



Assessment in contests of male lizards (*Anolis carolinensis*): how should smaller males respond when size matters?

THOMAS A. JENSSEN*, KRISTI R. DECOURCY* & JUSTIN D. CONGDON†

*Department of Biology, Virginia Polytechnic Institute and State University

†Savannah River Ecology Laboratory, University of Georgia

(Received 16 May 2003; initial acceptance 21 September 2003;
final acceptance 27 July 2004; published online 7 April 2005; MS. number: A9612R2)

Within a female-defence polygynous mating system, males of the lizard *A. carolinensis* use an array of stereotyped signals and aggressive tactics to acquire and defend long-term territories containing multiple, sedentary females. In competition, body size appears to be important because size of free-ranging males correlates positively with volume of male territories and number of patrolled females. Therefore, an ability to assess body size during territorial contests should be an adaptive attribute that would influence the tactics of intermale aggression. To examine this premise, we staged contests between 10 pairs of males matched for size (i.e. symmetric contests) and 10 pairs mismatched for size (i.e. asymmetric contests), while all 20 pairs of males were matched for habitat resources, a mate, and resident status. Overall, we found (1) contest profiles best fit the features of a 'fixed-phase, sequential assessment' model of game theory, (2) body size and mass were highly correlated with contest outcome, (3) none of 12 signal variables predicted contest outcome, and (4) paired males generally matched aggressive tactics and signalling behaviours. We also examined the asymmetric contest profiles for deviations from the profiles of symmetric contests. We tested the proposition that smaller males of size-mismatched contests would assess their disadvantage and choose a bluff strategy to mitigate risky behaviour and avoid fighting. We found, however, that the risk-mitigation hypotheses were unsupported. Smaller males were not playing a bluff strategy, but rather a hawk strategy. They initiated risky tactics by (1) invading the habitats of their larger opponents, an act that invited retaliation, (2) showing no tendency to stay away from larger opponents, (3) maintaining high levels of aggressive signalling as encounters intensified, and (4) engaging larger opponents in physical fighting, despite losing 90% of their encounters. These empirical results support a recent game theoretical construct ('Napoleon complex') that models size-asymmetric contests in which smaller males initiate fights that they usually lose. Our data suggest that, if smaller males of *A. carolinensis* have breeding territories, then they will engage in costly contests, despite a low probability of defeating larger and equally motivated opponents.

© 2005 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Although intermale conflict over resources and mates is a conspicuous component of most mating systems (Huntingford & Turner 1987), this aggression is particularly intense in polygynous species where males compete directly for immediate access to multiple females, such as in female-defence polygyny (Emlen & Oring 1977). Male reproductive success is highly variable in female-defence polygynous mating systems because it is

dependent on the outcome of intermale contests, which, in turn, result in few males with high success and many males with little or no success (Andersson 1994). Consequently, the study of species with conspicuous male-controlled polygyny can provide insight into the tactics of conflict resolution, including the dynamics of signalling behaviour, within highly contended social encounters.

The green anole, *Anolis carolinensis*, is an excellent species with which to examine the role and pattern of aggressive signalling within intense intermale contests for three reasons. First, field studies have documented *A. carolinensis* as an intrasexually selected, sexually size dimorphic species that practices female-defence polygyny (Ruby 1984; Jenssen et al. 1995a, b, 2001; Nunez et al.

Correspondence: T. A. Jenssen, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, U.S.A. (email: tjenssen@vt.edu). K. R. DeCourcy is now at the Fralin Biotechnology Center, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, U.S.A. J. D. Congdon is at the Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29801, U.S.A.

1997; Jenssen & Nunez 1998). Second, the repertoire of *A. carolinensis* signals has been described for both sexes, including the temporal structure, ontogeny, interpopulation variance, and social use for the species' three headbob display patterns (DeCourcy & Jenssen 1994; Lovern et al. 1999; Jenssen et al. 2000; Lovern & Jenssen 2003; Orrell & Jenssen 2003). Third, the distribution of reproductive females in space and time sets the conditions for strong intrasexual selection. Because females establish small, overlapping home ranges (Nunez et al. 1997) in early spring before either sex is reproductive (Jenssen et al. 1996, 2001) and continuously lay single-egg clutches at about weekly intervals throughout the ensuing 4-month breeding season (Licht 1973; Andrews 1985; Michaud 1990), males can use intermale aggression to directly acquire and defend long-term polygynous breeding territories. In this intrasexually selected system, male body size is positively correlated with male territory size, number of patrolled females, and potential reproductive rate (Ruby 1984; Jenssen & Nunez 1998). Large competitive males control access to an average of three resident females (Ruby 1984; Jenssen et al. 1995a; Jenssen & Nunez 1998) by attempting to exclude the remaining two-thirds of adult males who, at least through territorial tactics, have access to few or no females.

We make use of the 'big male' advantage in the *A. carolinensis* mating system to explore signal function and cues to the outcome of contests by assuming that opponents are aware of, and act on, size asymmetries. Because field data consistently relate large males with the acquisition and maintenance of polygynous breeding territories (see references above), males should be selected to assess the size of an opponent relative to themselves and respond accordingly to the probability of winning a contest. Through assessment, a smaller male has the opportunity to choose tactics that would minimize the risk of injury from dangerous fighting with a larger opponent (e.g. superior biting force of a larger foe; Meyer et al. 2002; Lailvaux et al. 2004). Given the evidence for cognition in *A. carolinensis* (e.g. individual recognition; Qualls & Jaeger 1991; Orrell & Jenssen 2002), selection for assessment of opponent body size is quite likely in the contest-oriented polygyny of *A. carolinensis*.

We guided our analysis of conflict resolution with predictions from game theory in which players of a game assess relative asymmetries, such as size, that are important to the outcome of contests (e.g. Hammerstein 1981; Parker & Rubenstein 1981; Maynard Smith 1982; reviews of Johnstone 1998; Riechert 1998). We gave particular emphasis to predictions from sequential assessment games that featured fixed-phase contests, phase-dependent signalling, and dangerous fighting (e.g. Enquist & Leimar 1983, 1987, 1990; Enquist et al. 1990) because these characteristics are found in the intermale contests of *A. carolinensis* (DeCourcy & Jenssen 1994). In formulating our assessment-based hypotheses, we made four assumptions. First, as conditions for game theoretical models (e.g. Ross 2003), players of games are assumed to be 'economically rational' in that they can (1) assess outcomes, (2) consider alternative outcomes, and (3) choose actions that yield the most preferred outcome given the actions of the

other players. Second, when evenly matched (i.e. symmetric contests) for factors correlated with contest outcome, opponents have difficulty making an assessment, leading to (1) longer contests, (2) signal matching within a phase, (3) progressively more intense signals and signal frequency with subsequent phases, and (4) frequent escalated fighting (e.g. Enquist & Leimar 1983; Enquist et al. 1990). Third, when unevenly matched (i.e. asymmetric contests) for factors correlated with contest outcome, opponents easily make an assessment, leading to (1) shorter contests, (2) signal frequencies that may diverge within later phases between the ultimate winner and loser, and (3) infrequent escalated fighting (e.g. Enquist & Leimar 1983; Enquist et al. 1990). Fourth, signalling during the assessment process is a mixture of honest and deceptive signals (e.g. Maynard Smith 1982; Krebs & Dawkins 1984; Grafen 1990; Johnstone & Grafen 1993; Adams & Mesterton-Gibbons 1995), where (1) signallers, tempered by the risk of retaliation and injury, should bluff in an attempt to manipulate receivers, and (2) receivers should attempt to find honest information from a background of deception. Therefore, in the interplay of honest and deceptive signalling, we assumed that less competitive males (ultimate losers), through an assessment process with more competitive opponents (ultimate winners), should adopt a bluffing strategy (i.e. play 'hawk', but retreat if challenged) by signalling aggressively, while taking actions that would predictably decrease risks from injury if challenged (e.g. Maynard Smith 1982; Enquist 1985).

We staged two types of size-related contests, one of size-matched opponents (symmetric contests) and the other of size-mismatched opponents (asymmetric contests). In the symmetric contests, pairs of males were matched for resident status, similar habitat, presence of a female, and body size. In the asymmetric contests, pairs of males were also matched for resident status, similar habitat, and presence of a female, but they were mismatched for body size. With resident advantage and resource quality held constant, we expected opponents of size-matched contests to produce an aggressive profile of long, intense interactions in which opponents initially have limited cues with which to assess their likelihood of winning or losing. In contrast, we expected the opponents of size-mismatched contests to quickly assess their likelihood of winning or losing and respond in a particularly differential manner. We quantified and compared the latency, frequency and duration of specific signals and intention behaviours during symmetric and asymmetric contests for evidence of assessment and for correlates for eventual contest winners and losers.

METHODS

Subjects

During April, we collected 40 male *A. carolinensis* from Palatka, Florida, U.S.A., and transported them to Virginia Polytechnic Institute and State University for our study. We individually marked males by toe clipping and

measured their snout-vent lengths (SVL) ($\bar{X} \pm \text{SE} = 60.8 \pm 0.44$ mm) and body mass (nearest 0.01 g) ($\bar{X} \pm \text{SE} = 5.08 \pm 0.079$ g). Males were housed separately in $0.6 \times 0.6 \times 0.7$ -m cages, each containing a female. Cage habitat consisted of a peat and Spanish moss substrate, small vertical tree bases, horizontal branches and artificial plants. Two 40-W fluorescent lights and one 150-W incandescent light were positioned over each cage to provide light and heat. The photoperiod (14:10 h light:dark cycle) and temperature gradient (24°C at night to 35°C under the floodlight) were set to facilitate and maintain gonadal recrudescence (Licht 1970, 1973). Water (in earthen dishes and from misting) and food (crickets, *Acheta domesticus*, dusted with calcium lactate and powdered vitamins) were replenished daily. After completion of experiments, all lizards were returned to their site of collection.

Experimental Protocol

We performed the following two types of intermale encounters by manipulating the relative body size of paired contestants: (1) 'symmetric' contests: 10 pairs of males matched for body size ($\bar{X} \pm \text{SE}$ SVL differential = 0.5 ± 0.19 mm; $\bar{X} \pm \text{SE}$ body mass differential = 0.3 ± 0.08 g); and (2) 'asymmetric' contests: 10 pairs of males mismatched for body size ($\bar{X} \pm \text{SE}$ differential = 5.0 ± 0.54 mm; $\bar{X} \pm \text{SE}$ body mass differential = 1.1 ± 0.26 g). However, the average size of the two groups was comparable (symmetric males: $\bar{X} \pm \text{SE}$ SVL = 61.6 ± 0.36 mm; $\bar{X} \pm \text{SE}$ body mass = 5.2 ± 0.08 g; asymmetric males: $\bar{X} \pm \text{SE}$ SVL = 60.2 ± 0.71 mm; $\bar{X} \pm \text{SE}$ body mass = 5.0 ± 0.14 g).

For a specific contest, two males (one with a white acrylic dot on its tail for visual identification) were moved from their holding cages into a large wooden observation chamber ($2.4 \times 0.6 \times 0.8$ m; Fig. 1) that was set at the same light and temperature conditions as the holding cages. The males were separated by an opaque, removable partition that bisected the chamber. Habitat on each side

of the partition was constructed in a mirror image of equal complexity, and each habitat contained a female. The habitat was configured to minimize 'blind spots' during videotaping and to encourage maximum initial separation distance between the males. At the far ends of the chamber, simulated 'trunks' were made from large-diameter tree limbs and positioned vertically either free-standing or against the walls. To the trunks were attached sloping branches; the highest branches were at the rear of the chamber and the lowest were towards the front. The branches radiated from each end of the chamber towards the central partition. To produce long, initial intermale separation distances (≥ 2 m), a favoured perch site was created at either end of the chamber by incorporating the highest trunk, a concentration of artificial vegetation, and an overhead flood lamp. All observations and videotaping were made 1.5 m from the observation chamber within a separate, black-out room and through a 100 (L) \times 10 (H) cm viewing slit overlaid with black window screen to diminish any observer effects (Sugarman 1990).

We did not remove the partition to start a contest until both subjects showed two behaviours associated with territoriality in free-ranging males (Jenssen et al. 1995a): patrolling (i.e. periodic perch shifts about the habitat without evidence of escape-motivated wall climbing) and advertisement displaying (i.e. nondirected displaying from a perch or while moving between perch sites). Development of territory-related behaviours within the observation chamber took 4–7 days, during which time the subjects were cared for as when they were in their holding cages. Once the partition was removed to start an encounter, one male voluntarily became an 'invader' by advancing into his opponent's habitat, and the other a resident 'defender'. Contest durations were determined by the subjects and concluded when one male showed flight behaviour by repeatedly fleeing and withdrawing in response to the other male. The retreating male was deemed the loser, and his pursuer, the winner. Except for two stalemates, contest durations ranged from 12 to 68 min.

Each contest was recorded with two video cameras (Panasonic Model WV 1550, fitted with 16–160-mm zoom

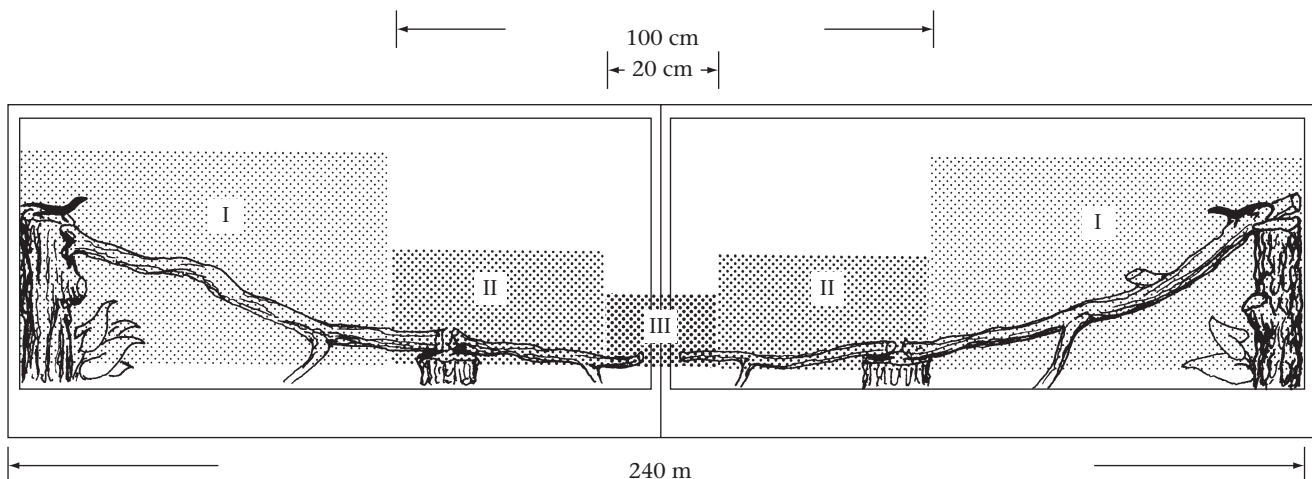


Figure 1. Scaled schematic of the observation chamber and the relative lengths of three stages of intermale separation distances (Phase I > 100 cm; Phase II 100–20 cm; Phase III < 20 cm).

lenses); each male was followed by a separate camera. Outputs from the two cameras were simultaneously juxtapositioned by a split-screen generator (Vicon Model V27OSP), superimposed with elapsed time in 0.01-s increments (Odetics time-date generator, Model G-77), and stored with a Panasonic (Model AG-1950) videocassette recorder. An audio track was also used to record observer notes and estimated separation distances between males. Accuracy of separation distances was facilitated by a measuring tape (in cm increments) affixed along the front of the chamber. From this videotape record, we quantified the following variables.

Variables

Categories. The presence, latency, frequency and duration of four classes of potential signals (skin colour, headbob displays, postural modifiers and intention movements) were analysed from the videotapes. We related the categories of signals to three 'phases' of an encounter that were defined by the following decreasing intermale separation distances: the initial long-range contact (Phase I, 2.4→0.1 m); intermediate distance as males approach (Phase II, 0.1→0.02 m); and immediate proximity in which physical contact may occur (Phase III, 0.02 m→physical contact) (Fig. 1). These ranges of separation distances are known to represent shifting uses of signals by males of *A. carolinensis* (DeCourcy & Jenssen 1994). The progressive decrease in intermale separation distance from Phase I to Phase III also represents increasing duration of the contest and an increasing risk of an escalated fight.

Skin colour. The skin colour of *A. carolinensis* can shift between bright green and deep chocolate brown by means of endocrine and neuroendocrine effects on melanophores; thus, colour states can provide evidence of the physiological state of a lizard (e.g. Cooper & Greenberg 1992). We used a 1–5 number system (bright green–dark brown) to track skin colour as males progressed from green to dark brown when they first sighted one another, and then back to green. In addition, an 'eye spot' of darkened skin behind the eye becomes evident as males regain a green body colour. We tracked the formation and persistence of the eye spot as another possible signal of internal state.

Headbob displays. Male *A. carolinensis* have three headbob displays of distinct cadence patterns (display types A, B and C; Jenssen et al. 2000); each display type is performed with or without a throat fan extension (DeCourcy & Jenssen 1994). When the throat fan (i.e. dewlap) is extended, its area is allometrically related to SVL of the signaller (quadratic regression: $R^2 = 0.895$; Jenssen et al. 2000). Therefore, the proportion of dewlap area to body size might provide a recipient with an honest cue to the signaller's absolute body size; in our sample, there was an 8% differential in SVL between the largest and smallest male and a 28% differential in dewlap area.

Postural modifiers. We tracked the occurrence of three postural 'modifiers': raised nuchal crest, lowered throat,

and sagittal body compression. These temporary modifications of body configuration can accompany headbob displays (Jenssen 1979), but also occur independently of headbobbing displays. When viewed from the lateral aspect of a signalling lizard, postural modifiers increase the apparent body size of the signaller. Consequently, these three modifiers are considered deceptive signals designed for intimidation (Jenssen 1977).

Intention behaviours. Directional orientation of a male relative to an opponent while signalling and moving (parallel, towards and away), as well as three risky behaviours (invasion, jaw sparring and jaw locking), were recorded as possible expressions of intention and motivational state (e.g. fight or flee). Invasion of an opponent's habitat is a risky act of aggression because it invites retaliation. Moving together to jaw-spar (Jenssen 1979) closes the last physical space between males and is the ritualized act that precedes physical combat. Jaw locking (Jenssen 1979) is the ritualized act of an escalated fight, where males lock their snouts and lower jaws to wrestle an opponent from its perch.

Statistics

Descriptive statistics are given as mean and standard error of the mean. We used nonparametric procedures to test for trends and sample differences of continuous and ordinal data because the data need not be normally distributed and the procedures are relatively robust to small sample sizes (Siegel & Castellan 1988). The Wilcoxon two-sample test was used for individual variables in two-sample cases, the Kruskal–Wallis analysis of variance for k -sample cases, and the Spearman correlation procedure for measures of association. As recommended by Hardy & Field (1998), we used a logistic regression (Hosmer & Lemeshow 1989) as the multivariate procedure for revealing any variable associated with contest outcome. The logistic regression is structured for a binary outcome variable, where the dependent variable is either win or lose and the independent variables can be continuous or categorical. As with our other procedures, the logistic regression does not carry restrictive normality assumptions and remains robust with small sample sizes. The α level ($P \leq 0.05$) was applied to two-tailed tests for nonspecific null hypotheses and one-tailed tests when applied to a priori hypotheses with predicted directionality. In cases of multiple testing, we used a modified Bonferroni procedure (Hommel 1988) to adjust P values to avoid making a type I error, where the null hypothesis is rejected when it is true. Statistical procedures were computed using SAS version 8.2 (SAS, Cary, North Carolina).

RESULTS

Contest Outcomes

In the 10 asymmetric matches, the larger male of a pair won eight times, the smaller male once, and one contest ended in a stalemate; even in the 10 symmetric matches,

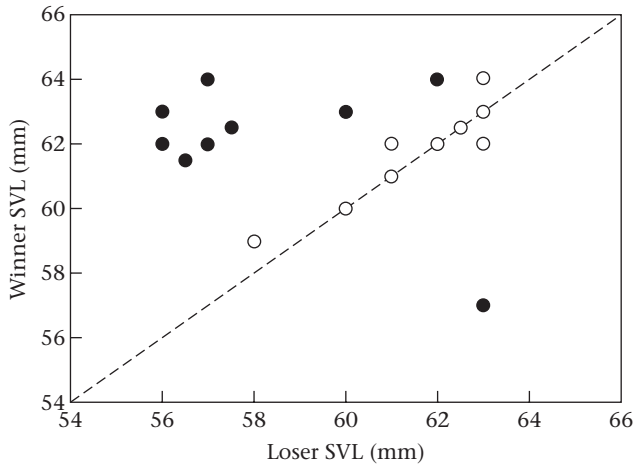


Figure 2. Body size (snout-vent length, SVL) relationship between winning and losing male *A. carolinensis* during size-matched (symmetric, ○) and size-mismatched (asymmetric, ●) contests. Dashed line indicates a size-matched condition: for contests above the line, the larger male won; for contests below the line, the smaller male won.

where males were closely matched in size, a smaller male won only once (Fig. 2). The SVL and body mass differentials of opponents significantly predicted the outcome of the contests (logistics regression, likelihood ratio: SVL $G_1^2 = 11.43$, $N = 36$, $P = 0.0007$, body mass $G_1^2 = 10.85$, $N = 36$, $P = 0.0010$). Smaller males had only a 0.1 probability of success. Thus, our laboratory-staged contests quantified our basic premise: body size is a critical factor in predicting the winner of male-male contests. Therefore, if size predicts contest outcome, can smaller males in asymmetric contests assess their size disadvantage, and, if so, do they modify their behaviour to mitigate their disadvantage? To gain answers, we examined seven possible actions that smaller males might take if playing a bluffing strategy (Table 1), as opposed to signalling honestly about their disadvantage.

Potential Actions by Smaller Male (Bluff and Risk Avoidance)

Action 1

Smaller males of size-mismatched contests should maintain large intermale separation distances for longer durations than males of size-matched contests to increase opportunity for low-risk bluff. Durations of Phase I (males > 100 cm apart) averaged longer for asymmetric matches (9.34 ± 2.04 min) than symmetric matches (6.45 ± 1.89 min) as proposed by Action 1, but the difference was not statistically significant (Wilcoxon, two-sample test: $Z = 0.43$, $N = 18$, one-sided $P = 0.34$).

Action 2

At long intermale distances, smaller males of size-mismatched contests should signal sooner and more frequently than larger opponents to increase low-risk bluff. Mean

Table 1. Proposed actions by the smaller of two male *A. carolinensis* in size-mismatched contests* if males assess their size disadvantage and choose a bluff strategy (i.e. play hawk, but avoid escalation)

Proposed actions	Results
1. Phase I: prolong long-distance intermale distances	Increase duration for low-risk aggressive signalling
2. Phase I: use aggressive signals sooner and more frequently than larger opponent at long intermale distances	Increase low-risk bluff
3. Phase I/II: do not invade the habitat of the larger opponent	Retain resident advantage and decrease risk of retaliation
4. Phase II: prolong intermediate intermale distances rather than coming head-to-head to jaw-spar	Decrease risk of physical engagement
5. Phase III: use fewer aggressive signals than larger opponent when in close proximity	Decrease risky provocation
6. Phase III: prolong jaw sparring with larger opponent and avoiding jaw locking	Avoid escalated fighting
7. Phase III: retreat early to end fight	Avoid escalated fighting

*Contests of *A. carolinensis* are phase-based, where decreasing intermale separation distances (Phase I, 2.4→0.1 m; Phase II, 0.1→0.02 m; Phase III, 0.02 m→physical contact) are associated with shifts in signalling behaviour and increased risk of escalated fighting (DeCourcy & Janssen 1994).

latencies in the asymmetric matches for the initial appearance of the six potential signals were similar for smaller and larger males, with only raised crest occurring sooner for smaller males (Fig. 3). None of these six latency variables differed significantly between smaller and larger males ($Z_s = 1.33$ – 0.01 , $N = 18$ for each test, $P_s = 0.16$ – 0.96).

Mean frequency of Phase I displaying (all display types, with and without dewlap extension), expressed as display rate (Fig. 4), was greater for smaller males (125 ± 55.6 /h) than for larger males (67 ± 21.9 /h), as proposed by Action 2, but the difference was not statistically significant ($Z = 0.446$, $N = 18$; one-tailed $P = 0.33$).

Mean durations for Phase I bouts of lowered throat, sagittal compression, raised crest and eye spot were greater for smaller males (31 ± 26.2 s, 216 ± 78.6 s, 30 ± 25.2 s and 83 ± 71.6 s, respectively) than for larger males (2 ± 1.8 s, 63 ± 23.7 s, 3 ± 1.7 s and 19 ± 12.8 s, respectively), as proposed by Action 2, but the differences were not statistically significant ($Z_s = -1.37$ to -1.18 ; $N = 18$ for each test; one-tailed $P_s = 0.08$ – 0.42).

We examined the above latency, frequency and duration variables of Phase I together using a multivariate analysis to determine whether these variables reflected any differential use by size class (i.e. smaller versus larger males) during asymmetric contests. No overall significance (MANOVA: $F_{1,10} = 0.94$, $N = 18$, $P = 0.59$) was found in the model, and no F and P values for each of the 11 individual variables reached significance ($F_s = 3.01$ – 0.01 , $P_s = 0.11$ – 0.91).

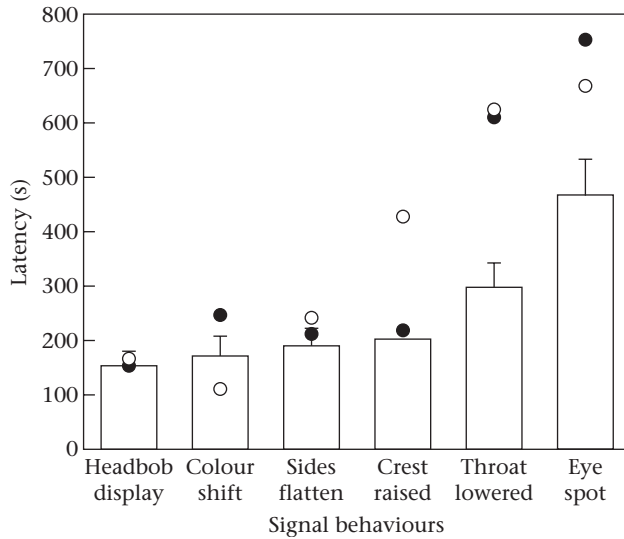


Figure 3. Mean + SE latency (s) to initiate signals by 18 male *A. carolinensis* in size-matched (symmetric, □) contests and by nine smaller (●) and nine larger (○) male *A. carolinensis* in size-mismatched (asymmetric) contests.

Action 3

Smaller males of size-mismatched contests should not invade the unfamiliar habitat of larger opponents, but rather maintain resident advantage and avoid retaliation. In asymmetric contests, a significant number of smaller males (7 of 9; Fisher's exact test: $P = 0.03$) voluntarily left their habitat to intrude into the habitat of their larger opponents, a tactic that was contrary to Action 3. Moreover, the decision to invade was an unsuccessful tactic because only one of seven smaller male invaders won (Fig. 5). Even in the symmetric contests, only a minority of males (3 of 9)

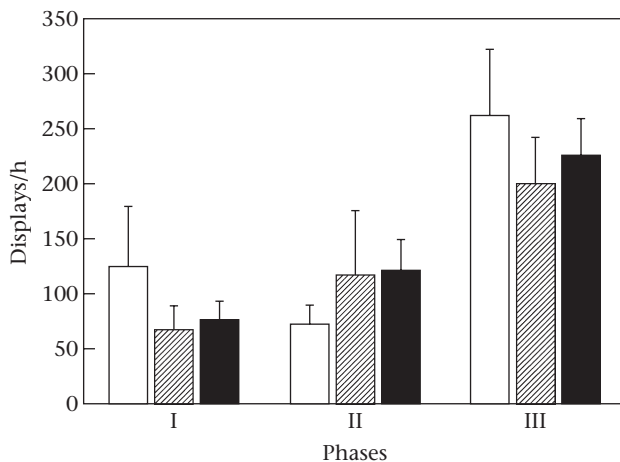


Figure 4. Mean + SE display rate (with and without dewlap extension) for 18 male *A. carolinensis* in size-matched (symmetric, □) contests and for nine smaller (○) and nine larger (●) male *A. carolinensis* in size-mismatched (asymmetric) contests when opponents progressively approached from far (Phase I > 100 cm), intermediate (Phase II 100–20 cm) and near (Phase III < 20 cm) separation distances.

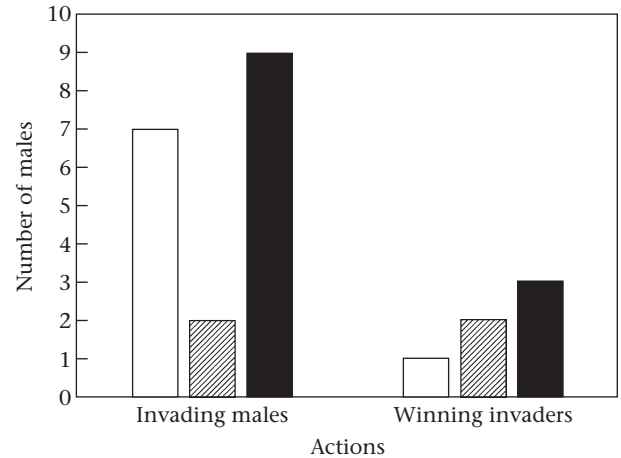


Figure 5. The number of male *A. carolinensis* that invaded the habitat of their opponents when they were smaller (□) or larger (▨) than their opponent (asymmetric contests, $N = 9$ pairs) or the same size as their opponent (■, symmetric contests, $N = 9$ pairs) and the number of invaders who won.

that opted to invade the habitat of their opponent won their encounters (Fig. 5).

Action 4

Smaller males of size-mismatched contests should maintain intermediate intermale distances for longer durations than size-matched males to avoid jaw sparring and decrease risk of physical engagement. Mean duration of Phase II (males 20–100 cm apart) was significantly longer for asymmetric matches (6.5 ± 1.62 min) than for symmetric matches (3.3 ± 0.72 min), as proposed by Action 4 (Wilcoxon two-sample test: $Z = 1.95$, $N = 18$, one-tailed $P = 0.026$).

Action 5

Smaller males of size-mismatched contests should signal less at short intermale distances than larger opponents to decrease risky provocation. Mean display rate in Phase III of asymmetric contests (males < 20 cm apart) was greater for smaller males (262 ± 60.5 /h) than for larger males (198 ± 43.4 /h), a direction contrary to Action 5 (Fig. 4), but a difference not reaching significance ($Z = -0.93$, $N = 18$, two-tailed $P = 0.35$).

Mean durations for Phase III bouts of lowered throat, sagittal compression, raised crest and eye spot for smaller males (251 ± 74.9 s, 207 ± 61.4 s, 252 ± 74.6 s and 300 ± 95.2 s, respectively) were similar to values for larger males (268 ± 66.2 s, 222 ± 45.6 s, 267 ± 66.5 s and 244 ± 110.2 s, respectively), with no statistically significant differences (Z s = 0.53 to -0.53 , $N = 18$ for each test, one-tailed P s = 0.30–0.59).

Action 6

Small males of size-mismatched contests should circle and prolong jaw sparring, while avoiding jaw locking with larger opponents to avoid injury. During Phase III, mean bouts of jaw sparring in asymmetric contests were brief, but of longer duration (12.1 ± 1.55 s) than in symmetric

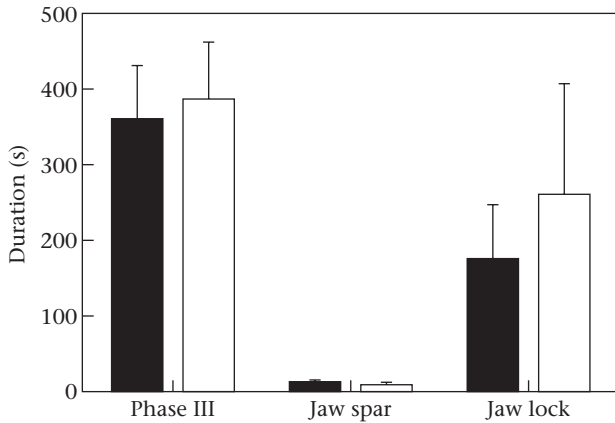


Figure 6. Mean + SE durations for Phase III and the associated jaw-sparing and jaw-locking behaviour between pairs of size-mismatched (asymmetric, ■, $N = 9$ pairs) and size-matched (symmetric, □, $N = 9$ pairs) male *A. carolinensis*.

contests (8.8 ± 1.188 s), as proposed by Action 6 (Fig. 6), but the difference was not statistically significant ($Z = 1.65$, $N = 18$, one-tailed $P = 0.055$). Bouts of jaw locking were of shorter mean duration (175 ± 73.4 s) in asymmetric contests than in symmetric contests (261 ± 147.1 s), as proposed by Action 6 (Fig. 6), but the difference was not statistically significant ($Z = 0.01$, $N = 18$, one-sided $P = 0.50$).

Action 7

Smaller males of size-mismatched contests should retreat earlier to end a contest than males of size-matched contests because of the futility of an escalated fight. Phase III, the intermale distance of highest risk (males < 20 cm apart), averaged about the same duration for asymmetric (6.1 ± 1.18 min) and symmetric contests (6.4 ± 1.26 min) before a winner and a loser were determined (Fig. 6), a result contrary to Action 7. This trend extended to total contest duration as well. Although a negative relationship might be expected between contest duration and the size differential of opponents, a regression analysis found no significant relation for either asymmetric or symmetric contests (REG, asymmetric: $F_{1,8} = 0.09$, $N = 9$ contests, $P = 0.77$; symmetric: $F_{1,8} = 1.86$, $N = 9$ contests, $P = 0.22$; Fig. 7).

Signal Variables as Predictors of Contest Outcome

Display and modifier latencies

Across the 18 contests that ended in a winner and loser, the latencies to the initial display or modifiers (lowered throat, sagittal compression, colour shift, erected crest, and eye spot) were not significantly related to the eventual winner and loser (logistic regression, likelihood ratio: $G_6^2 = 2.68$, $P = 0.87$; with headbob: $P = 0.36$; lowered throat: $P = 0.83$; sagittal compression: $P = 0.73$; colour shift: $P = 0.23$; erected crest: $P = 0.33$; eye spot: $P = 0.42$).

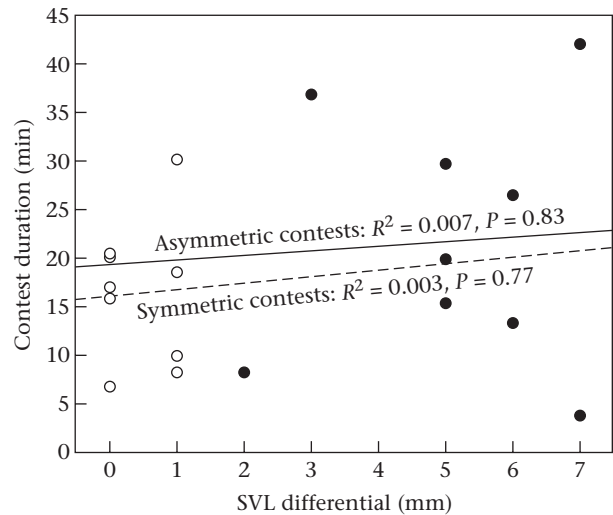


Figure 7. Linear regression of contest duration plotted against the size differential (snout-vent length, SVL) between pairs of size-matched (symmetric, ○, $N = 9$ pairs) and size-mismatched (asymmetric, ●, $N = 9$ pairs) male *A. carolinensis*.

As the number of modifiers significantly accumulated with phase (Spearman correlation: $r_s = 0.812$, $N = 36$, $P = 0.0001$), each male of a pair tended to match the signal latencies of his opponent (i.e. signal matching).

Display type frequencies

Across the 18 contests that ended in a winner and loser, the frequencies with which males used display types A, B and C were not significantly related to the eventual winner and loser (logistic regression, likelihood ratio: $G_3^2 = 3.03$, $P = 0.39$; A display: $P = 0.26$; B display: $P = 0.43$; C display: $P = 0.30$). As display rates significantly increased with phase (Spearman correlation: $r_s = 0.403$, $N = 36$, $P = 0.003$; Fig. 4), each male of a pair tended to match the display types and frequencies of his opponent (i.e. signal matching).

Modifier durations

Across all 18 contests that ended in a winner and loser, the total durations of all bouts of lowered throat, sagittal compression, erected crest and eye spot were not significantly related to the eventual winner and loser (logistic regression, likelihood ratio: $G_4^2 = 0.81$, $P = 0.94$; sagittal compression: $P = 0.67$; erected crest: $P = 0.54$; lowered throat: $P = 0.89$; eye spot: $P = 0.61$). As the durations of bouts of lowered throat, sagittal compression, erected crest and eye spot significantly increased with phase (Spearman correlation: lowered throat: $r_s = 0.609$, $N = 36$, $P = < 0.0001$; sagittal compression, $r_s = 0.339$, $P = 0.0003$; erect crest: $r_s = 0.358$, $P = 0.0001$; eye spot: $r_s = 0.532$, $P = < 0.0001$), each male of a pair tended to match the modifier durations of his opponent (i.e. signal matching).

Orientation and Contest Outcome

The directional orientation for signalling and movements, expressed as the proportion of phase duration, was quite variable (Fig. 8), but revealed several relationships. First, within respective contest types and phases, opponents were generally matching bouts of mutually presenting the longitudinal axis of their bodies towards one another (parallel orientation), mutual circling (parallel orientation), advancing (towards) and retreating (away). Second, during Phase I of both the symmetric and asymmetric contests, the tendency for eventual losers to move into the habitats of their opponents (see Action 3 above) was reflected in these males spending more time approaching than did eventual winners (Fig. 8), but this difference was not significant (Wilcoxon two-sample test: symmetric: $Z = 1.17$, $N = 18$, two-tailed $P = 0.23$; asymmetric: $Z = 1.48$, $N = 18$, two-tailed $P = 0.14$). Third, during Phase II, males of asymmetric contests averaged significantly less time in parallel orientation (i.e. less lateral signalling and circling) than symmetrically matched males ($Z = 2.75$, $N = 36$, two-tailed $P < 0.01$); this divergence would be expected if size-matched males required more time for assessment, and not expected if smaller males of asymmetric contests were attempting to prolong Phase II bluffing. Fourth, 'away' was the least common orientation, but occurred with greatest incidence during Phase III, when consistent retreat signalled the end of a contest (Fig. 8).

DISCUSSION

General Contest Profile

Males of *A. carolinensis* gain reproductive success through aggressive contests that feature a ritualized combat sequence, highly stereotyped display types, and predictable aggressive postures. The contest characteristics of

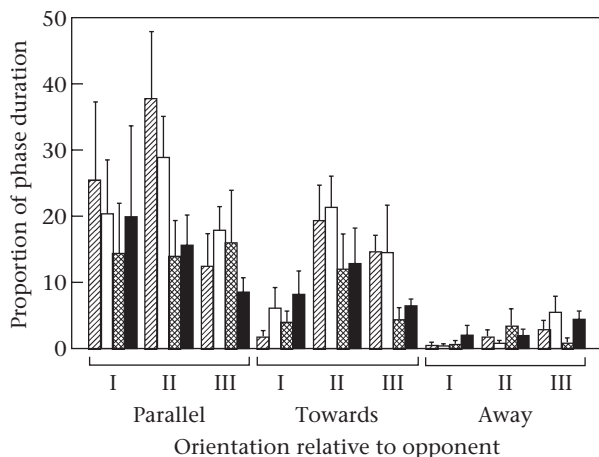


Figure 8. Mean + SE proportion of a phase (Phases I, II, III) in which winning and losing *A. carolinensis* males were oriented parallel to, towards, or away from a size-matched (▨: winners; □: losers; $N = 9$ pairs) or size-mismatched (▩: winners; ■: losers; $N = 9$ pairs) opponent.

A. carolinensis males reasonably fit a 'sequential assessment' game having 'fixed phases' in which assessment about an opponent's fighting ability becomes increasingly costly (e.g. Enquist & Leimar 1983; Enquist et al. 1990). The phases in *A. carolinensis* contests relate to decreasing intermale separation distances, with the following behavioural dynamics being aspects of the model. As males approach and progress from Phase I to Phase III, they (1) increase number of postural modifiers in a predictable order, (2) increase display rate, (3) change their choice of display types, dewlap exposure, and length of display volleys, (4) match signals with regard to signal types, latencies and display rates, (5) match relative time spent in oriented movement within a phase, (6) progress toward costly behaviours and (7) conclude with dangerous fighting (DeCourcy & Jenssen 1994; this study). The details of these generalizations are as follows.

Upon initial visual contact at long range (Phase I), males exchange extended volleys of predominantly type C displays, all of which are accompanied by extension of the dewlap (DeCourcy & Jenssen 1994; Jenssen et al. 2000). Thus, early in the encounter, size assessment appears to be facilitated by an uncheatable (i.e. honest) signal because dewlap area is allometrically scaled to SVL (Jenssen et al. 2000) and bite strength (Lailvaux et al. 2004). Concomitant with headbob displays, deceptive size-enhancing signals (sagittal compression, lowered throat and erected crest) are also deployed in a sequential manner (Fig. 3); these postural modifiers have been previously described for *A. carolinensis* (e.g. Greenberg 1977) and are a common feature in the contests of *Anolis* species (e.g. Jenssen 1977, 1979) and other lizards (e.g. Carpenter & Ferguson 1977; Ord & Blumstein 2002). Because size-deceptive postural modifiers are widespread among lizards (i.e. conserved), one may conclude that there has been a historic importance to large body size; perhaps such postural modifiers have generated a selective advantage by disrupting accurate size assessment by opponents. The mixture of honest and deceptive signals exchanged by *A. carolinensis* males may include changes in skin colour as males cycle from green (without an eye spot), to dark brown, and back to green (with an eye spot). The changes in colour state reflect shifts in catecholamine levels in response to stress-related social interactions (Summers & Greenberg 1994).

At intermediate distances (Phase II), both opponents may voluntarily approach, but only one male assumes the risky role of entering the habitat of his opponent. With increasing proximity, males (1) spend more time in parallel orientation (Fig. 8) due to mutual circling and laterally oriented displaying, (2) increase display rates (Fig. 4), and (3) shift their signalling profile (e.g. fewer C displays, more A and B displays, fewer displays with dewlap extension, and displays in shorter volleys) (DeCourcy & Jenssen 1994).

At close proximity (Phase III), males circle each other, and the pattern of signalling continues to shift. This phase features (1) the highest display rate of the three phases (Fig. 4), (2) the greatest proportion of type A and B displays (DeCourcy & Jenssen 1994), (3) infrequent dewlap extension with headbob displays (DeCourcy &

Jenssen 1994), and (4) displays performed singly or infrequently in short volleys of two to three displays (DeCourcy & Jenssen 1994). Energy costs mount due to (1) continued high display rates, (2) an adrenergic endocrine surge evidenced by altered body colour (Summers & Greenberg 1994), and (3) a potential lactate buildup from extended bouts of sagittal compression that can potentially compromise respiration efficiency (Brandt 2003). By Phase III, males are at the highest risk of physical engagement. If no male retreats, the interactions rapidly and predictably escalate. Opponents mutually open their mouths and jaw-spar as a ritualized act that most often leads to jaw locking. When jaw-locked, males test their strength, stamina, ability to inflict injury, and willingness to endure pain against that of their opponents. Assessment of relative fighting ability is now absolute and inflicted costs are size related (e.g. Meyer et al. 2002; Lailvaux et al. 2004). When the dual jaw holds are broken, as occurs when one male twists the other from the perch, males may choose to repeat the Phase III sequence of circling, jaw sparring and jaw locking, or one male may retreat and end the contest. The escalation of these contests to jaw locking carries the risk of injury that has been long noted as a feature of *A. carolinensis* combat (e.g. Greenberg & Noble 1944).

Correlated Asymmetries

Maynard Smith (1982) identified three primary asymmetries correlated with winning: resident status, quality of defended resources, and relative body size of opponents. Leuck (1995) and McMann (1993) have found evidence for the first two during staged contests with *A. carolinensis* males. In the present study, we document the third asymmetry, body size, as a correlate of contest outcome; this relationship has been reported for other lizard species as well (e.g. Tokarz 1985; Olsson 1992). In our study, the smaller of two males had only a 0.1 probability of defeating a larger and equally motivated opponent, even when the SVL differential was minimal (e.g. < 2 mm, symmetric contests; Fig. 2). In addition, the males who did not invade, but remained in their habitats, were more likely to win, both in symmetric and asymmetric contests (Fig. 5).

Outcome Predictors

Besides differential body size and mass of opponents as correlates of contest outcome, we also examined the latency, frequency and duration of three display types, five modifiers and six intention movements across three contest phases and two contest types for indicators of contest outcome. In general, paired males, regardless of their size differential and eventual win/lose status, matched signals within respective contest types and phases. None of the latency, frequency, or duration signal variables used in logistic regressions were significantly related to contest outcomes. This finding was even true of Phase III, where one might expect a divergence in behaviours between eventual winners and losers as an effect of cumulative assessment (Payne 1998). As a caveat,

however, we may have missed some biologically significant relationships (i.e. accepted the null hypothesis when it is false) because the variance for many compared variables was broad, while sample sizes of some tests were as small as nine.

In contrast to our results, some investigators have reported signal behaviour that predicted contest outcomes. Also using males of *A. carolinensis*, Summers & Greenberg (1994) found that short latencies to eye spot formation explained the eventual winner in 93% of staged contests. However, in their protocol, 'contest' duration was fixed and not determined by contestants; nine pairs of males were exposed in each of four exposure periods (1 h, 1 day, 1 week and 1 month). Because the actual latencies to eye spot formation were not reported, we could not compare their 1-h interactions with our data. Summers & Greenberg (1994) concluded that males with more rapidly activated adrenergic systems (evidenced by rapid eye spot formation) held an advantage for winning. Curiously, they found body size differences to be uncorrelated with winning, even though there was up to a 41% differential in mass of matched males. In another study, Brandt (2003) suggested that contesting male side-blotched lizards, *Uta stansburiana*, may use the duration of sagittal compression as a possible handicap signal (sensu Zahavi 1987) for eventual winners. The accumulated duration of sagittal compression during display production was related to accumulated lactate from compromised aerobic respiration, endurance capacity, and the ability to win an encounter (Brandt 2003). However, we found no significant difference in cumulative duration of sagittal compression between eventual winners and losers. Perhaps our *A. carolinensis* contests concluded before the effects of constrained respiration acted as an indicator of competitive fitness.

Assessment by Smaller Male

Low-risk tactics

To obtain evidence of the assessment process, we concentrated on the behaviour of smaller males in size-mismatched contests. These males have little chance of winning their contests. Therefore, as a class of contestants, we expected smaller males would show their assessment-driven decisions with signalling and intention behaviours that would diverge from the general contest profile of size-matched males. We asked, if smaller males are assessing their disadvantage, how should they diverge in relation to larger male opponents or from size-matched males? In a game for interacting territorial owners, Maynard Smith (1982, pp. 154–158) suggested three potential strategies: 'hawk': display at maximum level and escalate without retreat; 'honest': signal proportionate to assessment and retreat when opponent signals with greater intensity; and 'bluffer': act as a hawk, but retreat when challenged. We reasoned that a smaller male would not play hawk against a superior opponent and risk certain injury, with little prospect of winning. Conversely, it would not be of much benefit to signal honestly about a size disadvantage and an intention to retreat. The common-sense solution for

smaller males, and one that would have some prospect of gain, is to play bluff. To this end, we proposed seven potential actions that a smaller male might take when playing a low-risk, bluffing strategy within their fixed-phase contests. However, we found little statistically significant evidence from smaller males of size-mismatched contests to support our proposed actions (i.e. Table 1).

High-risk tactics

Instead of smaller males playing bluff in size-mismatched contests, their behaviours were consistent with playing a hawk strategy. The smaller males, in comparison with larger opponents, tended to initiate high-risk behaviours that would increase the probability of dangerous fighting, even though smaller males had little likelihood of winning their contests. As evidence of high-risk and escalating tactics, smaller males (1) did not maintain the safety of long intermale distances of Phase I, (2) initiated Phase II by invading the habitats of their larger opponent, a tactic that had a poor payoff even in symmetric matches (Fig. 5), (3) matched high signal rates at close quarters, (4) cooperatively engaged in jaw sparring and jaw locking at similar rates and durations to those of size-matched males (Fig. 6), and (5) showed no inclination for retreating early to avoid injury during Phase III (Fig. 7).

Game theoretical considerations

Our experimental protocol established both opponents as territorial owners. From a modelling perspective, smaller and larger opponents in our study assumed the same role, both were 'owners'. This 'same-role' status for opponents is not incorporated into most game theoretical models dealing with ownership; instead, they make a clear dichotomy between 'owner' and 'intruder' and provide owners with more motivation than intruders (i.e. owners have greater persistence before giving up; e.g. Leimar & Enquist 1984). This provision conveys a resident advantage to owners. In an early model of size assessment within an owner/intruder role context, Hammerstein (1981) seemed to have anticipated our experimental outcome. He concluded that when the risk of injury to an owner is compensated for by the reproductive success coming from the guarded resource, then the only evolutionarily stable strategy (ESS) open to an owner is to defend the territory (i.e. play hawk). Under this condition, a smaller owner that confronts an intruder with a sufficient size advantage so as to ignore the owner's resident advantage must 'paradoxically' engage in a near hopeless fight against an escalating intruder. In our size-mismatched contests, we may have a stark example of this game because each opponent may be evaluating the other as an intruder, yet it is the smaller of the pair that opts to escalate the contest.

This pattern of eventual losers being more aggressive than expected, even initiating escalated contests, has been occasionally observed (e.g. Dow et al. 1976; Enquist & Jacobsson 1986; Morris et al. 1995; Moretz 2003), but is now being considered less as an anomaly and more as a selected tactic. Just & Morris (2003) modelled the

aggressive behaviour of smaller males ('Napoleon complex' model), where likely losers (i.e. smaller males) are expected to attack first, even without a payoff asymmetry. If (1) the value of the resource exceeds the cost of losing a fight, (2) the cost of displaying is sufficiently small, and (3) assessment of an opponent's fighting ability is slightly less than perfect, then the ESS prompts those players who perceive themselves as the likely losers (i.e. smaller males) to initiate fights, while it prompts those players who perceive themselves as the likely winners (i.e. larger males) to wait for the adversary to attack or retreat.

In the field

A smaller male, with even a slight chance of maintaining a breeding territory (~10%) against a larger male, may stochastically gain more reproductive success by engaging in costly and dangerous behaviours than if he minimizes risky behaviours, but loses his territories with certainty. The results of our study, as well as the intrasexually selected nature of the *A. carolinensis* mating system, support the following observation by Riechert (1998): regardless of potential asymmetries that might influence the contest outcome, if the contested resource value is high, such as a breeding territory, then escalated fighting may be expected. This conclusion would be particularly true for species where the single contest is all important.

Acknowledgments

We are grateful to C. Miller for assistance videotaping and analysing data; M. Lovern and K. Orrell for comments on the manuscript; G. Holtzman at the Virginia Polytechnic Institute and State University Statistical Consulting Center for advice on statistical procedures; and anonymous referees and K. Holekamp for guiding the revision. Funding was provided through Financial Assistance Award Number DE-FC09-96SR18546 from the U.S. Department of Energy to the University of Georgia Research Foundation. We observed the ASIH/LH/SSAR Guidelines for Use of Live Amphibians and Reptiles in Field Research and followed an approved protocol by the Virginia Polytechnic Institute and State University Animal Care and Use Committee.

References

- Adams, E. S. & Mesterton-Gibbons, M. 1995. The cost of threat displays and the stability of deceptive communication. *Journal of Theoretical Biology*, **175**, 405–421.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Andrews, R. M. 1985. Ovarian frequency of *Anolis carolinensis*. *Copeia*, **1985**, 259–262.
- Brandt, Y. 2003. Lizard threat display handicaps endurance. *Proceedings of the Royal Society of London, Series B*, **270**, 1061–1068.
- Carpenter, C. C. & Ferguson, G. W. 1977. Variation and evolution of stereotyped behavior in reptiles. In: *Biology of the Reptilia, Vol. 7, Ecology and Behaviour A* (Ed. by C. Gans & D. W. Tinkle), pp. 335–554. New York: Academic Press.

- Cooper, W. E. & Greenberg, N. 1992. Reptilian coloration and behavior. In: *Biology of the Reptilia, Vol. 18, Physiology E: Hormones, Brain, and Behavior* (Ed. by C. Gans & D. Crews), pp. 298–422. Chicago: University of Chicago Press.
- DeCourcy, K. R. & Jenssen, T. A. 1994. Structure and use of male territorial headbob signals by the lizard, *Anolis carolinensis*. *Animal Behaviour*, **47**, 251–262.
- Dow, M., Ewing, A. W. & Sunderland, I. 1976. Studies on the behaviour of the cyprinodont fish III. The temporal patterning of aggression in *Aphyosemion stratum* (Boulenger). *Behaviour*, **59**, 252–268.
- Emlen, S. & Oring, L. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.
- Enquist, M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour*, **33**, 1152–1161.
- Enquist, M. & Jacobsson, S. 1986. Decision making and assessment in the fighting behaviour of *Nannacara anomala* (Cichlidae, Pisces). *Ethology*, **72**, 143–153.
- Enquist, M. & Leimar, O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology*, **102**, 387–410.
- Enquist, M. & Leimar, O. 1987. Evolution of fighting behaviour: the effect of variation in resource value. *Journal of Theoretical Biology*, **107**, 187–205.
- Enquist, M. & Leimar, O. 1990. The evolution of fatal fighting. *Animal Behaviour*, **39**, 1–9.
- Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y. & Segerdahl, N. 1990. A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. *Animal Behaviour*, **40**, 1–14.
- Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.
- Greenberg, B. & Noble, G. K. 1944. Social behavior of the American chameleon (*Anolis carolinensis* Voight). *Physiological Zoology*, **17**, 392–439.
- Greenberg, N. 1977. A neuroethological study of the display behavior in the lizard *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). *American Zoologist*, **17**, 191–201.
- Hammerstein, P. 1981. The role of asymmetries in animal contests. *Animal Behaviour*, **29**, 193–205.
- Hardy, I. C. W. & Field, S. A. 1998. Logistic analysis of animal contests. *Animal Behaviour*, **56**, 787–792.
- Hommel, G. 1988. A stagewise rejective multiple test procedure based on a modified Bonferroni test. *Biometrika*, **75**, 383–386.
- Hosmer, D. W. & Lemeshow, S. 1989. *Applied Logistic Regression*. New York: J. Wiley.
- Huntingford, F. & Turner, A. 1987. *Animal Conflict*. New York: Chapman & Hall.
- Jenssen, T. A. 1977. Evolution of anoline lizard display behavior. *American Zoologist*, **17**, 203–215.
- Jenssen, T. A. 1979. Display modifiers of *Anolis opalinus* (Sauria, Iguanidae). *Herpetologica*, **35**, 21–30.
- Jenssen, T. A. & Nunez, S. C. 1998. Spatial and breeding relationships of the lizard, *Anolis carolinensis*: evidence of intra-sexual selection. *Behaviour*, **135**, 981–1003.
- Jenssen, T. A., Greenberg, N. & Hovde, K. A. 1995a. Behavioral profile of free-ranging male *Anolis carolinensis* lizards across breeding and post-breeding seasons. *Herpetological Monographs*, **9**, 41–62.
- Jenssen, T. A., Congdon, J. D., Fischer, R. U., Estes, R., Kling, D., Edmands, S. & Anderson, R. A. 1995b. Morphological characteristics of the lizard, *Anolis carolinensis*, from South Carolina. *Herpetologica*, **51**, 401–411.
- Jenssen, T. A., Congdon, J. D., Fischer, R. U., Estes, R., Kling, D. & Berna, H. 1996. Behavioural, thermal, and metabolic characteristics of a wintering lizard (*Anolis carolinensis*) from South Carolina. *Functional Ecology*, **10**, 201–209.
- Jenssen, T. A., Orrell, K. S. & Lovern, M. B. 2000. Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard (*Anolis carolinensis*). *Copeia*, **2000**, 140–149.
- Jenssen, T. A., Lovern, M. B. & Congdon, J. C. 2001. Field-testing the protandry-based mating system for the lizard, *Anolis carolinensis*: does the model organism have the right model? *Behavioral Ecology and Sociobiology*, **50**, 162–172.
- Johnstone, R. A. 1998. Game theory and communication. In: *Game Theory and Animal Behavior* (Ed. by L. A. Dugatkin & H. K. Reeves), pp. 94–117. New York: Oxford University Press.
- Johnstone, R. A. & Grafen, A. 1993. Dishonesty and the handicap principle. *Animal Behaviour*, **46**, 759–764.
- Just, W. & Morris, M. R. 2003. The Napoleon complex: why smaller males pick fights. *Evolutionary Ecology*, **17**, 509–522.
- Krebs, J. R. & Dawkins, R. 1984. Animal signals: mind-reading and manipulation. In: *Behavioural Ecology: an Evolutionary Approach*. 2nd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 380–402. Oxford: Blackwell Scientific.
- Lailvaux, S. P., Herrel, A., VanHooydonck, B., Meyers, J. J. & Irschick, D. J. 2004. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society of London, Series B*, **271**, 2501–2508.
- Leimar, O. & Enquist, M. 1984. Effects of asymmetries in owner-intruder interactions. *Journal of Theoretical Biology*, **111**, 475–491.
- Leuck, B. E. 1995. Territorial defense by male green anoles: an experimental test of the roles of residency and resource quality. *Herpetological Monographs*, **9**, 63–74.
- Licht, P. 1970. Regulation of the annual testis cycle by photoperiod and temperature in the lizard *Anolis carolinensis*. *Ecology*, **52**, 240–252.
- Licht, P. 1973. Influence of temperature and photoperiod on the annual ovarian cycle in the lizard *Anolis carolinensis*. *Copeia*, **1973**, 465–472.
- Lovern, M. B. & Jenssen, T. A. 2003. Form emergence and fixation in social signals: ontogeny of headbobbing displays in green anole lizards (*Anolis carolinensis*). *Journal of Comparative Psychology*, **117**, 133–141.
- Lovern, M. B., Jenssen, T. A., Orrell, K. S. & Tuchak, T. 1999. Comparisons of temporal display structure across contexts and populations in male *Anolis carolinensis*: signal stability or lability? *Herpetologica*, **55**, 222–234.
- McMann, S. 1993. Contextual signalling and the structure of dyad encounters in *Anolis carolinensis*. *Animal Behaviour*, **46**, 657–668.
- Maynard Smith, J. 1982. *Evolution and Theory of Games*. Cambridge, Massachusetts: Cambridge University Press.
- Meyer, J., Herrel, A. & Birch, J. 2002. Scaling of morphology, bite force and feeding kinematics in an iguanian and a scleroglossan lizard. In: *Topics in Functional and Ecological Vertebrate Morphology* (Ed. by P. Aerts, K. D' Aout, A. Herrel & R. Van Damme), pp. 47–62. Maastricht: Shaker.
- Michaud, E. J. 1990. Geographic variation of life history traits in the lizard, *Anolis carolinensis*. Ph.D. thesis, University of Tennessee, Knoxville.
- Moretz, J. A. 2003. Aggression and RHP in the northern swordtail fish, *Xiphophorus cortezi*: the relationship between size and contest dynamics in male–male competition. *Ethology*, **109**, 995–1008.
- Morris, M. R., Gass, L. & Ryan, M. J. 1995. Assessment and individual recognition of opponents in the swordtails *Xiphophorus*

- nigrens* and *X. multilineatus*. *Behavioral Ecology and Sociobiology*, **37**, 303–310.
- Nunez, S. C., Jenssen, T. A. & Ersland, K.** 1997. Female activity profile of a polygynous lizard (*Anolis carolinensis*): evidence of intersexual asymmetry. *Behaviour*, **134**, 205–223.
- Olsson, M.** 1992. Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*. *Animal Behaviour*, **44**, 386–388.
- Ord, T. J. & Blumstein, D. T.** 2002. Size constraints and the evolution of display complexity: why do large lizards have simple displays? *Biological Journal of the Royal Society*, **76**, 145–161.
- Orrell, K. S. & Jenssen, T. A.** 2002. Male mate choice by the lizard *Anolis carolinensis*: a preference for novel females. *Animal Behaviour*, **63**, 1091–1102.
- Orrell, K. S. & Jenssen, T. A.** 2003. Heterosexual signalling by the lizard *Anolis carolinensis*, with intersexual comparisons across contexts. *Behaviour*, **140**, 603–634.
- Parker, G. A. & Rubenstein, D. I.** 1981. Role assessment, reserve strategy, and acquisition of information in asymmetric animal contests. *Animal Behaviour*, **29**, 221–240.
- Payne, R. J.** 1998. Gradually escalating fights and displays: the cumulative assessment model. *Animal Behaviour*, **56**, 651–662.
- Qualls, C. P. & Jaeger, R. G.** 1991. Dear enemy recognition in *Anolis carolinensis*. *Journal of Herpetology*, **25**, 361–363.
- Riechert, S. E.** 1998. Game theory and animal contests. In: *Game Theory and Animal Behavior* (Ed. by L. A. Dugatkin & H. K. Reeves), pp. 64–93. New York: Oxford University Press.
- Ross, D.** 2003. Game theory. In: *Stanford Encyclopedia of Philosophy*. Winter 2004 edn. (Ed. by E. N. Zalta). Stanford, California: The Metaphysics Research Lab Center for the Study of Language and Information, Stanford University. <http://plato.stanford.edu/archives/sum2003/entries/game-theory/>.
- Ruby, D. E.** 1984. Male breeding success and differential access to females in *Anolis carolinensis*. *Herpetologica*, **40**, 272–280.
- Siegel, S. & Castellan, N. J.** 1988. *Non-parametric Statistics for the Behavioral Sciences*. 2nd edn. New York: McGraw-Hill.
- Sugarman, R. A.** 1990. Observer effect in *Anolis sagrei*. *Journal of Herpetology*, **24**, 316–317.
- Summers, C. H. & Greenberg, N.** 1994. Somatic correlates of adrenergic activity during aggression in the lizard, *Anolis carolinensis*. *Hormones and Behavior*, **28**, 29–40.
- Tokarz, R. R.** 1985. Body size as a factor determining dominance in staged encounters between male brown anoles (*Anolis sagrei*). *Animal Behaviour*, **33**, 746–753.
- Zahavi, A.** 1987. The theory of signal selection and some of its implications. In: *International Symposium of Biological Evolution* (Ed. by V. P. Delfino), pp. 305–327. Bari, Italy: Adriatica Editrice.