differences were not significant. These results suggest that the resident may stand more to lose from invasion by a displaced neighbour than a stranger. A neighbour potentially knows the area better than a stranger, so the threat of a displaced neighbour can be considered higher than that of a stranger. Territory residents also know that their neighbours have adequate RHP to acquire and maintain a territory (because they previously had one), whereas intruding strangers may not. This, too, adds to the threat imposed by a displaced neighbour that is potentially trying to usurp a resident's territory when compared to a stranger. This same idea is supported by the results of McGregor & Westby (1992), where weakly electric fish (*Gymnotus carapo*) displayed shorter latencies and responded more aggressively toward displaced neighbours; however, they did not consider the idea that the displaced neighbour may represent more of a threat than a stranger. The fact that a resident increases aggression toward a displaced neighbour and is slightly more aggressive toward that displaced neighbour than toward a stranger suggests that, despite the familiarity of that neighbour, there is still an increased threat -- i.e., the dear enemy phenomenon is context-specific.

White-Throated Sparrows (*Zonotrichia albicollis*) have been shown to display a different order of intensity toward the same classes of intruders as that used in my study (Falls & Brooks 1975). Most aggression was directed toward strangers (ST), less toward displaced neighbours (OS), and much less toward neighbours at their normal location (FS). The explanation for the reduced aggression toward FS parallels that presented in this study (dear enemy phenomenon). The difference between OS and ST was minimal, and no explanations were offered for this order of intensity. It can be assumed that there are some different costs between territorial lizards and birds, but the overall trend of increased aggression toward both OS and ST should be consistent among territorial taxa

(and this is generally so). Response differences between OS and ST, however, will likely be taxon-specific and more empirical evidence is greatly needed for any generalizations to be made.

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Table 1. Dominant and submissive behaviour patterns quantified during intrusions.

Dominant Displays	
Approach	Directed movement toward intruder
Head bob	Subtle up and down motion of head, with or without limb flexion
Throat display	Dewlap extended, partially or fully
Lateral throat display	Dewlap fully extended, back arched, raised up on all four limbs and with laterally compressed body
Push up	During lateral throat display, body pushed all the way off substrate by limb extension
Superimposition	Resident covers intruder with body
Attack	Fast charge toward intruder, with contact
Bite	Resident bites intruder, then releases or maintains hold
Fight	Physical contact, rough-and-tumble combat
Circle	Resident moves in a circular pattern with intruder
Chase	Resident pursues intruder
Submissive Displays	
Retreat	Resident withdraws from intruder
Flee	Resident runs away from intruder

Table 2. Scores given to agonistic behaviour patterns recorded and used in the graded agonism analysis to weight relative cost to lizard.

Behaviour	Score
Flee	-1
Retreat	-1
Approach	1
Throat display	2
Lateral throat display	2
Head bob	2
Push up	2
Circle	2
Chase	2
Attack	3
Fight	3
Superimposition	3
Bite	3

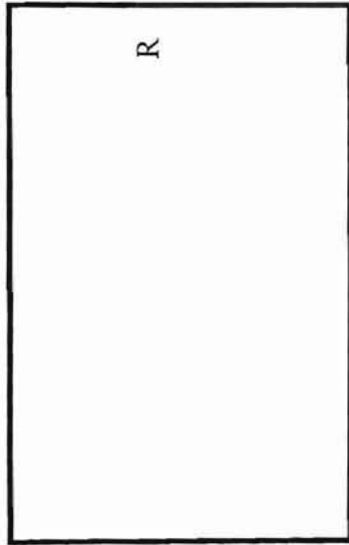
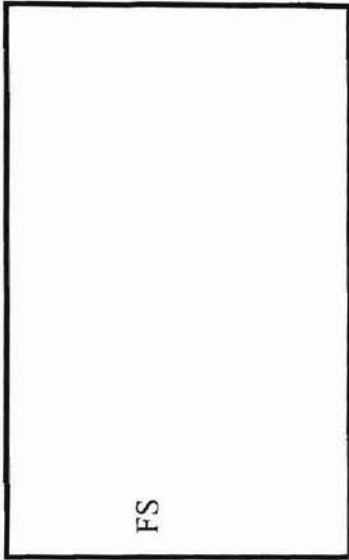
Table 3. Mean \pm 1 SE responses for four measures of aggression from neutral arena interactions (N = 13) between adult male collared lizards, *Crotaphytus collaris*, directed toward neighbours and strangers. P-values given are from a Wilcoxon signed-ranks test.

	Neighbours	Strangers	P-value
Latency (s)	42.9 \pm 8.1	24.8 \pm 1.9	< 0.01
Maximum Aggression	3.0 \pm 0.0	3.3 \pm 0.1	< 0.05
Total Aggressive Acts	5.8 \pm 0.4	16.5 \pm 2.0	< 0.001
Graded Agonism	10.8 \pm 0.9	30.7 \pm 3.7	< 0.001

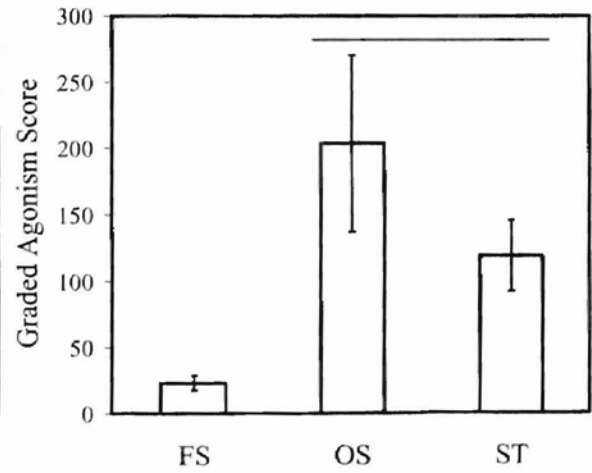
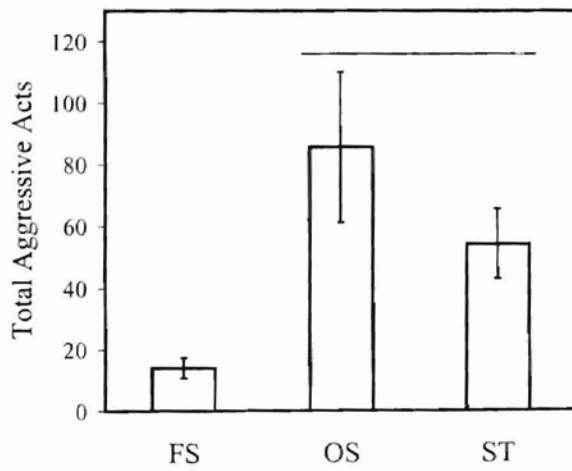
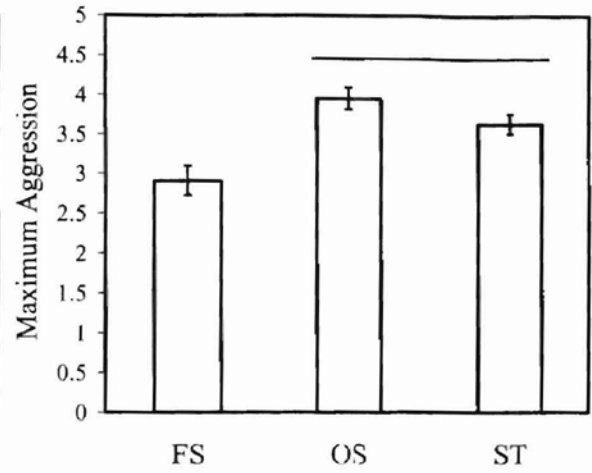
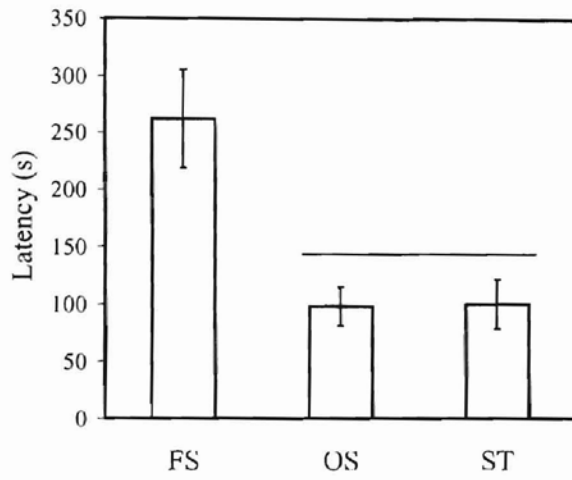
Figure Legends

Figure 1. Experimental design of intrusions, showing the locations of the resident lizard (R) and the intruders (FS - familiar side and OS - opposite side). R and FS represent the locations at territory boundaries where two territorial neighbours would normally encounter each other and interact. OS represents the displaced location for neighbour FS on the boundary opposite the shared boundary.

Figure 2. Mean responses (with ± 1 SEM error bars) for four measures of aggression from staged intrusions (N = 22) between adult male collared lizards, *Crotaphytus collaris*, directed toward neighbours on the familiar side (FS), neighbours on the opposite side (OS), and strangers (ST). Responses that were not significantly different have a line above the respective bars.



OS



SPATIAL ORGANIZATION AND THE DEAR ENEMY PHENOMENON IN
ADULT FEMALE COLLARED LIZARDS, *CROTAPHYTUS COLLARIS*

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Abstract: Reduced aggression toward territorial neighbors relative to strangers, the dear enemy phenomenon, is a widespread occurrence in many taxa, presumably because a stranger represents more of a threat to a resident than a neighbor. Several lizard species exhibit this phenomenon in males, including *Crotaphytus collaris*, but little is known about this phenomenon in females. Only one test for the presence of the dear enemy phenomenon has been conducted on female lizards, and no decrease in aggression toward neighbors was found. I introduced tethered neighbors or size-matched strangers in random order to 12 adult, non-reproductive female *C. collaris* and conducted 10-min focal observations, recording all behavior. I found no significant differences between responses to neighbors and strangers in latency, maximum aggression, total aggressive acts or a graded agonism score. This suggests that females of this population of *C. collaris* do not exhibit the dear enemy phenomenon, presumably because a stranger does not represent more of a threat than a neighbor. Changing costs associated with the reproductive cycle have allowed no favorable situations for the dear enemy phenomenon to evolve.

Key Words: Dear enemy phenomenon, female aggression, *Crotaphytus collaris*

In many taxa, territory residents respond less aggressively to neighbors than they do toward strangers, the dear enemy phenomenon (Fisher, 1954). Neighbors respect one another's boundaries with the "agreement" that they will not escalate encounters, especially if the costs of such encounters are high. Hypotheses based on familiarity (Ydenberg et al., 1988) and the relative threat of the intruder (Getty, 1987; Jaeger, 1981) have been proposed to explain the dear enemy phenomenon, but both have been criticized (reviewed in Temeles, 1994). Based on recent findings concerning neighbor relationships in which sometimes neighbors are more of a threat, and sometimes less of a threat, than strangers, the relative threat hypothesis has gained favor for explaining differences in aggression (Temeles, 1994). Among lizard species, the dear enemy phenomenon has been documented with male *Dipsosaurus dorsalis* (Glinski and Krekorian, 1985), *Anolis carolinensis* (Qualls and Jaeger, 1991), *Crotaphytus collaris* (Fox and Baird, 1992), and *Platysaurus broadleyi* (Whiting, 1999). Only the females of one species of lizard has been tested for the dear enemy effect (*Urosaurus ornatus*; Mahrt, 1998a), and the phenomenon was not found. Ironically, male *U. ornatus* have never been tested for the dear enemy phenomenon.

Most work on lizard social behavior has concentrated on males, neglecting females. This is mainly due to the fact that males are typically more showy and display more frequently (Stamps, 1977). Recently, however, some studies have been aimed strictly at female lizards and their role in a population's social organization (e.g., Mahrt, 1998a, 1998b; Sloan and Baird, 1999; Woodley and Moore, 1999a, 1999b). The collared lizard (*Crotaphytus collaris*) is a broadly distributed species of lizard in the southwestern United States whose behavior has been well studied. The behavior of female collared lizards is well documented (Baird et al., 1996; Fitch, 1956; Yedlin and Ferguson, 1973),

but only one paper deals strictly with their social behavior (Sloan and Baird, 1999). Female collared lizards have been found to be slightly aggressive with a great deal of spatial overlap (Baird et al., 1996), aggressive and arranged spatially with little overlap (Fitch, 1956; Yedlin and Ferguson, 1973), potentially defensive of the nest site (Yedlin and Ferguson, 1973), and "territorial" (Rostker, 1983). The population studied during this investigation (Husak and Fox, unpublished data), as well as others (Fitch, 1956; Rostker, 1983; Yedlin and Ferguson, 1973), shows some degree of female spacing that may offer appropriate conditions for the evolution of territoriality and the dear enemy phenomenon. The purpose of this study was to determine if females of this population exhibit the dear enemy phenomenon. It represents only the second test for the dear enemy phenomenon with female lizards, but the first on female *C. collaris*. Analysis of behavior patterns involving assessment of individuals requires field tests such as this study because such studies take into account the true *in situ* costs and benefits of territory ownership.

Methods

The study site was located on Sooner Lake dam in north-central Oklahoma on a substrate consisting of rip-rap boulders sprayed with a concrete slurry at the time the dam was constructed. In May 2000, lizards were captured by noosing and permanently marked with toe-clips and a unique pattern of colored beads attached with a short length of monofilament fishing line sewn through the base of the tail for visual identification at a distance (after Fisher and Muth, 1989). The base of the tail was cooled with ice before surgery to reduce discomfort as much as possible. When first captured, each lizard was weighed to the nearest 0.5 g and measured to the nearest 0.5 mm for total length and snout-vent-length (SVL).

The study area was surveyed and scale maps were generated and 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. The site was walked daily, lizards were observed with binoculars, and their locations were mapped so that home ranges could be defined by the minimum convex polygon procedure (Rose, 1982). Home range size and overlap was calculated for the females used in this study using ArcView GIS v. 3.1 (Environmental Systems Research Institute, Redlands, CA) to examine spatial relationships. Home range overlap was calculated as the percent overlap in home range for each resident female and the neighbor used as the intruder.

Once home range boundaries were defined, staged intrusions (see Fox and Baird, 1992) were conducted so that the order of intrusions (e.g., resident or neighbor) was random and no lizard was used in more than one trial on a given day. Conducting only one intrusion per day avoids potential problems associated with acute elevated hormone levels or other factors that may keep a lizard temporarily in an artificially aggressive state as a result of multiple intrusions in sequential order with little time for rest between them (see Mahrt, 1998a). This investigation was part of a larger study concerning collared lizard social behavior (Husak, 2001), so ages of all lizards were known with certainty. All intrusions were conducted between the first and second clutch of eggs, using only adult (1.5+ year-old) individuals. The “non-reproductive” time of the reproductive cycle was chosen because behavior should not be biased by post-ovipositional aggression (Sloan and Baird, 1999) or by a gravid condition, which may alter the costs and benefits of being aggressive (Mahrt, 1998a).

Twelve adult females were randomly chosen from the population to serve as focal residents. The following trials were conducted with these 12 residents against: 1) neighbor female at familiar boundary and 2) stranger female at the same boundary as case (1). Strangers were captured from areas away from the study site to ensure that subject lizards were not familiar with intruders. Neighbor or stranger adult females were introduced at the boundary of the home ranges of adult females by tethering them, with approximately 8 cm of monofilament fishing line, to a modified 4.5-m golfball retriever to avoid flight into otherwise accessible cracks and crevices. Ten-minute focal observations were conducted to quantify the behavior of each target resident during the encounter. Agonistic behavior was quantified by determining the frequency of aggressive and submissive displays (defined in Table 1) during encounters and the latency to the first aggressive act. All trials were size-matched such that strangers matched, within 1 mm SVL, the size of the neighbor that was normally encountered at that boundary. Data were collected only when the substrate temperature was between 30-40° C, the optimal temperature range for collared lizards in central Oklahoma (Uzee, 1990).

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 (sum of frequencies of behaviour patterns weighted by level of escalation: Table 2, modified from Fox & Baird 1992). All tests were conducted using SYSTAT (SPSS, Inc., 1998). One-tailed Wilcoxon signed-ranks tests (Conover 1999) were used to compare the response of a lizard to a neighbor and a stranger using the four measures of aggression described above. A sequential Bonferroni adjustment for four

related tests was used to confirm significance (Rice, 1989). Correlation analysis was used to test for a significant relationship between home range size and SVL, and home range overlap and SVL. Home range sizes and overlaps used in the analyses were for those females used as target residents during the intrusions.

Results

Results showed a trend in the predicted direction for the dear enemy phenomenon (Table 3), but no significant difference was found for latency ($z < 0.001$, $P > 0.99$), maximum aggression ($z = 1.414$, $P > 0.05$), total aggressive acts ($z = 1.101$, $P > 0.25$), or graded agonism ($z = 0.985$, $P > 0.25$).

Average home range size (± 1 SE) was 1794.2 ± 141.6 m². No relationship was found between home range size and SVL ($r = -0.48$, $P > 0.10$). There was extremely low home range overlap with a mean (± 1 SE) of 2.6 ± 0.9 %, and no significant relationship was found between home range overlap and SVL ($r = -0.30$, $P > 0.25$).

Discussion

There appears to be no dear enemy effect in this population of female collared lizards, in agreement with the one other dear enemy study conducted on female lizards (Mahrt, 1998a). Although the results are in the predicted direction for the dear enemy phenomenon, most probabilities did not approach significance and the mean responses were only slightly as expected for the dear enemy phenomenon to be present. The absence of the dear enemy phenomenon in this population suggests several things about the social organization of female collared lizards and the costs and benefits of territoriality. One possible explanation for these results is that both a stranger and a neighbor represent significant threats to the resident, but equal in magnitude. However, the low response levels, compared to that of males in the same situation (10-fold

difference: Fox and Baird, 1992; Husak, 2001), suggest that this is unlikely. There is likely little threat to a resident female from a neighbor, and there is also likely no more threat from a stranger (see below). Since there is little threat from either type of intruder, there is no benefit to warrant escalation in either case (Getty, 1987; Jaeger, 1981).

The definition of territoriality has remained controversial for many years (Brown and Orians, 1970; Maher and Lott, 1995; Mathis et al., 1995, Noble, 1939; Stamps, 1977), and the application of any one general definition of territoriality to various taxa should be done with caution (Sheldahl and Martins, 2000). Inherent in most definitions of territoriality are three components: 1) site fidelity, 2) defense of the site, and 3) exclusive use (Sheldahl and Martins, 2000). With respect to the first criterion, the data from this investigation suggest some degree of both intra- and inter-year site fidelity among female collared lizards. Females of this population have well-defined home ranges, and daily observations confirm that they do not leave those areas (except while gravid when there appears to be slightly more overlap among females; Husak and Fox, unpublished data). This study was part of a larger investigation of collared lizard social behavior, so I had spatial data for a subset ($N = 16$) of adult females that survived from 1999 to 2000. Fourteen of the sixteen females (87.5%) had home ranges in 2000 that overlapped $> 90\%$ of their 1999 home range. The two exceptions to this pattern were lizards that shifted their home ranges from 1999 to 2000 to fill a vacancy created by the disappearance of a large, dominant female (at least 5 years old; lizard marked in study by Yoshioka, 1996). Males of the species are also known to show such year-to-year site fidelity (Baird et al., 2001; Husak and Fox, unpublished data). The second criterion was only weakly met by this population of female lizards. I observed aggression toward neighbors and strangers (Table 3), but it was very low. The third criterion was strongly

met, with a very low degree of overlap among neighbors. Considerations of space use over the entire reproductive cycle may complicate these conclusions, however, as overlap tended to slightly increase while lizards were gravid (Husak and Fox, unpublished data).

Previous studies of female *C. collaris* have yielded mixed results in terms of whether or not they are territorial (Fitch, 1956; Rostker, 1983; Sloan and Baird, 1999; Yedlin and Ferguson, 1973). The population I studied appears to have relatively exclusive home ranges with little overlap, at least while in a non-reproductive state. The results of my study cannot definitively conclude whether or not these females are territorial, but they do suggest some degree of home range defense, albeit weakly so. The fact that there is little home range overlap (much less than in previous studies, e.g., Baird et al., 1996) suggests that there is some advantage to having an exclusive home range, but the advantages are most likely different than those conferred to males having an exclusive territory. Females are probably not defending access to mates as males of the species do, since a given adult male's territory may overlap numerous females (Baird et al., 1996; Husak and Fox, unpublished data). They may be excluding other females' access to other resources such as basking sites, nest sites, or food resources, but the homogeneous structure of the habitat suggests that basking sites, nest sites, and possibly food resources are not likely to be contested. In this situation there are not enough benefits to outweigh the costs of aggressively defending the boundaries of a home range (e.g., costs of patrolling, increased risk of injury). The lack of a significant relationship between either home range size or overlap and body size suggests that there may be no advantage to larger females having a larger home range with less overlap than smaller females. Assuming that there is a tight relationship between body size and food requirements, and

because there was no relationship between body size and home range size, it is unlikely that food resources are being defended.

The dear enemy phenomenon is advantageous only to highly territorial individuals that stand to lose a great deal to a stranger, but not a neighbor (Temeles, 1994; Ydenberg et al., 1988). Female *C. collaris* apparently have little to lose from either neighbors or strangers, suggesting that if they are territorial, they are not defending very valuable resources. These results agree with the hypothesis that responses during agonistic encounters between a territorial resident and an intruder are greatly influenced by the threat imposed by that intruder (Getty, 1987; Husak, 2001; Jaeger, 1981). In some species there is a greater aggressive response toward a neighbor than toward a stranger (Gordon, 1989; Dunn and Messier, 1999; Temeles, 1990) because the neighbor represents more of a threat than a stranger. If female collared lizards are territorial only while reproductive or post-reproductive, they should respond to neighbors and strangers differently at these times than at other times in the season. Defending a territory while carrying eggs is potentially costly due to the extra burden of the eggs (Sloan and Baird, 1999) and the heightened risk of injury or loss of eggs, so it may take the threat of a stranger to cause escalation to occur. In a recent study, heightened post-ovipositional aggression by female collared lizards was attributed not to nest defense, but instead to re-establishing social dominance after being absent for oviposition (Sloan and Baird, 1999). If this is true, then equal, but high, post-ovipositional aggression should be directed toward neighbors and strangers since they both represent equal threat. Perhaps since a neighbor may be more likely than a stranger to usurp portions of an absent female's territory, increased aggression may be directed even more toward neighbors than toward strangers. This is especially true if the resident expects to regain dominance upon return

from oviposition. Given these circumstances, it is unlikely that the dear enemy phenomenon could evolve among female collared lizards because the situation may never be uniformly advantageous all through the year. Added to this is the fact that females are not completely synchronous in their reproductive cycles, meaning, for example, that some may be post-ovipositional while others may be non-reproductive or still gravid. All of these ideas deserve further investigation and need empirical evidence through experimentation.

There was a great deal of individual variation in the responses to neighbors versus strangers, but no consistent pattern was apparent. Four (33.3%) females did not respond to either intruder, one (8.3%) female displayed equal aggression to both intruders, five (41.7%) females displayed more aggressive behavior toward strangers, and two (16.7%) females displayed more aggressive behavior toward neighbors. The somewhat lower response toward neighbors relative to strangers may simply be due to familiarity and muted aggression via habituation (Peeke, 1984). Individual recognition has been shown in adult male collared lizards (Husak, 2001), so there is the potential for females to also exhibit such behavior. Further tests in neutral arenas would be necessary to make any definitive statements concerning individual recognition and what the possible cues might be. Further studies should also examine the response of resident adult females to intrusion in the center of the home range where defense of space should be stronger (Giraldeau and Ydenberg, 1987).

Among-population differences in social and spatial organization of female collared lizards as reported by others (see Introduction) are probably attributable to variation in ecological factors such as density, resource availability, and predator density. Baird et al. (1996) placed tethered female intruders on the previously occupied perch of a

resident female (not at a boundary), and even there found very little aggression, suggesting that females do not aggressively defend a territory. However, the population they studied had much higher home range overlap, suggesting that other factors may be different than the population studied during this investigation. Yedlin and Ferguson (1973) observed female aggression during similar tethered intrusions, but it was less intense than the response of males. They made no speculations about whether or not the females might be territorial. The female collared lizards at Sooner Lake do not seem to aggressively defend a home range, as shown by the low degree of aggression during intrusions, but there is very little overlap. Density may be lower, predation rates may be higher, and resource availability may be spatially arranged differently than in the population studied by Baird et al (1996).

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Table 1. Dominant and submissive behavior patterns quantified during intrusions.

Dominant Displays	
Approach	Directed movement toward intruder
Head bob	Subtle up and down motion of head, with or without limb flexion
Throat display	Dewlap extended, partially or fully
Lateral throat display	Dewlap fully extended, back arched, raised up on all four limbs and with laterally compressed body
Push up	During lateral throat display, body pushed all the way off substrate by limb extension
Superimposition	Resident covers intruder with body
Attack	Fast charge toward intruder, with contact
Bite	Resident bites intruder, then releases or maintains hold
Fight	Physical contact, rough-and-tumble combat
Circle	Resident moves in a circular pattern with intruder
Chase	Resident pursues intruder
Submissive Displays	
Retreat	Resident withdraws from intruder
Flee	Resident runs away from intruder

Table 2. Scores given to agonistic behavior patterns recorded and used in the graded agonism analysis to weight relative cost to lizard.

Behavior	Score
Flee	-1
Retreat	-1
Approach	1
Throat display	2
Lateral throat display	2
Head bob	2
Push up	2
Circle	2
Chase	2
Attack	3
Fight	3
Superimposition	3
Bite	3

Table 3. Mean \pm 1 SE responses for four measures of aggression from intrusions ($n = 12$) between resident adult female collared lizards, *Crotaphytus collaris*, directed toward neighbors and strangers.

	Latency (s)	Maximum Aggression	Total Aggressive Acts	Graded Agonism
Neighbors	455.9 \pm 62.0	1.7 \pm 0.3	1.8 \pm 1.1	3.3 \pm 2.0
Strangers	437.9 \pm 56.5	2.3 \pm 0.3	5.8 \pm 3.2	11.2 \pm 7.1

VITA

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