

The effects of perch height, time in residence and distance from opponent on aggressive display in male lizards

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Abstract In antagonistic encounters individuals' displays reflect both the quality of the resource under dispute and their perception of the threat posed by their rival. All else being equal, as the value or threat to contested resources increases, so should an individual's level of aggression. Using a territorial species of Australian agamid lizard, the tawny dragon (*Ctenophorus decresii*), we tested three hypotheses about the relationship between territory quality and aggression. In three experiments we measured aggression whilst manipulating time in residence, perch height as a measure of territory quality and distance to an opponent's territory. Our measurement of aggression was a summary of behaviours used by tawny dragons in antagonistic displays (wrestling, hind-leg push-up display, chasing, raising of nuchal or vertebral crests, back arching, lateral compression, lowering dewlap, jerky walk and tail flick). Animals had significantly lower aggression scores when the opponent's territory was further away, but time in residence and perch height did not affect our measures of aggression. These experimental results provide good grounding for further tests of these hypotheses in field scenarios specifically manipulating distance between neighbours to determine what maintains the spatial distribution of tawny dragons in the wild.

Keywords Lizard · Motivation · Aggression · Individual recognition · Agonistic display

Introduction

Many factors interact to motivate an individual to enter antagonistic interactions (Hammerstein and Parker 1982; Knowlton and Keller 1982; Payne 1998; Taylor et al. 2001; Arnott and Elwood 2009). Broadly, such factors can be intrinsic or extrinsic (Nijman and Heuts 2000; Stocker and Huber 2001; Nosil 2002; Doake and Elwood 2010). Intrinsic factors can include physiological state such as hunger or reproductive condition (Stocker and Huber 2001; Nosil 2002), while extrinsic factors include the presence of a rival or potential mate and the quality of resources (Tachon et al. 1999; López and Martín 2002; Doake and Elwood 2010). As the value of a resource increases, an individual may be more likely to enter a contest or more likely to fight more aggressively despite no change in their inherent fighting ability (Stocker and Huber 2001; Nosil 2002). However, individuals' motivation to fight over a resource largely depends on their abilities/opportunities to assess the value of the resource (Arnott and Elwood 2009, 2008).

In some circumstances the value of a resource is clear. Aggression between male sand gobies (*Pomatoschistus minutus*), for example, increases with nest size, because a larger nest can hold more eggs (Lindström 1992). In other cases competitors must assess the value of a resource because simply holding or having experience with a resource (e.g. a territory) may be important in determining its value (Kokko et al. 2006; Arnott and Elwood 2008). A resident may be most likely to win a contest because of its status as a territory holder ('bourgeois' strategy; Maynard Smith and Parker 1976), or it might have a competitive edge through knowledge of the territory superior to that of the challenger (e.g. refuge sites, basking sites, food abundance, and presence of mates: Stamps 1987; Turner 1994; Olsson and Shine 2000; Hardy and Kemp 2001; Fayed et al. 2008). For example, in removal–replacement studies, resident males regularly win contests upon

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returning to their territory, dependent on the time elapsed since removal (Arnott and Elwood 2008). Rivals' perceptions of the value of a given resource may therefore be asymmetrical, and this can lead to asymmetries in aggressive displays (Mohamad et al. 2010). If such asymmetries affect contest outcomes, then rivals should send accurate signals to opponents to avoid unnecessary fighting (Peters and Ord 2003), for example by increasing the level of aggression displayed by changing the intensity or complexity of displays (Enquist et al. 1998; Husak 2004). Black-throated blue warblers (*Dendroica caerulescens*) produce a low-amplitude song that reliably precedes attack from that individual (Hof and Hazlett 2010). Territorial collared lizards (*Crotaphytus collaris*) exhibit increased rates of aggressive lateral displays directed towards strangers compared to neighbours, perhaps signalling their increased motivation to attack (Husak 2004). Similarly, hermit crabs' (*Pagurus bernhardus*) preflight displays are influenced by the quality of their shell (Arnott and Elwood 2007).

The purpose of this study was to investigate how aggressive display varies with factors that may affect territory quality in the territorial tawny dragon *Ctenophorus decresii*, a small arid zone agamid from Southern Australia. Agamid and iguanid lizards have highly complex displays (Jenssen 1977; Gibbons 1979; DeCourcy and Jenssen 1994; Peters and Ord 2003; Radder et al. 2006). It has been suggested that males with a greater motivation to fight will produce more aggressive displays by using a greater number of head bobs or increasing the number of elements such as postural movements (Jenssen 1977). *Ctenophorus decresii* males are highly territorial and aggressive towards other males (Osborne 2005a, b). Fights between males involve postures such as elevation of the body with the back arched, lateral compression, lowering of the gular region and erection of nuchal and vertebral crests (Gibbons 1977, Gibbons 1979; Osborne 2005a, b). Dynamic components of aggressive display include hind-leg push-ups where the rear of the animal is lifted in the air with the tail coiled over the back, often in conjunction with head bobbing and forearm waving (Gibbons 1977, 1979; Osborne 2005a). We predicted that residents would signal their motivation via aggressive displays to intruder males depending on three key variables: time in residence, height of perch and distance to intruder. Time in residence should increase male display intensity as it reflects an investment in a resource (Arnott and Elwood 2008). Male tawny dragons excavate tunnels under rocks as refuge sites (Gibbons 1977); thus, territory owners have more information on the quality of the tunnels than do the rivals, thus leading to an asymmetry in the rivals' knowledge about the quality of the resource (Rand and Rand 1976; Arnott and Elwood 2008). Also, we expected that taller perches would elicit aggressive displays since *C. decresii* are territorial and spend much of their time on top of rocks surveying their territory and because the higher the perch, the more of one's territory can be surveyed and threats

identified earlier (Cooper and Avalos 2010). Finally, we expect that distance to an opponent should also affect aggression, following the logic that lizards at great distance are less threatening compared to lizards close by (Dugan 1982; DeCourcy and Jenssen 1994).

In this study we conducted three different manipulations of territory quality and examined the aggression level of lizards' displays. The three manipulations were: (1) time in residence, (2) perch height and (3) distance to an opponent's territory (as a more easily controllable trait than distance to opponent). Our measure of aggression level was a combined score of four factors: (1) the number of display elements performed, (2) overall intensity of the display, (3) the number of head bobs and (4) the number of push-ups performed. Assuming that time in residence and perch height represent an increase in knowledge of the resource and an increase in resource value due to enhanced views across territory, respectively, we predicted that aggression levels would increase with time in residence and perch height, and decrease with increasing distance to the opponent's territory.

Methods

Mature adult males were collected from the Flinders Ranges in South Australia (snout–vent length >65 mm). Twenty-eight lizards were captured across four different localities in the Flinders Ranges to avoid collecting neighbours with prior knowledge of one another. Animals were caught by noosing using waxed dental floss on the end of a 5-m telescopic fishing pole and immediately transferred to textile bags. All individuals were recognisable by their unique gular patterns and colouration, and so it was not necessary to individually mark them. Animals were housed individually in outdoor enclosures for the duration of spring and summer in Canberra, Australia. The enclosures were 2 m in diameter and divided in half with one male in each side. The divider prevented males from visual or chemosensory contact with each other while in their home enclosures. Enclosures had a natural soil substrate, with tussock grass, refugia and basking sites (rocks and roof tiles). Food and water was available ad libitum in their home enclosures. Wild insects were available as a food source, which supplemented their diet of captive crickets.

Males were assigned to seven size-matched groups of four individuals according to a size index. The index was calculated by running a principal components analysis with data for mass, snout–vent length and head width, and ranking the regression factor scores obtained from the first principal component. The first PC accounted for 77.7 % of the variation. The regression factor scores from the first PC were highly correlated with all the direct measurements of size (snout–vent length, $r=0.868$; mass, $r=0.884$; head width, $r=0.891$). This method of size matching was preferred to using any one size

variable as it incorporated variability of the different measures of size. Snout–vent length, mass and head width are all important in determining male contest outcomes (Vitt and Cooper 1985; Olsson 1992). In each of our three experiments, animals were paired with a different member of their size-matched group (e.g. experiment 1: a vs. b, experiment 2: a vs. c, experiment 3: a vs. d). Pairs were constant within an experiment to control for opponent identity ($N=14$ pairs), but pairs were not re-used across experiments. Lizards did not have physical contact and thus did not resolve contests.

Experiments were conducted outdoors in November and December between 10:00 am and 3:00 pm when the animals are naturally active. Experiments were conducted in outdoor enclosures ($140 \times 50 \times 50$ cm; 0.35 m²) that had a wooden base with a plastic overlay and heat cord that was threaded between the two layers. Males' territories in nature are often around 10 m² and are adjunct to other males' and other females' territories. While our experimental enclosures were smaller than natural territories, they ensured that we could elicit antagonistic responses. One end of the enclosure had a 50×50 cm clear divider sheet on the front to allow filming, and the enclosure was split into two equal halves using a 50×50 cm clear divider sheet to prevent animals from having physical contact but allowing animals to see each other. A sheet of paper covered the clear divider partition securely and was only removed at the start of a trial. Both halves had a water dish and a refuge. The wooden base of the enclosure consisted of three sections, two of 50×50 cm and one 40×50 cm (total length of 140 cm). This allowed the middle section of the base to be removed as described in experiment 3. Live conspecifics were the most appropriate stimulus to use for this study. Although the behaviour of the stimulus lizard could not be controlled, the focal lizard's behaviour was compared only within experiments and thus with the same stimulus lizard.

Experiment 1: time in residence

In this experiment we used a repeated measures design to test whether the length of time a lizard had spent in a 'territory' (time in residence) affected its aggression level. Three different lengths of time in residence in the enclosures were used: 10 min (control), 1 h and 48 h before opponents were introduced. These times were chosen as 10 min is not long enough for an animal to adjust to a territory or assert ownership and so acts as a control. Animals are known to react aggressively after 1 h in a territory, and 48 h is sufficient time for animals to explore, become familiar with and mark a territory (Osborne 2005b). Time in residence was measured from when the animal was placed in the enclosure. To control for the treatment order, pairs were split into three groups (group 1: $N=5$ pairs, group 2: $N=5$ pairs, group 3: $N=4$ pairs). The order of treatments was different for each group: group 1: 10 min, 1 h,

48 h; group 2: 1 h, 48 h, 10 min; group 3: 48 h, 10 min, 1 h. For each experiment animals had a 48 h rest period between treatments.

Experiment 2: perch height

This experiment tested whether aggression levels were affected by territory quality, using perch height as a measure of quality in a repeated measures design. To increase the height of the perch without affecting the dimensions of the refuge space within, we placed stackable containers over each other. When placed upside down, they fitted neatly over each other leaving the internal space at the bottom of the pile unchanged. The heights of the perches were: 8.5, 12.5 and 16.5 cm; although these are smaller than perch heights commonly found in nature (30 cm, e.g.), they allowed us to use the same enclosures throughout the three experiments. Lizards were left to acclimate to the enclosures overnight for this experiment, and all three groups had 48-h rests between treatments.

Experiment 3: opponent territory distance

Using a repeated measures design, this experiment tested if the distance between rivals affected their aggression levels. To do this we manipulated the distance between opponents' territories because it was easier to measure accurately without having to account for the constant movement of rivals. Enclosures were separated by a divider for this experiment to allow filming. 50×50 cm clear divider sheets were placed over both ends of one half and at the front of the other half (Fig. 1). The two halves of each enclosure were then placed with three different distances between them: 20, 50 and 85 cm. These distances are the minimum distances between lizards (from the front of one enclosure to the front of the other). The maximum possible distances between lizards were 160, 190 and 225 cm (the minimum distance plus the length of the two enclosures combined (140 cm)). Distances could not exceed the distance that allowed both animals' behaviour to remain within the video camera's field of view.

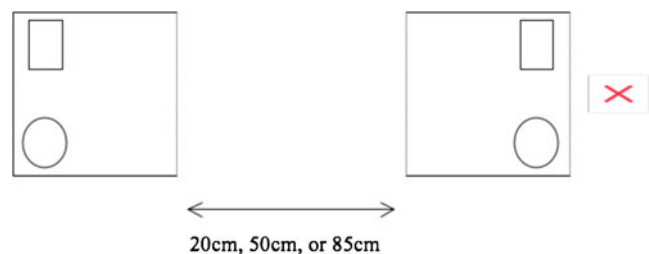


Fig. 1 Set-up of enclosures for experiment 3 'opponent territory distance'. Dashed lines represent clear divider sheets; each half of the enclosure contains a water bowl (circles) and a shelter (squares). Three different distances between rivals were tested (20, 50 or 85 cm), measured between the opposing transparent faces of the two enclosures

Animals were left to acclimate to the enclosures overnight for this experiment with the divider in place. Each individual was subjected to each of the three treatments, and each group of lizards had 48 h rest between treatments.

Measurement of aggression levels

We used a Panasonic NV-DS28 digital video camera mounted 50 cm from the side of the enclosure to film the lizards' behaviour. Both animals in an enclosure were filmed simultaneously for 20 min. Behavioural observations were taken from the videos to obtain a single measure of aggression. Aggression was scored according to the following index (scores in parentheses): attempt wrestle (3), hind-leg push-up display [lowering of dewlap, lateral compression, slow push-ups and tail coiling (3)], chase (2), aggressive posturing [raising of nuchal or vertebral crests, back arching, lateral compression, lowering dewlap (2)], jerky walk (1) and tail flick (1). The aggression score for each lizard was the sum of the product of the number of times a behaviour occurred by the score for that behaviour. The scores provide a conservative index of aggression and are analogous to standard scoring systems used in other studies of lizard contests (e.g. Fox and Baird 1992; Whiting 1999). Although more than one bout may be performed per interaction, individual displays were quite distinct as animals return to normal posture between bouts.

Ethical note

As described above, the enclosures used in this study were divided in half with a section of clear divider. This prevented animals from having physical contact with opponents. Although 'attempted wrestle' was measured as behaviour, this describes the animals approaching the clear divider, gaping and moving their head in order to mouth wrestle with the opponent. This wrestling is only attempted as the clear divider prevents actual contact. The animals were monitored continuously throughout the contests, and no signs of distress, such as lying prostrate, occurred. A lack of distress was an important part of experimental design, as animals that had lost against an opponent would not be aggressive to that opponent in the subsequent contest (Hoeffler 2002).

Statistical analyses

All statistical tests were conducted using SPSS 19.0. Not all aggression score data achieved the Kolmogorov–Smirnov test criteria for normality even after \log_{10} transformation (time in residence, 10 min: $Z_{13}=23.0$, $P=0.042$; 1 h: $Z_{14}=12.71$, $P=0.55$; 48 h: $Z_{15}=16.57$, $P=0.35$; perch height 8.5 cm: $Z_{12}=50.0$, $P<0.01$; 12.5 cm: $Z_{10}=60.0$, $P=0.10$; 16.5 cm: $Z_{10}=40.36$, $P<0.01$; distance from opponent 20 cm: $Z_9=33.43$, $P<$

0.01; 50 cm: $Z_{11}=30.29$, $P<0.01$; 85 cm: $Z_6=37.0$, $P=0.01$). Thus, we used non-parametric Friedman's tests and Wilcoxon's signed rank tests post hoc to tease apart differences between the treatments of each experiment.

Results

There was no effect of group on aggression levels for any experiment (time in residence: $\chi^2=0.60$, $N=24$, $P=0.74$; perch height: $\chi^2=1.75$, $N=24$, $P=0.42$; distance from opponent: $\chi^2=1.49$, $N=24$, $P=0.48$). For experiment 1, time in residence, we found no effect of the time a lizard had spent in a territory prior to the interaction on aggression levels ($\chi^2=0.55$, $N=28$, $P=0.76$). Experiment 2, manipulating perch height, also had no significant effect on aggression ($\chi^2=4.35$, $N=28$, $P=0.11$). However, our manipulation of distance between opponent's territories (experiment 3) strongly influenced rivals' aggression levels ($\chi^2=8.27$, $N=28$, $P=0.02$). Lizards that were 20 and 50 cm apart were more aggressive to each other than lizards that were 85 cm apart (20 vs. 85 cm: $T=-2.50$, $N=28$, $P=0.01$; 50 vs. 85 cm: $T=2.55$, $N=28$, $P=0.01$). For example, there was a significant effect of distance between opponents on the number of push-ups performed ($\chi^2=6.348$, $N=28$, $P=0.042$). But the aggression of lizards 20 and 50 cm apart did not differ ($T=-0.55$, $N=28$, $P=0.59$; Fig. 2).

Discussion

We found no difference in aggression levels in relation to the time a lizard had spent in residence or how high its perch was. These findings are contrary to our predictions that

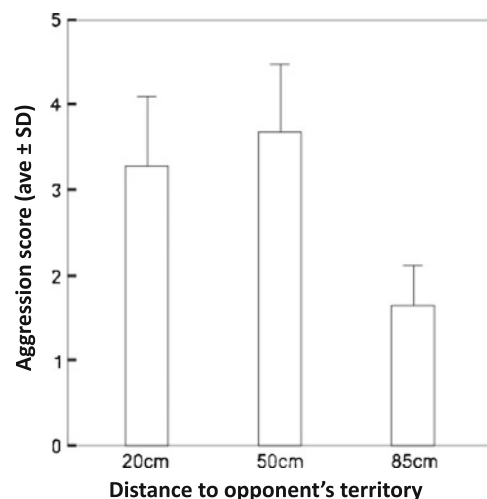


Fig. 2 The mean aggression score of male tawny dragons decreased as the distance to the opponent's territory increased. Bars show mean aggression score \pm standard deviation, $N=14$ pairs for each distance

increased resource quality defined as ‘time spent in a territory’ and ‘taller perches’ would cause lizards to be more aggressive towards each other. We suggest several explanations. Firstly, our manipulations (time spent in territory and relative and absolute perch heights) may not have been sufficient to elicit a response. Ideally, this study would be repeated in a natural environment where residents have invested in their territory for much longer and perch sizes are dictated by natural rock formations. Second, for perch height, the predation risk associated with sitting on a high perch may have confounded our treatment because—although tawny dragons may benefit from surveying their territories from atop tall rock perches (Gibbons 1977)—they may also place themselves at greater risk of attack by aerial predators. Third, our sample sizes, though not dissimilar to those in other studies (Stuart-Fox and Johnston 2005; Stuart-Fox 2006), may not have been large enough to detect an effect. Finally, there may be behaviours and display elements other than those we scored that better signal motivation to fight; more subtle cues such as amplitude of head bobs were outside the scope of this study.

In response to changes in the distance between males' territories, we found that *C. decresii* displayed different levels of aggression. Aggression was greater between rivals whose territories were 50 or 20 cm apart than when they were 85 cm apart. This suggests that *C. decresii* display increased motivation to fight when their rival is closer and by extension that the threat to their territory appears to be greater (Call 1999; McMann 2000; Számadó 2008). Other species of lizards show a similar pattern with a greater tendency to react to opponents when they are within a certain geographical limit. The green anole (*Anolis carolinensis*), for example, shows an increase in display rate with decreasing inter-male distance in laboratory contests (DeCourcy and Jenssen 1994). For the green iguana (*Iguana iguana*), the minimum tolerable distance is between 1 and 1.5 m, and Dugan (1982) suggests that this may be explained by lizard body size and/or visual acuity. Our study may indicate some threshold of *C. decresii*'s visual acuity, but this possibility must be further investigated with a controlled experiment. Our study suggests that there is a distance beyond which lizards' aggressive displays are diminished. Factors that maintain this threshold could be related to the visual acuity of individuals or to trade-offs between investing into territory defence, courtship or foraging.

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References

- Arnott G, Elwood RW (2007) Fighting for shells: how private information about resource value changes hermit crab pre-fight displays and escalated fight behaviour. *Proc Roy Soc B* 274:3011–3017
- Arnott G, Elwood RW (2008) Information gathering and decision making about resource value in animal contests. *Anim Behav* 76:529–542
- Arnott G, Elwood RW (2009) Assessment of fighting ability in animal contests. *Anim Behav* 77:991–1004
- Call J (1999) The effect of inter-opponent distance on the occurrence of reconciliation in stump-tail (*Macaca arctoides*) and rhesus macaques (*Macaca mulatta*). *Primates* 40:515–523
- Cooper WE, Avalos A (2010) Escape decisions by the syntopic congeners *Sceloporus jarrovi* and *S. virgatus*: comparative effects of perch height and of predator approach speed, persistence, and direction of turning. *J Herpetol* 44:425–430
- DeCourcy K, Jenssen TA (1994) Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. *Anim Behav* 47:251–262
- Doake S, Elwood RW (2010) How resource quality differentially affects motivation and ability to fight in hermit crabs. *Proc Roy Soc B* 278:567–573
- Dugan B (1982) A field study of the headbob displays of male green iguanas (*Iguana iguana*): variation in form and context. *Anim Behav* 30:327–338
- Enquist M, Ghirlanda S, Hurd PL (1998) Discrete conventional signalling of a continuous variable. *Anim Behav* 56:749–754
- Fayed SA, Jennions MD, Backwell PRY (2008) What factors contribute to an ownership advantage? *Biol Lett* 4:143–145
- Fox SF, Baird TA (1992) The dear enemy phenomenon in the collared lizard, *Crotaphytus collaris*, with a cautionary note on experimental methodology. *Anim Behav* 44:780–782
- Gibbons JRH (1977) Comparative ecology and behaviour of lizards of the *Amphibolurus decresii* species complex. PhD thesis, University of Adelaide
- Gibbons JRH (1979) Hind leg pushup display of the *Amphibolurus decresii* species complex (Lacertilia: Agamidae). *Copeia* 1:29–40
- Hammerstein P, Parker GA (1982) The asymmetric war of attrition. *J Theor Biol* 96:647–682
- Hardy ICW, Kemp DJ (2001) Skink skirmishes: why do owners win? *Trends Ecol Evol* 16:174
- Hoefler CD (2002) Is contest experience a trump card? The interaction of residency status, experience, and body size on fighting success in *Misumenoides formosipes* Araneae: Thomisidae. *J Insect Behav* 15:779–790
- Hof D, Hazlett N (2010) Low-amplitude song predicts attack in a North American wood warbler. *Anim Behav* 80:821–828
- Husak JF (2004) Signal use by collared lizards, *Crotaphytus collaris*: the effects of familiarity and threat. *Behav Ecol Sociobiol* 55:602–607
- Jenssen TA (1977) Evolution of anoline lizard display behaviour. *Amer Zool* 17:203–215
- Knowlton N, Keller B (1982) Symmetric fights as a measure of escalation potential in a symbiotic, territorial snapping shrimp. *Behav Ecol Sociobiol* 10:289–292
- Kokko H, Lopez-Sepulcre A, Morrell LJ (2006) From hawks and doves to self-consistent games of territorial behavior. *Am Nat* 167:901–912
- Lindström K (1992) The effect of resource holding potential, nest size and information about resource quality on the outcome of intruder-owner conflicts in the sand goby. *Behav Ecol Sociobiol* 30:53–58
- López P, Martín J (2002) Effects of female presence on intrasexual aggression in male lizards, *Podarcis hispanicus*. *Anim Behav* 28:491–498

- Maynard Smith J, Parker GA (1976) The logic of asymmetric contests. *Anim Behav* 24:159–175
- McMann S (2000) Effects of residence time on displays during territory establishment in a lizard. *Anim Behav* 59:513–522
- Mohamad R, Monge J-P, Goubault M (2010) Can subjective resource value affect aggressiveness and contest outcome in parasitoid wasps? *Anim Behav* 80:629–636
- Nijman VV, Heuts BA (2000) Effect of environmental enrichment upon resource holding power in fish in prior residence situations. *Behav Proc* 49:77–83
- Nosil P (2002) Food fights in house crickets, *Acheta domesticus*, and the effects of body size and hunger level. *Can J Zool* 80:409–417
- Olsson M (1992) Contest success in relation to size and residency in male sand lizards. *Anim Behav* 44:386–388
- Olsson M, Shine R (2000) Ownership influences the outcome of male–male contests in the scincid lizard, *Niveoscincus microlepidotus*. *Behav Ecol* 11:587–590
- Osborne L (2005a) Information content of male agonistic displays in the territorial tawny dragon (*Ctenophorus decresii*). *J Ethol* 23:189–197
- Osborne L (2005b) Rival recognition in the territorial tawny dragon (*Ctenophorus decresii*). *Acta Ethol* 8:45–50
- Payne RJH (1998) Gradually escalating fights and displays: the cumulative assessment model. *Anim Behav* 56:651–662
- Peters RA, Ord TJ (2003) Display response of the jacky dragon, *Amphibolurus muricatus* (Lacertilia: Agamidae), to intruders: a semi-Markovian process. *Austral Ecol* 28:499–506
- Radder RS, Saidapur SK, Shine R, Shanbhag BA (2006) The language of lizards: interpreting the function of visual displays of the Indian rock lizard, *Psammophilus dorsalis* (Agamidae). *J Ethol* 24:275–283
- Rand WM, Rand AS (1976) Agonistic behavior in nesting iguanas: a stochastic analysis of dispute settlement dominated by the minimization of energy cost. *Zeitschr f Tierpsychol* 40:279–299
- Stamps JA (1987) The effect of familiarity with a neighborhood on territory acquisition. *Behav Ecol Sociobiol* 21:273–277
- Stocker AM, Huber R (2001) Fighting strategies in crayfish *Orconectes rusticus* (Decapoda, Cambaridae) differ with hunger state and the presence of food cues. *Ethology* 107:727–736
- Stuart-Fox D (2006) Testing game theory models: fighting ability and decision rules in chameleon contests. *Proc Roy Soc B* 273:1555–1561
- Stuart-Fox DM, Johnston GR (2005) Experience overrides colour in lizard contests. *Behaviour* 142:329–350
- Számádó S (2008) How threat displays work: species-specific fighting techniques, weaponry and proximity risk. *Anim Behav* 76:1455–1463
- Tachon G, Murray A, Gray D, Cade WH (1999) Agonistic displays and the benefits of fighting in the field cricket, *Gryllus bimaculatus*. *J Insect Behav* 12:533–543
- Taylor PW, Hasson O, Clark DL (2001) Initiation and resolution of jumping spider contests: roles for size, proximity, and early detection of rivals. *Behav Ecol Sociobiol* 50:403–413
- Turner G (1994) The fighting tactics of male mouthbrooding cichlids: the effects of size and residency. *Anim Behav* 47:655–662
- Vitt LJ, Cooper WE Jr (1985) The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. *Can J Zool* 63:995–1002
- Whiting MJ (1999) When to be neighbourly: differential agonistic responses in the lizard *Platysaurus broadleyi*. *Behav Ecol Sociobiol* 46:210–214