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EFFECTS OF AN INDIVIDUAL'S REMOVAL ON SPACE USE AND BEHAVIOR IN TERRITORIAL NEIGHBORHOODS OF BROWN ANOLES (*ANOLIS SAGREI*)

ANN V. PATERSON

Department of Natural Sciences, Williams Baptist College, P.O. Box 3565, Walnut Ridge, AR 72476, USA

ABSTRACT: I conducted experiments using naturally established neighborhoods of *Anolis sagrei* to examine interactions between neighboring territorial males. I observed the behavior of groups of lizards before and after the removal of one lizard from the group. I measured space use using x and y coordinates of a 20 × 20 m grid. Focal lizards moved farther from the former resident's activity area center following his removal from the territory. Both neighbors and non-neighbors took over the newly vacated territories, suggesting that some neighbors were able to gain space. The behavioral display patterns of focal lizards did not change following the removal. These data indicate that neighboring males may pose a significant threat to territorial residents by taking space and resources. Additionally, these data provide no evidence that removal of one resident causes general social instability that harms neighbors. These findings have theoretical implications for studies of the "dear enemy" phenomenon and other relationships that are based on social contexts found in territorial neighborhoods.

Key words: Anole; *Anolis sagrei*; Dear enemy; Territorial neighborhood; Territoriality

DESPITE the evidence that territoriality is a central aspect of the social behavior of

many taxa, recent work suggests that we have a poor understanding of the complexity of natural territorial behavior (e.g., McMann, 2000; Sheldahl and Martins, 2000; Stamps and Krishnan, 1994a,b,

¹ CORRESPONDENCE: e-mail, apaterson@wbcoll.edu

1995, 1998). One reason is that we are only starting to understand the complexity of territorial neighborhoods. A given territory owner may react differently to neighbors, non-territorial individuals, and others for a variety of reasons. In addition, interactions between the above classes of individuals may differ based upon larger contexts (for example, the establishment of a new neighborhood in a seasonally territorial species, versus individuals maintaining territories, versus an event such as predation causing a single vacancy in an established neighborhood).

One example of a poorly understood aspect of territoriality is the “dear enemy” phenomenon (*sensu* Fisher, 1954). The dear enemy phenomenon describes the tendency of territorial residents to show less aggression towards familiar neighbors than towards unfamiliar non-neighbors (reviewed in Temeles, 1994). Two hypotheses that have been proposed to explain the dear enemy phenomenon are the social stability hypothesis, which relates level of aggression to the benefits of a stable territorial neighborhood, and the relative threat hypothesis, which predicts greater aggression towards the individual that poses a greater threat.

The purpose of my study was to use the territorial lizard (*Anolis sagrei*) (1) to examine whether neighbors or non-neighbors are more likely to take territorial space from a resident, given the opportunity, in a territorial lizard, (2) to provide baseline data on territorial interactions in a natural setting in this species, and (3) to begin to elucidate the basis of dear enemy behavior. Adult males of *A. sagrei* are known to exhibit the “dear enemy” phenomenon, showing reduced aggression towards former neighbors in a neutral arena (Paterson, 1999). However, their behavior in a natural territorial neighborhood is less clear (Paterson, 1999).

By examining display behavior and space use before and after the removal of a resident from a natural territorial neighborhood, I examined the following two questions. Do neighbors or non-neighbors gain territorial space more often when a resident loses its territory? If neighbors

gain space more often, then neighbors are willing to take territorial space. This action suggests that they pose a threat to a resident even though they already have a territory and is inconsistent with the relative threat hypothesis if *A. sagrei* shows the “dear enemy” phenomenon. According to the relative threat hypothesis, non-neighbors (either unfamiliar floaters or unfamiliar territorial males) would be expected to pose the greater threat.

Do neighbors face changes in defensive costs (reflected by display behavior and intrusion rates) when a resident loses its territory? The social stability hypothesis predicts that defensive costs increase following a change in territorial ownership. A change in display behavior could also indicate increased higher (or lower) aggression towards a new neighbor versus familiar, established neighbors. Another possible cost of territorial turnover could be the loss of territorial space by neighbors. Following a change in territory ownership, neighbors may lose space to the new intruder or to other neighbors as a result of the instability and re-negotiation of boundaries. Alternatively, neighbors may gain space during re-negotiation.

The above information can be used in conjunction with other studies to examine the relative threat hypothesis, increasing the external validity of more manipulative studies (both in the laboratory and in the field) by showing that experimental protocols truly reflect natural situations and behaviors (*i.e.*, Nelson, 1998). Additionally, *A. sagrei* and other anoles are frequently used in a variety of behavioral studies, making knowledge of their territorial neighborhoods particularly useful.

Anolis sagrei is a medium-sized anole that generally occurs on, and around, the bases of trees and in other structurally complex habitats. Males are territorial during the breeding season, which runs from approximately March to early August (Lee et al., 1989; Tokarz et al., 1998). When former neighbors are placed together in a neutral arena, they show less aggression than pairs of unfamiliar individuals in the same context (Paterson, 1999).

METHODS

I conducted this study at Castellow Hammock Park in southern Florida during the March–August breeding season of *A. sagrei* (Lee et al., 1989; Tokarz et al., 1998). The vegetation of the study site is subtropical hardwood hammock forest, similar to forests that occur in many parts of the Caribbean where *A. sagrei* is found (e.g., Snyder et al., 1990). The area had been disturbed by a hurricane in 1992 and, therefore, provided a habitat with abundant light gaps combined with structural complexity in the lowest few meters (e.g., fallen trees and secondary regeneration; Horvitz et al., 1995, 1998). Therefore, this habitat was grossly similar to others that have supported the high population densities that are common for *A. sagrei* (Lister, 1976; Schoener and Schoener, 1980). Individuals of *Anolis sagrei* establish their territories on the ground, on low rocks/outcroppings, and on the lower portions of vegetation (Schoener and Schoener, 1980, 1982; Tokarz, 1998).

I established eight gridded plots (20 × 20 m) with surveyor's flags placed at 2-m intervals. I selected the sites for the plots by walking through the forest and looking for areas that were sufficiently open to allow observation of lizards. The grids gave a two-dimensional measure of lizard location, consistent with location data used in previous studies of home ranges of *A. sagrei* (Schoener and Schoener, 1982).

I marked all visible adult males with permanent bead tags within eight of these plots, using the technique of Fisher and Muth (1989). I did not begin to collect data in a plot until several successive observations indicated that all visible adult males in the plots had been marked. Seven plots were used between April and July 1997, while the eighth was used in March 1998. Because plot setup, extensive marking of lizards, and the experiment itself were time consuming, the number of plots used was the maximum that time constraints, such as the length of the *A. sagrei* breeding season, allowed. The eighth plot was included a year after the others in order to increase the sample size.

I made focal animal observations on adult males of *A. sagrei* based upon several criteria. First, a male was chosen for observation if it had been observed to display in an area without being chased from the area by a conspecific for several days prior to data collection (i.e., the individual was a territory owner). Second, I chose males located near the centers of their respective plots to reduce the likelihood of interactions with unmarked lizards.

For each of the eight replicates, I observed two groups of lizards within a 20 × 20 m plot; each group consisted of an adult male focal animal and its three nearest adult male territorial neighbors. For each plot, none of the lizards in one group were immediately adjacent neighbors to the lizards in the second group (i.e., patches of habitat with displaying males separated the groups, and the groups were chosen to maximize the distance between them). One four-male neighborhood was designated the experimental group, meaning that the focal animal would be removed. The other four-male neighborhood was designated the control group. For each of the experimental and control groups, I sequentially observed the four males during 15-min periods throughout a morning activity period (4 h of observation, with a total of four 15-min observation periods, approximately 1 h apart, for each male). This observation protocol was followed during all days of observation. During these observations, I recorded location and behavior using the variables discussed below.

To record location, I used x and y coordinates written on the surveyor's flags placed at 2-m intervals to form a grid. I recorded the coordinates of the flag nearest to the lizard under observation as well as the orientation of the lizard with respect to the flag (e.g., northeast of 2,4). Therefore, locations for all lizards observed in a plot could be estimated to the nearest meter, placing them within 1-m squares within the entire 20 × 20 m plot (Fig. 1). I used the location at the center of each square for all calculations. For each observation, I noted the lizard's starting location and each new location. I used these data

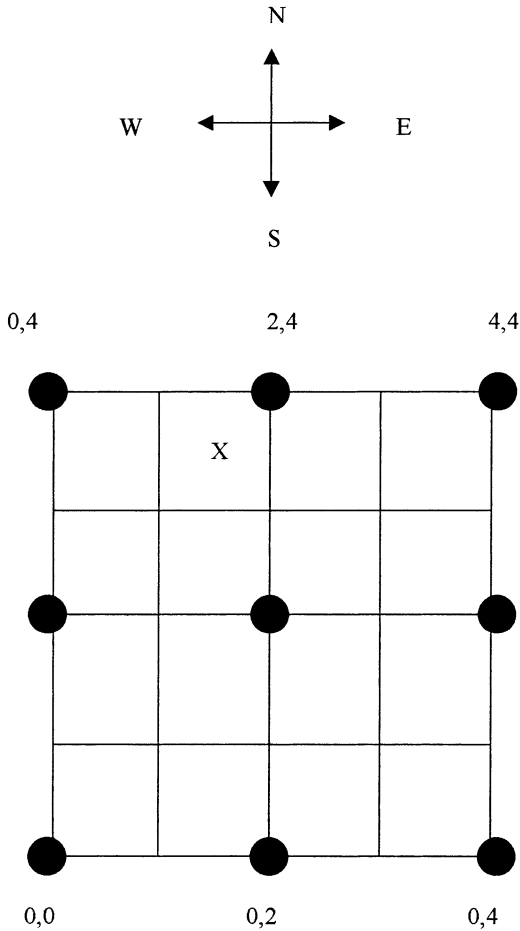


FIG. 1.—Locations of lizards observed in a plot could be mapped onto a grid of the entire 20×20 -m plot, placing them within 1-m squares. The grid below represents a portion of a 20×20 -m plot. The circles represent the locations of surveyor's flags (placed at 2-m intervals). The location of the lizard "X" is SW of 2,4. In this way, the lizard's location is known within a 1-m square.

to estimate an "area of activity" (the part of the home range used within 4 h).

To record social behavior, I noted the times and locations of activities such as displays, chases, fights, and copulations. Although males may engage in physical fighting, they accomplish territorial defense primarily through easily quantifiable visual displays (described in McMann, 1998, 2000). The most common visual displays are two types of headbob displays: nodding and bobbing displays. A nodding display consists of a volley of continuous

dorso-ventral oscillations of the head, whereas a bobbing display is a discontinuous series of movements that form a specific temporal pattern. I recorded headbob displays by classifying them as nodding displays or bobbing displays using the classification system of McMann (2000; see also Paterson, 1999). I also recorded each extension of the brightly colored dewlap, or throat fan, and noted whether the dewlap extension coincided with a bobbing display (the dewlap is not extended during a nodding display; McMann, 2000; Paterson, 1999). Following each 15-min observation period, I examined the surrounding area to note locations of other displaying adult males (neighbors) to determine their markings (or to note if an unmarked male was present).

Approximately 72 h from the first morning of observation for each group (or the next non-rainy morning after 72 h), I observed the same group for an additional 4 h using the same protocol. This time period was chosen to allow for consistent observations and to allow lizards 72 h to shift their home ranges after the removal of one resident. The above protocol was the same for the control and experimental groups.

I conducted additional observations of the experimental group. On the morning of the next non-rainy day following the second observation of the experimental group, I attempted to remove the most central (focal) lizard in the experimental group (all lizards that were removed were captured using a noose on the end of a fishing pole). On two occasions, it was necessary to remove a neighboring lizard when the most central lizard did not appear or was inaccessible. I then watched the newly vacant territory using the same protocol as described above for 4 h of the morning activity period. Approximately 48 h after the removal, I again watched the experimental group using the same protocol. I observed the three neighbors and the new resident of the vacated territory (if present) using the same protocol used prior to the removal. I designed the observation schedule to keep conditions as similar as possible between each experi-

TABLE 1.—Observation schedule for experimental and control groups.

Day	Observation group
1	Experimental group (preliminary)
3	Control group
4	Experimental group (before removal)
5	Experimental group (immediately following removal)
6	Control group
7	Experimental group (after removal)

mental and control group in a plot (Table 1).

To determine whether neighbors gain territorial space more often than non-neighbors when a resident loses its territory (testing the relative threat hypothesis), I examined (1) whether neighbors or non-neighbors were more likely to move into new territorial space after a resident was removed and (2) whether neighbors or non-neighbors were responsible for apparent territorial takeovers observed during pre-manipulation observations (in other words, natural and unmanipulated movement of a lizard into the mean location/activity area center previously occupied by another lizard; see below for explanations of terminology). For the purposes of data analysis, I defined a neighbor as a lizard that (1) had been observed previously within the plot and (2) had been observed to display without being chased or challenged (engaged in an escalated interaction) within 10 m of a focal animal. I defined a non-neighbor as a lizard that had not previously been observed in the plot over the weeks prior to use of a particular plot (all lizards observed in a plot were marked prior to the start of observations in that plot; see above). All observed lizards fit into one of these categories. Therefore, potential non-neighbors under my classification system include both non-territorial floaters that may periodically roam across a resident's territory as well as territorial males from farther away that might be searching for a better territory.

I compared display rates before and after the removal of a resident to examine whether neighbors encounter increased defensive costs when a resident loses its

territory. An increased proportion of headbob displays that are bobbing displays is found in higher-intensity encounters such as fights between individuals that are close together (McMann, 1998, 2000; Paterson, 1999, unpublished data). Therefore, an increase in the proportion of headbob displays that are bobbing displays suggests that they may increase energy expenditure, accompanied by an increased risk of injuries from the associated fighting. Initially, I calculated the proportion of headbob displays that were bobbing displays, which can be used as an indicator of aggression as described above (see also McMann, 2000; Paterson, 1999). I used Wilcoxon paired tests to compare changes in proportion of bobbing displays between observations in the experimental group (comparing the 72 h with a removal and the 72 h without a removal) and between the control and experimental groups (during the 72 h without a removal for each) in each plot. In the same manner, I compared displays by examining the following variables: number of nodding displays, number of bobbing displays, number of dewlap extensions, and number of displays with a clearly visible dorso-nuchal crest (Paterson, 1999; Tokarz, 1995).

To examine which type of conspecific was more likely to engage in escalated interactions with the focal males (reflecting level of relative threat), I examined the proportion of escalated interactions (interactions involving displays in which at least one lizard has a clearly visible dorso-nuchal crest and in which the lizards are less than 2 m apart) between neighbors and non-neighbors (see Paterson, 1999; Tokarz, 1995 for discussions of crests). In addition, I examined which conspecifics took resources by copulations and foraging within the boundary of a resident's territory during control and pre-removal observations. Lizards were considered to be within the boundary of another male's territory if they entered a square of the grid in which the resident male had been sighted and in which the resident had not been challenged or chased.

I examined space use by calculating the activity area center (the mean location of

TABLE 2.—Summary of escalated interactions. Observations are listed as preliminary observations of the experimental group, observations before the removal, and observations after the removal (see Table 1). Lizards are identified by abbreviations for their individual combinations of bead colors (*um represents an unmarked lizard). Note that some dyads interacted more than once.

Date	Plot	Group	Observation	Interacting lizards	Neighbor?
30 April 1997	1	experimental	preliminary	RDWHRD and BDRDRD	yes
3 May 1997	1	experimental	before	RDWHRD and BDRDRD	yes
3 May 1997	1	experimental	before	RDWHRD and BDGRBD	yes
6 May 1997	1	experimental	after	RDWHRD and BDGRBD	yes
15 May 1997	2	control	after	YOBKKB and um*	no
25 May 1997	3	experimental	preliminary	BDBBBD and WHGRBD	yes
27 May 1997	3	control	before	RDRDGR and um*	no
30 May 1997	3	control	after	RDRDWH and GRGRRD	yes
7 July 1997	5	experimental	preliminary	YOYOBK and BDGRBD	yes

each lizard) for each day of observation. These mean locations were used as an alternative to home range calculations for several reasons. First, this short-term behavioral study was intended to measure small-scale, short-term fluctuations in space use rather than to document home ranges. Second, the observations of locations for each lizard were close together, violating the independence of observations that should be used when calculating home ranges. Thirdly, the number of different locations in which each lizard was sighted was relatively low, making estimates of home range size inaccurate. Therefore, I chose the term “activity area center” in order to clarify the fact that I am not attempting to relate my results to the complete home ranges of the lizards, but rather to a specific short-term area of activity that represents part of a home range. Rather than estimate inaccurate home range sizes, I chose to estimate the mean location of a lizard on a given day.

To calculate mean locations, I multiplied (weighted) each location by the time spent at that location. To examine whether neighbors changed their patterns of space use following a resident's removal, I compared neighbors' mean locations before and after the removal. To control for normal variations in space use, I measured the difference in location of activity area centers between the following pairs of observations: (1) observations of the experimental group before and after the removal of one of its members, (2) observations of the experimental group 72 h apart during

which no lizard was removed, and (3) observations of the control group 72 h apart in which no lizard was removed. I then used Wilcoxon tests to determine whether there were differences in the distances moved: (1) in the experimental group over 72 h periods during which a lizard was removed compared with 72 h periods in which no lizard was removed, and (2) in the experimental group over 72 h periods during which a lizard was removed compared with the control group over 72 h in which no lizard was removed. I similarly used Wilcoxon tests to examine whether the activity area centers were closer to, or farther from, the former mean activity area of a focal lizard after the focal lizard had been removed. In this way, I examined whether neighbors may have gained or lost space during the instability caused by the removal of the focal lizard.

RESULTS

When residents were removed, seven of eight were replaced at their activity area center by another lizard within 72 h. Of the seven, four were neighbors (lizards that had displayed previously within 10 m without being challenged) while three were non-neighbors (lizards that had not been observed previously in the plot over the weeks prior to use of a particular plot). In one case, no lizard was visible in the area previously occupied by the removed lizard after 72 h.

Five of seven observed escalated interactions were between immediate neighbors (Table 2; note that a total of nine in-

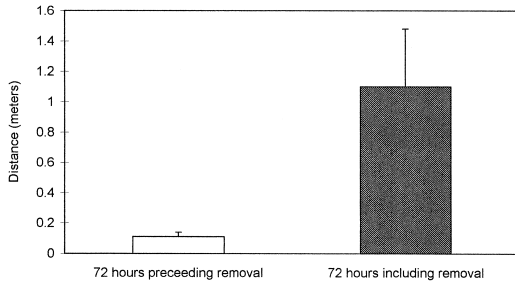


FIG. 2.—The difference (+1 SE) in location of activity area centers over 72-h periods. The activity area center represents the mean location of a lizard within a plot. This figure shows the average amount of change in mean location during 72 h in which no lizard was removed compared with 72 h during which a lizard was removed. There was more change in space use when a lizard was removed, vacating a territory.

teractions were observed but that some pairs of lizards had repeated interactions). At least one neighbor was observed to enter a resident's territory to capture an earthworm, followed by an escalated interaction with the territory owner that led to his return to his own territory (after consuming the earthworm). No non-neighbors were observed to intrude prior to a removal. Additionally, the only natural (pre-manipulation) takeover observed was by a neighboring resident.

A resident's removal did not affect the locations of the activity area centers (the mean location in which lizards were observed) during the 72 h including the removal of a resident in the experimental group compared with the 72 h without a removal in the control. In other words, between the first and second sets of observations, the activity area centers did not move either a greater or smaller distance than did the activity area centers of neighbors of a control male. The mean difference in activity area center in the experimental plots was 0.30 ± 0.11 m, compared with 0.35 ± 0.1 m in the control plots (Wilcoxon paired test, $Z = 1.5$, $P = 0.8438$, $n = 6$), suggesting that lizards were using similar areas on both days.

However, there was a difference in activity area center between different observation days in the experimental plots, suggesting a change in space use. During the

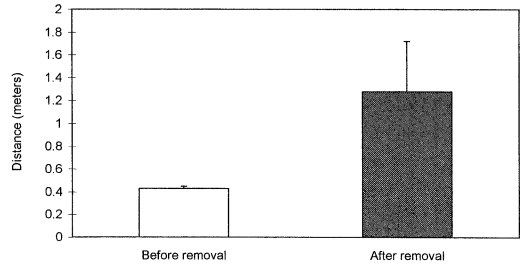


FIG. 3.—The mean distance of activity area centers (+1 SE) of neighbors from the activity area center of the resident that was removed. The activity area center represents the mean location of a lizard within a plot. This figure shows the average difference in location between the neighbors and the mean location of the removed lizard before and after the removal. Lizards tended to be farther from the location of the removed lizard following his removal.

24 h before and 48 h after a resident was removed, activity area centers moved 1.1 ± 0.38 m, compared with 0.11 ± 0.03 m during the previous 72 h (Wilcoxon paired test, $Z = 18$, $P = 0.0078$, $n = 8$; Fig. 2). This test remains significant if a correction for multiple comparisons is used (considering the comparison of experimental and control and the comparison of experimental observations as two tests of the same hypothesis; Bonferroni correction, $P = 0.0156$).

Prior to a removal, the mean activity area center of neighbors was 0.43 ± 0.20 m from the activity area center of the resident that would later be removed. Following the removal, the mean activity area center of neighbors was significantly farther from the former activity area center of the removed resident (1.28 ± 0.44 m; Wilcoxon, $Z = 14$, $P = 0.0156$, $n = 8$; Fig. 3).

Following the removal of a resident, there was no change in the proportion of headbob displays that were bobbing displays (Wilcoxon paired test, $P > 0.05$, $n = 8$). The proportion of headbob displays that were bobbing displays also did not differ between the experimental and control groups (Wilcoxon paired test, $P > 0.05$, $n = 6$). There were no differences in any of the behavioral variables, either between days of observation of the experimental group or between the experimental and control groups (Wilcoxon paired tests, $P >$

0.05 in all cases, $n = 8$). Display, chase, and copulation frequencies are summarized in Tables 3 and 4.

DISCUSSION

I set out to test the predictions that (1) neighbors gain territorial space more often than non-neighbors when a resident loses its territory, and (2) neighbors face increased defensive costs (reflected by display behavior and intrusion frequency) when a resident loses its territory. Neither prediction was clearly supported by the data. However, residents were affected by the removal in several ways.

If neighbors gain territorial space more often than non-neighbors when a resident loses its territory, then the majority of the lizards sighted in the activity area center of the removed resident should have been neighbors. Four of seven times that a lizard was sighted in the activity area center of the resident that had been removed, the lizard sighted was a marked individual that had previously been identified as a neighbor (a lizard that had previously displayed within 10 m without being challenged). The other three times that a lizard occupied the vacated area, the lizard involved was unmarked and therefore had not previously been sighted within the plot (a non-neighbor).

There was no evidence of a change in defensive costs following the removal of a resident. Overall display frequencies did not change. Of particular interest, the proportion of headbob displays that were bobbing displays did not change, suggesting no increase in aggression following the removal. Frequencies of chases and copulations were low, making conclusions difficult, but there was no evidence of a treatment effect.

However, patterns of space use changed following the removal of a resident. Some neighbors took over the center of a vacated territory (they were observed, unchallenged and unchased, in the square of the grid that was the center of the former resident's activity area). However, the mean location of all neighbors was farther from a focal male's territory following his removal, suggesting that neighbors needed

to devote less time and energy to defending that side of their territory.

The above findings have implications for both the relative threat and social stability hypotheses. Both hypotheses attempt to explain why territorial animals often show less aggression towards neighbors than towards non-neighbors (unfamiliar individuals).

Depending upon whether they primarily may take resources, part of a territory, or all of a territory, different classes of individuals pose varying levels of threat to a resident. The relative threat of neighbors versus strangers may play an important role in determining whether the dear enemy phenomenon is observed (the "relative threat hypothesis," Temeles, 1990, 1994). If an individual poses little threat to a resident, then a highly aggressive attack by the resident may have a large cost and little benefit. If an individual poses a great threat, then the cost of not fighting may be high and it may be worthwhile to engage in a costly aggressive interaction (e.g., Emlen, 1971; Weeden and Falls, 1959). The relative threat hypothesis predicts that more aggression is shown towards conspecifics that pose the greatest threat. It is closely related to the social stability hypothesis because the latter predicts that residents should be less aggressive towards neighbors if such behavior reduces the risk of territorial intrusion or takeover.

Neighboring males of *A. sagrei* take territorial space when possible, suggesting that they may pose a threat to residents. At least one neighboring male took food from another's territory, suggesting that neighbors also threaten resources to some extent. These findings are consistent with the findings of Tokarz (1998) that marked male lizards on a single *Ficus* tree (presumably neighbors) may replace each other on territories and that males may court females on neighbors' territories. Although it is unclear whether neighbors posed a greater or equal threat than non-neighbors, there is no evidence to suggest that neighbors posed a lesser threat in either the natural or artificial territorial neighborhoods. The proportion of nonaggressive takeovers by neighbors is similar to

TABLE 3.—Summary of display behavior in the experimental and control groups. Values are presented as mean \pm SE and median. Display definitions are based on McMann (2000).

Behavior	Experimental group observations (<i>n</i> = 8)				Control group (<i>n</i> = 6)	
	Preliminary	Before removal	Day of removal	After removal	Before	After
Nodding displays	17.08 \pm 3.76 17.75	22.54 \pm 7.69 15.33	12.13 \pm 3.18 12.33	17.83 \pm 4.11 18.50	19.96 \pm 2.83 16.5	28.17 \pm 8.61 19.54
Bobbing displays	8.42 \pm 2.77 7.00	7.31 \pm 1.87 6.42	5.65 \pm 1.84 4.00	6.83 \pm 1.13 6.92	12.21 \pm 2.55 11.17	12.39 \pm 3.36 11.17
Dewlap extensions	41.38 \pm 7.88 47.00	50.35 \pm 13.70 45.33	37.79 \pm 9.82 38.25	54.83 \pm 13.14 47.25	66.28 \pm 7.35 65	62.99 \pm 17.21 57.25
Proportion of headbob displays that were nodding displays	0.599 \pm 0.067 0.66	0.59 \pm 0.12 0.76	0.63 \pm 0.14 0.74	0.62 \pm 0.11 0.717	0.60 \pm 0.05 0.62	0.64 \pm 0.052 0.69

TABLE 4.—Summary of display behavior, chases, and copulations in the experimental and control groups. Values are presented as mean \pm SE standard error and median. Display definitions are based on McMann(2000)

Behavior	Experimental group observations (<i>n</i> = 8)				Control group (<i>n</i> = 6)	
	Preliminary	Before removal	Day of removal	After removal	Before	After
Headbob displays with crests	3.13 \pm 1.79 0.00	1.38 \pm 1.17 0.00	0.00 \pm 0.00 0.00	0.73 \pm 0.48 0.00	0.46 \pm 0.46 0.00	2.39 \pm 1.82 0.00
Total chases	0.19 \pm 0.097 0.00	0.042 \pm 0.042 0.00	0.014 \pm 0.014 0.00	0.083 \pm 0.055 0.00	0.13 \pm 0.085 0.00	0.042 \pm 0.042 0.00
Chases of neighbors	0.15 \pm 0.07 0.00	0.042 \pm 0.042 0.00	0.00 \pm 0.00 0.00	0.083 \pm 0.055 0.00	0.00 \pm 0.00 0.00	0.00 \pm 0.00 0.00
Chases of unmarked lizards	0.042 \pm 0.042 0.00	0.00 \pm 0.00 0.00	0.014 \pm 0.014 0.00	0.00 \pm 0.00 0.00	0.13 \pm 0.085 0.00	0.042 \pm 0.042 0.00
Copulations	0.10 \pm 0.07 0.00	0.00 \pm 0.00 0.00	0.00 \pm 0.00 0.00	0.063 \pm 0.063 0.00	0.29 \pm 0.16 0.13	0.056 \pm 0.056 0.00

the proportion of nonaggressive takeovers in song sparrows, in which case neighbors are considered to pose a relatively high level of threat (Stoddard et al., 1991 discussed in Stoddard, 1996). My data show no difference in the risk of non-aggressive territorial takeover posed by neighbors and non-neighbors. Therefore, if territorial takeovers are the most serious threat to a resident, then the relative threat hypothesis predicts no difference in aggression towards neighbors versus non-neighbors in *A. sagrei*.

This study shows that neighbors will take over territorial space when a resident is removed, not that they are capable of taking space when the resident is present. However, it demonstrates the questionable nature of the premise that neighbors pose less of a threat because they already have territories (e.g., Fox and Baird, 1992; Getty, 1987; Temeles, 1994). This is important to take into account when considering the review of Temeles (1994). In Temeles' test of the relative threat hypothesis, the above premise is used to justify the prediction that the dear enemy phenomenon would occur more frequently in multi-purpose territories than in feeding territories (Temeles, 1994). A large-scale study monitoring a substantial marked population over an entire breeding season is needed in order to determine which individuals are responsible for aggressive takeovers and to provide the type of baseline data that have already been gathered in more intensively studied species (e.g., red-winged blackbirds, Beletsky and Orians, 1996; Searcy and Yasukawa, 1995). At least one *A. sagrei* neighbor took resources from another's territory in my study. Additionally, Tokarz (1998) observed that males intrude to court females on neighbors' territories. However, it is important to consider that neighbors might take resources more openly than non-neighbors, which influences these results.

The majority of escalated interactions occurred between immediate neighbors, suggesting that (1) one of the neighbors was posing some kind of threat (e.g., trying to take food or other resources), and (2) more time and energy may be spent fight-

ing neighbors than non-neighbors. In order to determine the importance of the latter, additional work is needed to determine how energetically costly these fights are. However, it is important to remember that more interactions may be between neighbors simply because residents encounter neighbors more frequently than strangers. Therefore, it is not possible to conclude that neighbors pose more of a threat to a resident than non-neighbors.

Additionally, the relative threat hypothesis may explain some differences in aggression without being the primary cause of the dear enemy phenomenon. Aggression has been demonstrated to be related to the immediate level of threat posed by an intruder. For example, the presence of a food item causes more aggression towards intruders by female cicada-killer wasps (Pfennig and Reeve, 1989). In female harriers, relative threat appears to be closely related to the level of aggression shown (Temeles, 1989, 1990, 1994). Aggressiveness has been demonstrated to be related to resource availability, which may affect relative threat (e.g., Armstrong, 1991; Ewald, 1985; Stamps and Tanaka, 1981). Differences in behavior based on context (i.e., at the center versus the edge of a territory) may result from differences in threat (e.g., Giraldeau and Ydenberg, 1987; Stoddard, 1991). In the case of anoles, it is possible that a territorial male would show more aggression towards an intruder if that intruder was near a female lizard than if the intruder was on a bare patch of territory. In this way, there may be some interaction between relative threat and familiarity.

The social stability hypothesis (Beletsky, 1992) suggests that territory owners should show less aggression towards their territorial neighbors than towards other potential challengers because of benefits to maintaining stability in the territorial neighborhood. Instability, reflected by frequent challenges and turnovers of territory ownership, may attract intruders and increase the probability of successful takeovers of territorial space by intruders (Beletsky, 1992; see Paterson, 1999, for a discussion). Therefore, residents may show

less aggression towards neighbors than towards non-neighbors in order to reduce the frequencies of intrusions and territorial takeovers.

It is also unclear whether neighbors gain or lose when social instability arises. There were no differences in display behaviors, chase frequencies, or copulation frequencies in observations before and after a removal. However, following a removal, neighbors moved their mean activity area centers significantly farther from the center of the removed resident's activity area. This finding could mean that neighbors have benefited because they can concentrate territorial defense away from the newly established territorial resident, who may be a weaker competitor. Alternatively, this finding could mean that neighbors have lost territorial space to the new resident. Additional experimental work is needed to distinguish between these possibilities. However, the former hypothesis best explains the results of another experiment, examining the effects of the removal of an established neighbor and his replacement with an unfamiliar individual in an artificial territorial neighborhood. In artificial territorial neighborhoods, neighbors took over territories, taking advantage of the fact that the former neighbor was no longer present to defend it (Paterson, 1999).

There is no evidence that neighbors pose less of a threat than non-neighbors; rather, it appears that neighbors may pose a significant threat to residents. Additionally, there is no evidence that social instability, reflected by relocations of lizards, is detrimental to territory owners. Therefore, additional hypotheses must be examined in order to determine the causes of the "dear enemy" phenomenon in *A. sagrei*.

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LITERATURE CITED

- ARMSTRONG, D. P. 1991. Aggressiveness of breeding territorial honeyeaters corresponds to seasonal changes in nectar availability. *Behavioral Ecology and Sociobiology* 29:103–111.
- BELETSKY, L. D. 1992. Social stability and territory acquisition in birds. *Behaviour* 123:290–313.
- BELETSKY, L. D., AND G. H. ORIANS. 1996. Red-winged Blackbirds: Decision-making and Reproductive Success. University of Chicago Press, Chicago, Illinois, U.S.A.
- EMLEN, S. T. 1971. The role of song in individual recognition in the indigo bunting. *Zeitschrift für Tierpsychologie* 28:241–246.
- EWALD, P. W. 1985. Influence of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. *Animal Behaviour* 33:705–719.
- FISHER, J. 1954. Evolution and bird sociality. Pp. 71–83. *In* J. Huxley, A. C. Hardy, and E. B. Ford (Eds.), *Evolution as a Process*. Allen and Unwin, London, U.K.
- FISHER, M., AND A. MUTH. 1989. A technique for permanently marking lizards. *Herpetological Review* 20:45–46.
- FOX, S. F., AND T. A. BAIRD. 1992. The dear enemy phenomenon in the collared lizard, *Crotaphytus collaris*, with a cautionary note on experimental methodology. *Animal Behaviour* 44:780–782.
- GETTY, T. 1987. Dear enemies and the prisoner's dilemma: why should territorial neighbors form defensive coalitions? *American Zoologist* 27:327–336.
- GIRALDEAU, L.-A., AND R. YDENBERG. 1987. The center-edge effect: the result of a war of attrition between territorial contestants. *Auk* 104:535–537.
- HORVITZ, C. C., S. MCMANN, AND A. FREEDMAN. 1995. Exotics and hurricane damage in three hardwood hammocks in Dade County parks. *Florida Journal of Coastal Research* (SI No. 21) 18:145–158.
- HORVITZ, C. C., J. B. PASCARELLA, S. MCMANN, A. FREEDMAN, AND R. H. HOFSTETTER. 1998. Functional roles of invasive non-indigenous plants in hurricane-affected subtropical hardwood forests. *Ecological Applications* 8:947–974.
- LEE, J. C., D. CLAYTON, S. EISENSTEIN, AND I. PEREZ. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. *Copeia* 1989:930–937.
- LISTER, B. C. 1976. The nature of niche expansion in West Indian *Anolis* lizards I: ecological consequences of reduced competition. *Evolution* 30:659–676.
- MCMANN, S. 1998. Display Behavior and Territoriality in the Lizard *Anolis sagrei*. Ph.D. Dissertation, University of Miami, Coral Gables, Florida, U.S.A.
- . 2000. Effects of residence time on displays during territory establishment in a lizard. *Animal Behaviour* 59:513–522.

- NELSON, D. A. 1998. External validity and experimental design: the sensitive phase for song learning. *Animal Behaviour* 56:487–491.
- PATERSON, A. V. 1999. Relationships in Territorial Neighborhoods: Factors Influencing Interactions in a Lizard, *Anolis sagrei*. Ph.D. Dissertation, University of Miami, Coral Gables, Florida, U.S.A.
- PFENNIG, D. W., AND H. K. REEVE. 1989. Neighbor recognition and context-dependent aggression in a solitary wasp, *Sphecius speciosus* (Hymenoptera: Sphecidae). *Ethology* 80:1–18.
- SCHOENER, T. W., AND A. SCHOENER. 1980. Density, sex ratio, and population structure in some Bahamian *Anolis* lizards. *Journal of Animal Ecology* 49: 19–53.
- . 1982. Intraspecific variation in home range size in some *Anolis* lizards. *Ecology* 63:809–823.
- SEARCY, W. A., AND K. YASUKAWA. 1995. Polygyny and Sexual Selection in Red-winged Blackbirds. Princeton University Press, Princeton, New Jersey, U.S.A.
- SHELD AHL, L. A., AND E. P. MARTINS. 2000. The territorial behavior of the western fence lizard, *Sceloporus occidentalis*. *Herpetologica* 56:469–479.
- SNYDER, J. R., A. HERNDON, AND W. B. ROBERTSON, JR. 1990. South Florida Rockland. Pp. 230–277. In R. L. Myers and J. J. Ewel (Eds.), *Ecosystems of Florida* University of Central Florida Press, Orlando, Florida, U.S.A.
- STAMPS, J. A., AND V. V. KRISHNAN. 1994a. Territory acquisition in lizards: I. First encounters. *Animal Behaviour* 47:1375–1385.
- . 1994b. Territory acquisition in lizards: II. Establishing social and spatial relationships. *Animal Behaviour* 47:1387–1400.
- . 1995. Territory acquisition in lizards: III. Competing for space. *Animal Behaviour* 49:679–693.
- . 1998. Territory acquisition in lizards: IV. Obtaining high status and exclusive home ranges. *Animal Behaviour* 55:461–472.
- STAMPS, J. A., AND S. K. TANAKA. 1981. The relationship between food and social behavior in juvenile lizards (*Anolis aeneus*). *Copeia* 1981:422–434.
- STODDARD, P. K. 1991. Recognition of individual neighbors by song in the song sparrow, a species with song repertoires. *Behavioral Ecology and Sociobiology* 29:211–215.
- STODDARD, P. K. 1996. Vocal recognition of neighbors by territorial passerines. Pp. 356–374. In D. E. Kroodsma and E. H. Miller (Eds.), *Ecology and Evolution of Acoustic Communication in Birds*. Comstock Publishing Associates, Ithaca, New York, U.S.A.
- TEMELES, E. J. 1989. The effect of prey consumption on territorial defense by harriers: differential responses to neighbors versus floaters. *Behavioral Ecology and Sociobiology* 24:239–243.
- . 1990. Northern harriers on feeding territories respond more aggressively to neighbors than to floaters. *Behavioral Ecology and Sociobiology* 26:57–63.
- . 1994. The role of neighbours in territorial systems: when are they “dear enemies”? *Animal Behaviour* 47:339–350.
- TOKARZ, R. R. 1998. Mating pattern in the lizard *Anolis sagrei*: implications for mate choice and sperm competition. *Herpetologica* 54(3):388–394.
- . 1995. The importance of androgens in male territorial acquisition in the lizard *Anolis sagrei*. *Animal Behaviour* 49:661–669.
- TOKARZ, R. R., S. MCMANN, L. SEITZ, AND H. JOHNALDER. 1998. Plasma corticosterone and testosterone levels during the annual reproductive cycle of male brown anoles (*Anolis sagrei*). *Physiological Zoology* 71:139–146.
- WEEDEN, J. S., AND J. B. FALLS. 1959. Differential response of male ovenbirds to recorded songs of neighboring and more distant individuals. *Auk* 76: 343–351.

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