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Influence of Age and Prior Experience on Territorial Behavior and the Costs of Defense in Male Collared Lizards

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Abstract

In polygynous species where males maintain strong interseasonal philopatry to the same breeding territories, older individuals have prior experience defending their areas, whereas younger individuals are defending a territory for the first time. Theoretical and empirical studies predict that under such conditions the cumulative costs of defense may be lower for older experienced males as a consequence of familiarity with environmental and/or social conditions in their particular local habitats. We used quantitative data from focal observational studies and introduction experiments to test the hypothesis that older collared lizard males (*Crotaphytus collaris*) with prior territorial experience (3 yr+ males) acquire larger territories allowing them to court more, different females, with greater frequency without incurring higher defense costs. Consistent with this hypothesis, 3 yr+ males controlled significantly larger territories and courted more females, without having significantly higher rates of territory patrol, frequencies of advertisement display, or aggressive interactions with same-sex competitors. Moreover, the intensity of responses to size- and age/experience-matched tethered intruders by 3 yr+ males was lower than that by 2 yr males in their first season of territory defense. Our results support the hypothesis that age/prior occupancy of territories lowers defense costs allowing males to defend larger areas and increase opportunities to court females, perhaps increasing mating opportunities. By contrast, 2 yr males may need to respond more aggressively to intruders because their ownership of territories is tenuous as a consequence of shorter territory occupancy.

Introduction

Territory defense evolves when the benefits of maintaining exclusive access to areas containing one or more resources essential for survival and reproduction exceed the costs of excluding competitors (Brown 1964; Brown & Orians 1970; Emlen & Oring 1977; Davies & Houston 1984; Stamps 1994). Defense costs may include the time and energy expended in aggressive contests and displays (Marler & Moore 1988, 1989; Vehrencamp et al. 1989; Marler et al. 1995; Hack 1997) especially when asymmetries in the physical attributes of competitors are small (Parker 1974; Leimar & Enquist 1984). Territorial defense may also increase mortality as a consequence of high energetic costs (Marler & Moore 1988; Dufty 1989) or increased predation risk (Tuttle & Ryan 1981; Ryan et al. 1982; Bradbury et al. 1989; Whitehouse 1997a; Lange & Leimar 2001). Lastly, defense of territories may interfere with opportunities to court and mate with females (Clutton-Brock et al. 1979: Baird et al. 2001).

Because territorial defense is costly, it is reasonable to hypothesize that natural selection may act on the behavior of defenders in ways that reduce costs and hence increase the net benefit of spatial defense. Territory owners sometimes reduce defense costs by decreasing aggression towards familiar occupants of neighboring territories (dear-enemy phenomenon; Jaeger 1981; Krebs 1982; Ydenberg et al. 1988; Fox & Baird 1992; Temeles 1994; Husak & Fox 2003), and by utilizing displays that are 'honest signals' of resource holding power but are less costly than overt aggression (Whiting et al. 2003; Husak 2004). Males defending breeding territories may maximize advertisement to same-sex competitors when these behaviors detract the least from courtship of females (Baird et al. 2001). Familiarity with specific territory attributes (e.g. local terrain; Baugh & Forester 1994) acquired through prior occupancy may promote effective detection and defense against intruders (Alcock & Bailey 1997; Eason et al. 1999; Sloan & Baird 1999). Experienced males may also be more successful in agonistic contests with same sex competitors and have greater access to females because they have prior knowledge of the locations and phenotypic qualities of both (Waser & Wiley 1980; Austad 1983; Holberton et al. 1990; Kim & Zuk 2000).

Economic approaches have proven useful for modeling the conditions under which defense of space is adaptive (Brown 1964; Davies & Houston 1984). Because reproductive success of males is often limited by access to females (Trivers 1972), males are predicted to maximize the size of defended areas to exclude same-sex competitors from the home ranges of numerous females (Davies 1991; Zamudio & Sinervo 2003). These models generally predict that both the cumulative benefits and costs of territory defense increase as some function (linear or curvilinear) of increasing territory area (Davies & Houston 1984; Hixon 1987). Territories of a given size are expected to be economically defensible at axial coordinates where the elevation of the cumulative benefit curve exceeds the curve describing the cumulative defense costs (Fig. 1). If there is an upper limit on the capacity of individuals to exploit the defended resources (e.g. food), then the benefit curve should asymptote (Brown 1964; Davies & Houston 1984). However, assuming that the number of females that males can mate with is not limited, the benefit curve for breeding territories should continue to increase to the extent that males are able to expand to overlap additional female home ranges.

The shapes of cumulative defense cost curves will be influenced by any factor(s) that alter the costs of excluding competitors vying for the defended resource(s). Under the hypothesis that prior experience defending the same territory reduces one or more costs, the elevation and/or slope of the curve for older experienced males is expected to be lower than that for younger males lacking prior experience (Fig. 1). Older males, therefore are predicted to acquire larger territories without increasing the defensive behavior patterns that are costly (aggression and display). Conversely, some studies predict that the likelihood of winning contests increases as a function of the tenure of territory occupancy (e.g. Hatchwell & Davies 1992; Dale & Slagsvold 1995). If selection acts on experienced males to reduce defense costs, displays have evolved as honest signals of resource holding power, and/or RHP increases with territory tenure, then when confronted by intruders these males are expected to adopt less costly defensive tactics such as lower-intensity displays. By contrast, males defending a territory for the first time should use higher intensity aggressive tactics (Switzer et al. 2001; Husak & Fox 2003). We test these predictions in male collared lizards (*Crotaphytus collaris*), by determining the size of male territories, and rates of advertisement displays and aggression in relation to age and prior territorial experience. We also staged intrusions by size- and age-matched competitors to compare the defensive tactics of older, more experienced and younger, less experienced territory owners.

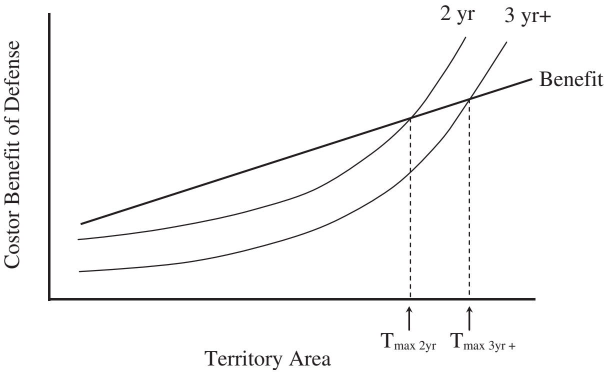

Fig. 1: Hypothesized relationship between benefits and costs and territory area for males with and without prior experience defending their territories

Methods

Study Site, Species, and General Methods

We conducted this study from April 15 to July 10 1992; and 1997–2003 at the Arcadia Lake Dam (AL) located 9.6 km east of Edmond, Oklahoma on State Highway 66. At AL, collared lizards occur on three separate patches of granite boulders used to construct flood-control channels (boulder patch area = 1505–19, 850 m^2). Boulder patches are separated from one another by 50–260 m of open grass not inhabited by these lizards (Baird et al. 1996; Baird & Timanus 1998; Baird et al. 2001).

We captured lizards by noose, marked them permanently by clipping the terminal phalange of three digits in unique combinations, and for identification from a distance by applying spots of acrylic paint to the dorsum. Lizards were released at the precise capture location within 10-min to minimize any influence of handling on social conditions. At each capture, we recorded snout-vent length (SVL), tail length (both ± 1.0 mm), and total body mass (±1.0 g). We know the ages of all of the males used in this study from mark-recapture of hatchlings since 1990 (Baird et al. 1996, 2003). Study areas were marked with grids of reference points (10 m apart) mapped to the nearest meter using GPS equipment of the U.S.A.F (Baird & Timanus 1998; Baird et al. 2001).

Male collared lizards at AL are good subjects in which to examine the influence of age and prior experience on costs of territorial defense because previous studies have documented the size-age structure and ontogeny of social behavior of both males and females (Baird et al. 1996; Baird & Timanus 1998; Baird & Sloan 2003; Baird et al. 2003). Although they become reproductively mature during their first activity season, males usually do not acquire a territory until their second season (Baird & Timanus 1998). There is very strong between-season stability in the locations of territories defended by males. Males spend the winter burrowed near to their defended areas rather than dispersing (Baird 1999), and they hold all of the same territory (or more) until they die (Baird et al. 2001, 2003). Because 40–50% of territorial males die each winter, at the beginning of the next season (April) there are openings for 2-yr-old males to acquire their first territories. Therefore, each season surviving males that have held the same territories throughout one or more previous seasons (hereafter, 3 yr+ males) and males that are competing to establish and maintain their first territories (2 yr males) co-occur throughout the study site (Baird et al. 2001). Because males almost always acquire a territory for the first time as 2-yr olds, age and prior experience in territory occupancy co-vary, and age cannot be controlled like in studies of captive animals (e.g. Groothuis & Van Mulekom 1991; Fleming et al. 1997).

Male Social and Spatial Behavior

We examined the influence of variation in age/prior occupancy on the costs and benefits of territory defense by recording focal observations (*sensu* Altmann 1974) on males of known age and social history. Focal observations involved tracing the travel path and recording all social behavior initiated by males (described below) for 20 min periods on scale-drawn maps (Baird et al. 1996, 2001). We recorded 15 focal observations per male for a total observation time of 300 min on each individual. Because the behavior of *C. collaris* males varies seasonally, for all males (1992, 1997–2000) we recorded five focal observations during May when male activity is increasing, and five focal observations during both the first, and second 2-wk of June when male activity is highest (Baird et al. 2001). We recorded only one focal observation on any given male on any given day, and males were observed in random order from 09:00 to 14:00 h when substrate temperature was optimum (30–38°C) for *C. collaris* (Baird et al. 1996, 2001). We recorded focal observations on all territorial males that were present in all years. To avoid pseudoreplication, we only included data for each male from one season (chosen randomly) in statistical analyses. All of the 2 yr males ($n = 42$) were in their second activity season and were defending a territory for the first time. Of the 24 older, more experienced males, 20 were 3 yr old and in their second season of defending the same territories. The remaining older males were in their fourth seasons of territory defense (5-yr old). We did not compare the behavior of males with 2 and 3 yrs of previous territory occupancy because male survival to a third season is relatively rare (average male life span = 2.7 yr, T.A. Baird, unpubl. data).

Male collared lizards at AL exhibit social behavior in two distinct contexts; when they are displaying distantly from conspecifics, and when they engage in proximate social encounters with a conspecific of either sex (behavior patterns described in Baird et al. 1996, 2001, 2003). Distant displays were head bobs, pushups, and lateral compression and elevation of the torso with the dewlap extended when focal males were >5 m from conspecifics. Male–male encounters were defined as focal males approaching to within 1 m of another male while initiating one or more of these displays (listed above), chases, and sometimes attacks including bites on the head and torso of opponents (Baird et al. 1996, 2001, 2003). We also recorded the frequency of courtship encounters and the number of different females courted. Courtship encounters involved focal males closing to within one body length of a female, the mutual exchange of displays, either or both lizard making physical contact with their partner including nudging with snout, superimposition of the torso, limbs and tail, turning circles while maintaining contact, and males grasping females by the neck and mounting them dorsally (behavior patterns described in Baird et al. 1996, 2001, 2003; Baird 2004).

To quantify the social behavior of each 2 and 3 yr+ male, we calculated hourly frequencies of distant displays, proximate encounters with other males, and courtship encounters with females (separately), by dividing the total number of each type of event tallied during 15, 20 min focal observations by the total observation time (5 h) for that focal male. We determined rates of territory patrol for each male by measuring (using a Planix 5000 planimeter; Sokkia Corporation, Overland Park, USA) the total distance traveled during 15 focals, by the total observation time for that male (5 h). For each of these variables, the cumulative data for each male were the independent replicate data points used for statistical analyses (see following paragraphs).

We prepared maps of territories using the minimum convex polygon method (Turner et al. 1969; Rose 1982; Worton 1987). We constructed territory maps based on census sightings together with the beginning and the ending points of focal observations, except for rare focals when males did not travel, in which case we only recorded that single location (Stone & Baird 2002). In all males and years, the number of sightings used to map territories (60–65) equaled or exceeded the minimum number ($n = 60$) required in this population for territory area to asymptote when graphed against the number of sightings (Stone & Baird 2002). Territory area was measured using a digital planimeter (Planix 5000).

We pooled social and spatial variables on males from different years because ANOVA revealed no differences among years for all variables ($p = 0.13$–0.61). We examined the possible effects of body size (SVL) on male behavior using least-squares regression of male SVL on all social and spatial variables. We used t-tests to examine the influence of male age/experience level (2 yr vs. 3 yr+) on all dependent variables derived from focal observations and censuses (separate tests for: patrol rate, frequencies of distant displays, male–male and courtship proximate encounters, the number of different females courted), which all met the assumptions for parametric tests. We used one-tailed probabilities for comparison of these variables in 2 and 3 yr+ males because the hypothesis that age/prior experience lowers defense costs predicts that 3 yr+ males should defend larger territories that promote increased courtship opportunities, without higher frequencies of patrol, display, and encounters with other males. Because we used the same set of focal/census observations to determine these variables, we applied the sequential Bonferroni technique (Rice 1989) for related tests.

Intrusion Experiments

To test the hypothesis that 3 yr+ males exhibit less costly, lower intensity responses to males intruding onto their territories, we experimentally introduced an intruder to 2 yr males ($n = 22$) and 3 yr+ males ($n = 12$) during 1999–2003 (n; 1999 = 12; 2000 = 7; 2001 = 11; 2002 = 2; 2003 = 2). We conducted intrusion experiments from 10 to 29 May for both groups of males early in the season to minimize the potential for 2 yr males to acquire experience during naturally occurring agonistic contests, which occur only infrequently early in the season (Baird et al. 2001). Because both differences in body size and age may influence the outcome of male contests (Baird et al. 1997), we matched intruders with territory defenders for age/experience level and size (mean SVL disparity between territory defenders and intruders = 2.7 mm ± 0.32) and the SVL disparity between defenders and intruders was not different ($z_{1,33} = 0.184$, $p = 0.854$) for 2 yr and 3 yr+ male defenders. Because familiarity with neighbors influences defensive responses in *C. collaris* and other lizards (Fox & Baird 1992; Lopéz & Martín 2002; Husak & Fox 2003), we did not pair neighboring individuals that likely had previous social experience. Each male was used once as an intruder and once as a defender, and the order that males were run as each was randomized.

We recorded a 10 min focal observation on each defender prior to intrusions for comparison with their behavior during intrusions. In order to minimize the extent to which behavior by intruders influenced responses by residents, we tethered intruders around the waist on a short (10 cm) monofilament loop attached to the tip of 3-m long pole. When defenders were near the centers of their territories, intruders were placed 5 m away by laying the pole down on a flat rock chosen because it allowed an unobstructed view by the defender. The observer then retreated at least 15 m and recorded on audiotape all social behavior initiated by the defender male for 10 min while observing through binoculars. We tallied all approaches and displays (lateral compression of the torso with dewlap extension, pushups) initiated by defenders, noting the time at which defenders first responded (latency to first response). Responses sometimes involved fights where defenders approached intruders to within one body length, lunged towards and bit intruders (Husak & Fox 2003). None of the 10-min trials involved such intense aggression that it was necessary to stop the trials prematurely. Following trials, the introduced males were returned to their territories, and both introduced and defender males survived in good health for at least the duration of that activity season (throughout July).

To test whether responses by 2 yr males were more intense than those by 3 yr+ males, we calculated the ratio of displays to bites. Because intrusion experiment data did not meet the assumptions necessary for parametric tests despite transformation, we used Mann–Whitney U-tests (Bonferroni corrected, Rice 1989) to compare each of these response variables in 2 yr and 3 yr+ male territory residents. We also determined a categorical aggressive score for each trial using criteria developed for *C. collaris* (Fox & Baird 1992; Husak & Fox 2003), as follows: fight then display = 5, display then fight = 4, display but no fight = 3, display then flee = 2, no response = 1, flee = 0. We used a contingency chi-square to test if the categorical aggressive score was higher in 2 yr males. We used 1-tailed probabilities in these analyses because the hypothesis predicts more intense responses by 2 yr males. We also examined correlations between displays and bites in our two classes of males to the test the hypothesis that in male collared lizards, display functions as an honest signal of motivation to attack (Husak 2004).

Results

Male Social and Spatial Behavior

Consistent with our cost-benefit model (Fig. 1), regression analyses revealed that advertisement behaviors that carry costs were both positively correlated (displays/h, $t_{1,65} = 1.96$, $p = 0.055$; rate of patrol, $t_{1,65} = 4.30$, $p < 0.0001$) with male territory area, as were both estimates of male access to females (courtship encounters/h, $t_{1,65} = 3.34$, $p = 0.001$, number of females courted, $t_{1,64} = 4.09$, $p = 0.001$). Although 3 yr+ males were larger ($\bar{x}$ SVLmm ± 1.0 SE = 110.6mm ± 0.75, $t_{1,65} = 3.14$, $p = 0.025$) than 2 yr–males ($\bar{x}$ SVLmm ± 1.0 SE = 107.5 ± 0.63), none of the social and behavioral variables that we recorded during focal observations were correlated with male SVL ($t_{1,65} = -0.668$–1.82, $p = 0.0739$–0.501).

The average territory area of 3 yr+ males was 1.4 times larger ($t_{1,65} = 2.86$, $p_{1\text{-tailed}} = 0.003$) than that of 2 yr males (Table 1). By contrast, the hourly frequencies of display ($t_{1,65} = 0.74$, $p_{1\text{-tailed}} = 0.231$), male–male encounters initiated ($t_{1,65} = 1.08$, $p_{1\text{-tailed}} = 0.141$) and rate of patrol ($t_{1,65} = 1.32$, $p_{1\text{-tailed}} = 0.096$) were not statistically higher in 3 yr+ males than in 2 yr males (Table 1). Three year and older males courted more different females (i.e. different individuals; $t_{1,64} = 3.13$, $p_{1\text{-tailed}} = 0.0013$) than 2 yr males, and initiated courtship encounters more frequently ($t_{1,65} = 2.21$, $p_{1\text{-tailed}} = 0.0153$) although the latter result was no longer statistically significant (after sequential Bonferroni adjustment] (Table 1).

Table 1: Social and spatial behavior ($\bar{x} \pm 1.0$SE) in 2 yr and 3 yr+ males

Behavioral variable	2 yr males	3 yr+ males
Male–male encounters/h	0.25 (0.05)	0.34 (0.07)
Courtship encounters/h	1.60 (0.16)	2.11 (0.18)
No. different females courted	3.1 (0.2) *	4.4 (0.4)
Territory area (m^2)	1198.6 (97)*	1716.2 (168.9)
Patrol (m/h)	68.5 (4.2)	77.8 (5.7)
Displays/h	93.0 (4.1)	101.0 (7.6)

*Statistically higher ($p < 0.05$, see text) values in 3 yr+ males.

Intrusion Experiments

Defender males responded to intruders in 31 of 34 (91.1%) of trials as exemplified by defenders displaying 2.1 times more frequently ($z_{1,33} = 4.24$, $p < 0.0001$). Although 3 yr+ male territory defenders were larger ($\bar{x}$ SVL ± 1.0 SE = 110.8 mm ± 1.03, $z_{1,33} = 2.27$, $p = 0.023$) than 2-yr male defenders (107.1 ± 0.84), there were no significant correlations between male SVL and the dependent variables that we measured during intrusion experiments (Spearman Rank Correlations, $z = -1.16$–1.18, $p = 0.23$–0.59), or between the disparity in intruder and defender SVL's and any of the response variables ($z = -1.24$–0.43, $p = 0.22$–0.79). The frequency of displays and overt physical aggression (bites) were not correlated in 2 yr ($z_{1,21} = 0.07$, $p = 0.94$), or 3 yr+ males ($z_{1,11} = 1.46$, $p = 0.14$), or when the two male classes were pooled ($z_{1,33} = 0.62$, $p = 0.54$).

Neither latency to first response ($z_{1,33} = 0.595$, $p = 0.28$) nor the number of displays per trial ($z_{1,33} = 0.018$, $p = 0.49$) were higher in 2 yr males (Table 2). By contrast, 2 yr males bit intruders 4.6 times more frequently ($z_{1,33} = 2.95$, $p = 0.002$) than did 3 yr+ males, whereas the ratio of displays to bites was nearly two times higher ($z_{1,33} = 3.06$, $p = 0.001$) in 3 yr+ males (Table 2). In 21 of 22 (95.5%) trials, 2 yr males bit intruders at some point during contests, whereas 3 yr+ males bit intruders in nine of 12 (75.0%) trials. Two-year males had higher aggressive scores ($\chi^2_{1,33} = 6.09$, $p = 0.024$) giving the most aggressive response (= 5.0, biting before any other behavior) in six of the 22 trials (27.3%; Table 2). By contrast, in trials when

Table 2: Social behavior ($\bar{x} \pm 1.0$SE) by 2 yr and 3 yr+ males in response to introduction of tethered intruders

Behavior pattern	2 yr males	3 yr+ males
Latency to first response	91.5 (26.7)	114.8 (35.4)
Displays/10-min trial	38.0 (4.0)	37.0 (5.8)
Bites	15.3 (3.2)*	3.3 (0.9)
Displays/bites	7.4 (3.2)*	13.7 (3.9)
Aggressive score	4.2 (0.1)*	3.8 (0.1)

*Statistically significant differences ($p < 0.05$, see text) between male age classes.

3 yr+ males bit intruders, they always displayed prior to biting (aggressive score < 5.0).

Discussion

Results of focal observations support the hypothesis that prior experience occupying the same areas allows collared lizard males to acquire larger territories without significantly increasing activities that carry energetic and temporal costs (distant display, patrol), and without increasing the frequency of aggressive encounters with same-sex competitors that require energy and time as well as increase risk of injury (Marler & Moore 1988, 1989; Marler et al. 1995). When contest outcome is influenced by body size like it is in *C. collaris* (Baird et al. 1997), the intensity of aggression is expected to be highest during contests between similarly sized opponents (Sigurjonsdottir & Parker 1981; Yasukawa & Bick 1983; Robinson 1985; Ruby & Baird 1993; Lopéz & Martín 2001). Therefore, the diminished intensity responses to closely size-matched intruders by 3 yr+ males in our study strongly supports the hypothesis that older, more experienced collared lizard males adopt less costly defensive tactics.

Because male age and prior occupancy of territories co-vary in our population, we cannot unequivocally separate whether observed differences between 2 yr and 3 yr+ males are a consequence of age or previous experience. Optimal reproductive effort may increase as a function of age (e.g. Forslund & Pärt 1995; Fleming et al. 1997). Therefore, acquisition of larger territories and increased frequency of courtship with more females might be a consequence of increased reproductive effort. However, the fact that 3 yr+ males held larger territories without investing significantly more effort in patrol, displays, and aggression suggests that they learn through experience to increase the efficacy of territory defense and increase opportunities to court females without increasing costs.

Numerous other studies have shown that experience in social encounters may alter agonistic behavior patterns (e.g. Kodric-Brown 1995; Whitehouse 1997b; Johnsson & Ackerman 1998; Kim & Zuk 2000). Similar to our results, studies on fishes, birds, and other lizards have shown behavioral modifications by experienced individuals that likely reduce defense costs. Dominant male swordtail fish that had experienced long-term stable social groups reacted less aggressively to intruders than did inexperienced subordinates, and experienced males mediated their aggressiveness depending upon the behavior of opponents (Franck & Ribowski 1987, 1989). Experienced Atlantic salmon males spent less time in aggression, which allowed them to monopolize more spawnings (Fleming et al. 1997). Similar to male collared lizards, as they became experienced male black-headed gulls changed from using more costly overt aggression to lower cost displays (Groothuis & Van Mulekom 1991). In other lizards, both the intensity and duration of contests decreased as males gained experience during repetitive interactions with the same opponents (Olsson 1994; Lopéz & Martín 2001).

Our results add to several previous findings indicating that the behavior of collared lizard males has been selected to reduce cumulative defense costs. Male collared lizards respond less aggressively to familiar same-sex intruders (Fox & Baird 1992), and appear to recognize their neighbors and gauge the intensity of responses depending upon whether neighbors intrude from familiar or unfamiliar shared boundaries (Husak & Fox 2003). Finally, strong inter-season fidelity to the same areas allows experienced males to secure ownership of the territories that they occupied during previous seasons without high rates of aggression and display early in the season when it would interfere with their ability to court potential female mates (Baird et al. 2001). In this previous study, males with prior experience did not have larger territories, whereas, the present larger present data set revealed strong differences in territory area based on age/experience level. This discrepancy is probably a consequence of smaller sample size and relatively few observations recorded early in the season by Baird et al. (2001).

Reducing the long-term costs of territory defense may have important implications for male lifetime reproductive success. Although males at AL sometimes survive to defend the same territories for as long as 5 yr, average male lifespan is 2.7 yr, and 40–50% of territory owners die each winter (T.A. Baird, unpubl data). Therefore, if reducing defense costs allows males to store energy and emerge in robust enough condition to defend their territory for another season, they would substantially increase their lifetime reproductive success. Reduced intensity responses to intruders and expansion of territories by experienced males are consistent with the reduced energy expenditure hypothesis. Because 3 yr+ males courted more females (different individuals), and tended to have higher frequencies of courtship, an important advantage of fidelity to the same site over successive seasons and expanding the size of territories appears to be increased opportunities to court (and presumably mate with) females. Increased mating success should be especially advantageous if 3 yr+ males achieve it without higher defense costs, as our data indicate.

Based on positive correlations between the frequency of displays and aggression during introduction trials, Husak (2004) proposed that display postures that accentuate body size in *C. collaris* signal fighting ability, stamina and motivation. If this hypothesis is correct, then in our introduction trials, higher ratios of displays to bites and lower aggressive scores (more reliant on displays) by 3 yr+ males might also suggest that displays are effective signals of resource holding power (Husak 2004) that carry lower cumulative costs. Inconsistent with this hypothesis, however, frequencies of displays and bites were not correlated in our introduction trials. In addition, in Husak's (2004) study, frequencies of display were negatively correlated with male SVL in two of three treatment groups, and frequency of aggression was negatively correlated with SVL in one of the three treatment groups. Because SVL increases with age, such correlations with body size suggest that age and/or experience level may have also influenced the behavior of males in the latter study.

Why might it be advantageous for 2 yr males to exhibit higher intensity responses to intruders? Indeed, this result is opposite those of some empirical studies that have revealed a positive relationship between the intensity of aggression and length of territory occupancy because the likelihood of winning encounters, and therefore, the pay-off of aggression is higher for long-term residents (e.g. Hatchwell & Davies 1992; Dale & Slagsvold 1995). For male collared lizards, the 'pay-off' is opportunities to court females. Non-territorial first year males court females only infrequently and females often reject their mating efforts by fleeing (Baird et al. 1996; Baird & Timanus 1998). Therefore, successful acquisition and defense of a breeding territory as 2 yr olds and the correlated increased opportunity to court receptive females (Baird et al. 1996, 2003) may yield the pay-off of substantially increased mating success. As a consequence of their relative inexperience, ownership of territories by 2 yr males may be more tenuous than that of 3 yr+ males. Therefore, if 2 yr males have a higher risk of being displaced from territories unless they respond aggressively to challengers, reproductive success would be severely diminished, especially if they died prior to the next reproductive season. Theory predicts escalated contests when the pay-off for winning is large relative to the potential costs (Maynard-Smith & Parker 1976). Because 2 yr males do not yet have a history of highly successful reproduction, the consequences of losing mating opportunities to intruders is probably very high relative to the costs involved in confrontations, perhaps selecting for intense aggression when 2 yr males are challenged.

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