



Morphological and behavioural correlates of contest success in male yellow-headed geckos, *Gonatodes albogularis*: sequential assessment or self-assessment?

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Abstract

Gonatodes albogularis is a small diurnal gecko that lives in Central and northern South America and whose behaviour has been rarely analysed. This study describes the behaviour patterns occurring during agonistic encounters between male geckos, assesses the effect of morphological and behavioural traits on aggressive intensity and contest outcome, and tests predictions of the sequential assessment and self-assessment models of animal contests. We staged encounters between randomly paired wild-caught males in a neutral arena. The behaviour of both males was recorded and a winner was determined for most encounters. Aggressive patterns exhibited during the contests included ‘throat depression’, ‘push-ups’, three types of ‘tail display’, ‘whole body waving’ and ‘bites’. Contest winners did not differ from losers in any of the morphological variables examined. However, winners performed longer or more frequent aggressive behaviours than losers, and frequency of ‘throat depression’ and duration of ‘whole body waving’ significantly predicted final status of geckos. These results show that some behaviours are good predictors of the outcome of aggressive encounters in *G. albogularis*. Moreover, winner SVL significantly predicted the aggressive intensity of the contest. Early theoretical models hypothesized that there should be mutual assessment between contestants, but our results for *G. albogularis* agree more with a recent model of ‘self-assessment only’ of intrasexual competition.

Keywords

agonistic displays, intrasexual competition, contests, yellow-headed gecko.

1. Introduction

Several morphological, physiological and behavioural traits affect the intensity, duration and outcome of contests between individuals of the same sex (Maynard-Smith, 1974; Parker, 1974). Intrasexual contests have been modelled using game theory (Maynard-Smith & Price, 1973; Maynard-Smith, 1974), which predicts that the outcome of fights depends on costs and benefits, fighting ability, resource value and ownership status of every contestant (Maynard-Smith & Parker, 1976). In earlier models, individuals were assumed to have information on the fighting ability (or resource holding power, Parker, 1974) of the other contestant. More realistic approaches have emphasized that individuals would gain information about their opponents during the fight and that fighting behaviour might function to assess the opponent's fighting ability (Maynard-Smith, 1974; Parker, 1974; Enquist & Leimar, 1983). Assessment of the relative fighting ability of an opponent may enable individuals to avoid potentially costly, escalated contests (Maynard-Smith & Harper, 2003). Thus the 'sequential assessment game' model of Enquist & Leimar (1983) proposed the gradual acquisition of information by contestants during the contest. The model predicts that: (1) the probability of victory for the animal with the greater fighting ability will decrease with the difference in fighting ability between the contestants; (2) fight duration will be negatively correlated with the difference in fighting ability between contestants; and (3) the frequency of aggressive behaviour will be higher when contestants are of similar size. Contests have been analysed mostly in males as members of this sex commonly compete for access to females (Andersson, 1994). During contests, males may use multiple signals because each signal may convey different information ('multiple messages') regarding fighting ability, and thereby may facilitate a more accurate opponent assessment (Johnstone, 1996; Ord et al., 2001).

Previous results supported predictions of the sequential assessment game model (fish, Enquist et al., 1990; Arnott & Elkwood, 2009; lizards, Molina-Borja et al., 1998; Huyghe et al., 2005; crickets, Briffa, 2008). A cumulative assessment model has also been developed (Payne, 1998) in which a contestant's decision whether to persist or to flee is based upon a cumulative sum of its adversary's actions. Following the seminal work of Taylor & Elwood (2003), an alternative model of 'self-assessment only' has begun to be used (Taylor et al., 2001; Elias et al., 2008). In summary, this model proposes that the outcome of an intrasexual contest would depend more on the resource

holding potential (RHP) of the loser (Taylor & Elwood, 2003) than on a mutual assessment of the contestants (as proposed by the Enquist & Leimar's model).

Male aggressive behaviours have been described in *Gonatodes* and *Sphaerodactylus* (Demeter & Marcellini, 1981; Leuck et al., 1990; Regalado, 2003b), and male contests have been analysed in some eublepharid species (Kratochvil & Frynta, 2002). It has been argued that most gekkonids are nocturnal and, therefore, adaptation to living in scotopic conditions could have constrained the evolution of visual signals, and favoured instead the evolution of relatively static postures (Regalado, 2003b). However, since even nocturnal geckos may have colour vision (Roth & Kelber, 2004) visual signals could be more developed in these species than previously thought. Though chemical (Brillet, 1993; Hoare et al., 2007) and auditory signals (Regalado, 2003a; Hibbitts et al., 2007) may also be used in intrasexual challenges, diurnal geckos should have acquired a more diverse repertoire of visual signals. Several aspects of the behaviour of geckos have been studied in nocturnal (Regalado, 2003a, b; Kondo et al., 2007) and in a few diurnal species (Ellingson, 1994; Regalado, 2003a), but male contests have been analysed in detail for only a few nocturnal species (Bolger & Case, 1992; Kratochvil & Frynta, 2002; Regalado, 2003b).

The genus *Gonatodes* (Fam. Sphaerodactylidae) is a monophyletic group comprising 23 species, most of them small-bodied diurnal geckos distributed in a wide range from Southern Mexico to Brazil, Bolivia and many islands of the Caribbean (Rivero-Blanco, 1979; Cole & Kok, 2006; Schargel, 2008).

Gonatodes albogularis is a small diurnal gecko living in coastal to open tropical dry forest habitats (up to 1500 m a.s.l.) of Central and South America (Rivero-Blanco, 1979). Populations of this species have been reported in several localities of Colombia (Serrano-Cardoso et al., 2007; Carvajal-Cogollo & Urbina-Cardona, 2008; Bohórquez-Alonso et al., 2010). Individuals live in tree trunk crevices, under logs, in stone walls, and in rock piles both in undisturbed habitats and near buildings. This gecko shows a striking sexual colour dimorphism: adult males have an orange to yellowish head and dark brown body color, while the tip of the tail can be light grey to white; females are more cryptic, with a grey background and spotted mosaic of dark grey to dark brown patches (Rivero-Blanco, 1979). Between the yellow-orange head and the dark body of adult males there is a thin stripe of light blue at each shoulder. Natural predators of this species include large lizards, snakes,

birds, and mammals (Fitch, 1973; Bello, 2000). In the field, males usually defend small territories in tree trunks, logs and rocks, and can be seen near adult females (unpublished observations). Reproduction is associated to two annual peaks of raining (October and April, Serrano-Cardoso et al., 2007).

There are almost no behavioural studies of wild yellow-headed geckos. Ellingson (1994) analysed different aspects of their behaviour, mainly by means of intra- and inter-sexual controlled encounters. Males with a yellowish head won more frequently in aggressive contests with other males and were preferred by females over those with an orange head (Ellingson, 1994). Social displays in this species are very striking including gular extension, push-ups and tail displays, but they have not been analysed in detail. Antipredator behaviour was analysed recently in field conditions (Bohórquez-Alonso et al., 2010), but details of social and reproductive behaviours of this gecko are largely unknown.

In this paper we report the results of analysing male aggressive behaviours in experimentally staged intrasexual encounters. Our specific aims were: (1) to detect and describe the aggressive behaviour patterns exhibited by males; (2) to analyse experimentally the effects of body traits and behaviours of contestants on the outcome and intensity of contests; and (3) to ascertain if results fit to a mutual assessment or self-assessment model of intrasexual competition.

2. Methods

2.1. Animals

Adult male *Gonatodes albogularis* (snout-to-vent length (SVL) 50–58 mm) were collected by hand in Pandi (SE of Bogotá, Colombia) from widely-spaced locations to avoid previous experience between experimental individuals.

2.2. Housing

Males were transported in small Styrofoam containers to the lab where they were kept singly in cages measuring 55 × 40 × 40 cm inside an insulated room of the laboratory. There was a 12L:12D light cycle (lights were on between 08:00 and 20:00 h local time), and temperature was maintained at 27.5 ± 0.5°C. Light during the photo-phase was provided by daylight fluorescent lamps (Philips, TLD 18W/95) suspended over the lizards' cages.

Relative humidity varied between 50–60%. Each cage was provided with small logs and leaves as shelter for the gecko. Water was sprayed every day to provide humidity. Food was provided every two to three days in the form of live *Tenebrio* larvae and cat food containing vitamins.

2.3. Testing cage and recording protocol

The lizards were kept in the above cages for at least ten days before their first contest. From 62 available males, 31 pairs were randomly established for testing. However, in 9 out of these 31 male contests no gecko appeared as a clear winner or loser and their data were not included in the analyses. Therefore, we performed statistical analyses with twenty two pairs of geckos. Each pair was randomly selected from the 44 males and transferred to a test cage (30 × 30 × 45 height, in cm) located in a neighbouring chamber; this cage included a half-cylinder block (16 cm diameter, 30 cm height) covered by cork and its flat side was attached to the rear wall of the terrarium; geckos could climb over this block and stay in the upper platform. Light and temperature in this cage were regulated as above. The cage had an incandescent lamp (100 W, Tungsrapp flood) to provide heat on the cage floor where the temperature ranged between 35 and 39.7°C. Contests were always staged between 12:00 and 13:00 h.

Contests were viewed from a darkened hide and also recorded on video tape. The video recordings were first watched to describe in detail all behaviour patterns shown by the geckos. Subsequently, from every recorded contest we scored all occurrences of each behaviour pattern shown by each animal: ‘tongue-flicking’, ‘head shaking’, ‘throat depression’ (occurring together with body compression), ‘push-up’, three types of ‘tail display’ (see Results), ‘bite’ and ‘whole body waving’ (see descriptions in the Results section). Contests started when one of the geckos resumed locomotor activity after putting both of them in the experimental terrarium and finished 30 min later. This contest duration was long enough to ascertain which gecko was the winner. Several aggressive episodes could occur within a contest and geckos were classified as losers when they ceased aggressive behaviour towards their opponent and moved away from them. The aggressive intensity of each contest was calculated as the total number of occurrences (and durations) of all aggressive behaviour patterns (all the above except ‘tongue-flicking’). Contests never resulted in physical damage to the contestants, none of the observed bites drawing any blood.

Immediately after the contest, the following traits were measured for each gecko: SVL, body mass (BM), head width (HW, distance between head laterals at ear opening level) and height (HH, distance between dorsal head plate and lower jaw), fore- and hind-limb lengths (FLL, HLL, distances between groin and the tip of the longest digit from each limb), and area of the gular-coloured patch (GPA, yellow–orange patch on the throat skin). The latter was measured by placing the ventral side of the geckos against a plastic sheet provided with a millimetered scale and taking a picture with a digital camera; once the pictures were imported to a computer, we used UTHSCSA Image Tool v2.0 to calculate GPA in mm². In 7 of 22 valid contests, this area was not clearly defined and could not be measured in one or both individuals; therefore, we had a smaller sample size for the analysis of GPA. All animals were released unharmed after the experiments at their places of capture.

2.4. Data analysis

Data were analysed for normality and homoscedasticity requirements and when these were not supported, non-parametric tests were used. Except for a few cases (see below) tests were two-tailed and the significance level was set at $p < 0.05$.

2.4.1. Morphological traits

Most biometric traits were significantly correlated among them and with SVL; therefore, to detect winner and loser morphological differences, we performed a principal component analysis (PCA, varimax rotation based on correlation matrix; Budaev, 2010) of all biometric variables (log-transformed) and, afterwards, we compared PC1 and PC2 factor scores between winner and loser geckos; this comparison was performed with Mann–Whitney *U*-test as factor scores did not fulfil normality and homoscedasticity requirements. For some analyses we used the GPA, standardized as arcsin of its square root divided by SVL.

To examine the relationship between body and head traits of the contestants and the intensity of aggressive contests, stepwise backward multiple regression analyses were conducted. Taylor & Elwood (2003) considered that composite measures based on differences between contestants (as independent variables) could fail to reveal the effect of each contestant trait, considered separately, on contest duration. Therefore, in a first step, we calculated the relationship between winner traits and, separately, that of

loser traits to the contest aggressive intensity (rate of total aggressive behaviours — arcsin transformed, for frequencies and durations (in separate tests) — from both winners and losers). In a second step we calculated regressions with aggressive intensity as dependent variable, both winner and loser traits as independent variables and we also included a cross-product term — winner trait \times loser trait — (Elias et al., 2008).

2.4.2. Behavioural traits

There were high correlations among several behaviour patterns, both within frequency and duration data. Therefore, we applied PCA separately to each type of data (standardized as $\log(x + 2)$) and, afterwards, the corresponding factor scores for PC1 and PC2 compared (Wilcoxon exact test) between winner and loser geckos. As each type of tail display was performed with a low frequency, we pooled up all three for statistical analyses.

Additionally, to analyse behaviour patterns affecting winner or loser status, backward logistic regressions were applied considering as the dependent variable gecko's status and frequencies (or durations, in a separate test) of behaviour patterns shown during the contests as the independent variables.

3. Results

3.1. Behaviour pattern descriptions

In Table 1 we present the behaviour patterns detected during *G. albogularis* male contests with a short description of their characteristics.

3.2. Agonistic behaviour sequence during contests

Aggressive encounters were initiated when one gecko remained still or walked slowly towards the other with a depressed throat (plus body compression); after both individuals placed with their bodies aligned laterally, they could perform 'push-ups', 'head shaking', 'whole body waving' or one of the tail displays. This sequence could be repeated and, eventually, one of the geckos withdrew quickly from the other. If one gecko did not withdraw after the initial displays, the other could bit and/or chase him. Thus, the sequence of agonistic behaviours shown by males was first least costly displays and more costly ones later on, if the contest escalated.

Table 1.

Behaviour patterns detected in the aggressive encounters of males of *G. albogularis* together with their descriptions.

Behaviour	Description
Throat depression	The gecko keeps the body laterally compressed and lightly elevated from the substrate and, at the same time, extends the gular skin downwards; occasionally accompanied by 'head shaking' or lateral tail display (see below).
Head shaking (headbobbing)	Short (low amplitude) up and down head movements (between 3 and 8 per bout) in the sagittal plane. It could be repeated at different times throughout the aggressive encounter.
Push-ups	The gecko flexes and extends the fore-legs or all four legs several times in a sequence. In some occasions, it may at the same time elevate the tail vertically and afterwards move it laterally.
Tail displays	Three types of tail movements were detected: (1) surface tail display that consisted in lateral movements of the tail while it rested in the substrate; (2) horizontal tail display: the tail was undulated from its base up to its tip while held lightly separated from the substrate; (3) vertical tail display: the tail was elevated vertically and then moved laterally.
Whole body waving	All four legs are initially extended, keeping the body and the tail separated from the substrate. Afterwards, the gecko moves the whole body length in a waving manner, firstly lowering the fore part (by flexing the fore limbs) while extending the rear legs and elevating the tail, followed by elevating the anterior part of the body and lowering the rear part and the tail (by extending the fore-limbs and flexing the hind-limbs). This sequence can be repeated several times.
Bite	The gecko bit its rival, often in the head but also in the trunk or the base of the tail.
Stereotyped patterns	Some behaviour patterns were performed in a stereotyped way such as for 'whole body waving' that always was expressed in the way described, a sequence that could be continuously repeated and last between 40 s and up to more than one minute. While other behaviour patterns could be performed when both geckos were very close each other, 'whole body waving' always occurred when they were separated by about 20 cm.

3.3. Morphological and behavioural correlates of winners and losers

3.3.1. Body traits

Mean \pm SE and minimum and maximum values for each biometric trait of winner and loser geckos are shown in Table 2. Winners had somewhat larger SVL than losers (Table 2, marginally significant, one-tailed paired t -test, $t = 1.98$, $df = 42$, $p = 0.053$). SVL was highly correlated with head and limb traits (Table 3). Winner males had absolute GPA somewhat larger than losers (difference marginally significant, exact Mann–Whitney U -tests, $Z = -1.5$, $N_1 = 19$, $N_2 = 15$; $p = 0.068$) but there was no significant difference in size-adjusted patch area (exact Mann–Whitney one-tailed U -test, $Z = -0.05$, $N_1 = 19$, $N_2 = 15$; $p = 0.48$).

PCA applied to all biometric traits resulted in two main components accounting for 78.19% of the variance (Table 4). PC1 was mainly defined by GPA, FLL, HW and HH, while PC2 was by HLL, BM and SVL. Factor scores from PC1 and PC2 did not significantly differ between winners and losers (exact Mann–Whitney two-tailed U -test, $Z = -0.32$, $p = 0.76$, and $Z = -1.40$, $p = 0.16$, respectively).

3.3.2. Behavioural traits

PCA results showed that variation in the frequency and duration of behaviour patterns could be explained by the first two principal components (Table 5). PC1 from behaviour frequency analysis was more highly correlated with ‘push-ups’, ‘whole body waving’ and ‘tail displays’, while PC2 was correlated with ‘throat depression’ and ‘bite’ (Table 5). PC1 from behaviour duration analysis correlated more with ‘push-ups’, ‘tail displays’, ‘whole body waving’ and ‘throat depression’, while PC2 was highly correlated only with ‘bite’ (Table 5).

PC1 factor scores from frequency analysis did not significantly differ between winners and losers (Wilcoxon test, $Z = -1.38$, $p = 0.168$) but PC2 factor scores from winners were significantly higher than those of losers ($Z = -2.549$, $p = 0.01$). PC1 and PC2 factor scores from duration analysis were significantly higher in winners than in losers ($Z = -3.133$, $p = 0.002$, and $Z = -2.321$, $p = 0.020$, respectively, Wilcoxon exact one-tailed test). In Figure 1 a comparison of mean values for each behaviour pattern between winner and loser geckos is presented as reference.

Table 2. Mean \pm SE, and minimum and maximum values (in parentheses) of biometric traits from winner and loser geckos used in contest experiments.

	SVL	BM	HW	HH	FLL	HLL	GPA
Winners	37.92 \pm 0.51 (29.1–41.82)	1.53 \pm 0.05 (0.74–1.87)	5.88 \pm 0.10 (4.59–6.60)	4.63 \pm 0.10 (3.55–5.31)	12.71 \pm 0.29 (10.35–14.77)	16.15 \pm 0.27 (12.45–17.67)	59.38 \pm 1.9 (38.13–72.42)
Losers	36.33 \pm 0.61 (29.10–41.82)	1.43 \pm 0.06 (0.74–1.96)	5.84 \pm 0.10 (4.59–6.48)	4.43 \pm 0.13 (2.86–5.65)	12.92 \pm 0.31 (9.81–15.55)	16.13 \pm 0.46 (11.79–19.71)	40.70 \pm 6.06 (0.0–85.93)

N = 22, except for GPA (*N* = 19 for winners and *N* = 15 for losers). For abbreviations, see text.

Table 3.

Correlations (Pearson’s ρ) between biometric traits for winner geckos (above diagonal) and losers (below diagonal).

		SVL	HW	HH	FLL	HLL	GPA
SVL	Pearson’s ρ		0.611*	0.427	0.426*	0.492*	0.609*
	p		0.002*	0.054	0.048*	0.024*	0.006*
	N		22	21	22	21	19
HW	Pearson’s ρ	0.539*		0.497	−0.010	0.153	0.593*
	p	0.010*		0.022	0.966	0.507	0.007*
	N	22		21	22	21	19
HH	Pearson’s ρ	0.314	0.178		0.265	0.024	0.663*
	p	0.154	0.428		0.246	0.919	0.003*
	N	22	22		21	20	18
FLL	Pearson’s ρ	0.231	0.626*	0.132		0.353	0.456*
	p	0.301	0.002*	0.560		0.116	0.050*
	N	22	22	22		21	19
HLL	Pearson’s ρ	0.498*	0.281	0.131	0.019		0.252
	p	0.026	0.230	0.583	0.936		0.298
	N	20	20	20	20		19
GPA	Pearson’s ρ	0.395	0.525*	−0.377	0.307	0.456	
	p	0.145	0.044*	0.166	0.266	0.101	
	N	15	15	15	15	14	

For abbreviations, see text.

* Most significant values.

Table 4.

Rotated factor loadings of biometric traits on the first two components of PCA.

Trait	PC1	PC2
SVL	0.584	0.735*
BM	0.610*	0.748*
HW	0.742*	0.387
HH	0.702*	0.261
FLL	0.822*	−0.027
HLL	0.026	0.945*
GPA	0.821*	0.395
% Variance explained	44.39	33.8

* Higher loadings.

Table 5.

Rotated factor loadings of behaviour frequencies and durations (separate analyses) on the first two components of PCA, and percentage of variance accounted for by each component.

Behaviour	Frequency		Duration	
	PC1	PC2	PC1	PC2
Bite	0.576	0.648*	0.008	0.966*
Throat depression	0.194	0.926*	0.670*	0.419
Push-ups	0.914*	0.140	0.791*	0.034
Tail displays	0.671*	0.525	0.768*	0.050
Whole body waving	0.738*	0.423	0.7428	-0.031
% Variance explained	43.9	35.0	44.3	22.2

* Higher loadings.

3.4. *Aggressive intensity as a function of contestant’s traits*

3.4.1. *Morphological traits*

The aggressive intensity (total frequencies or durations of all aggressive patterns performed by both contestants) lightly increased with a decreasing difference in body size of the contestants (Figure 2), but the relationships

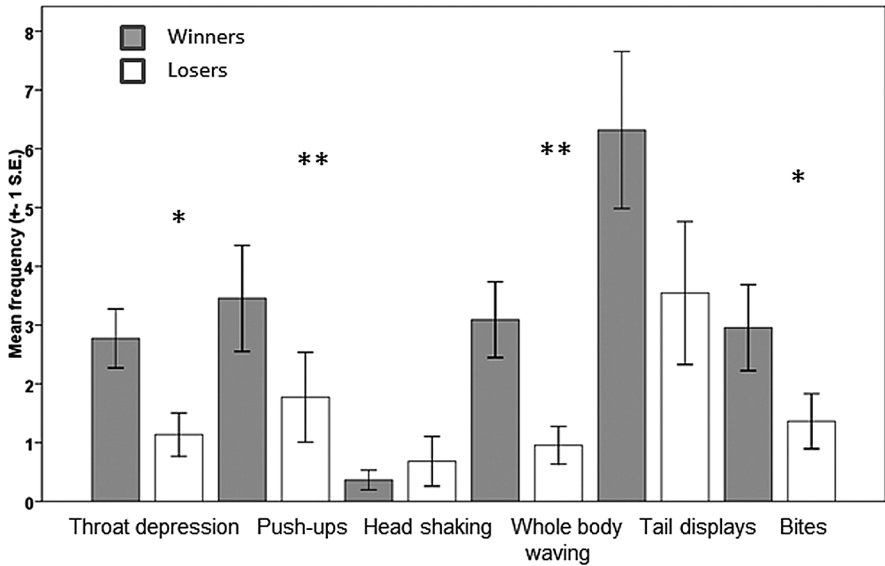


Figure 1. Mean values (± 1 SE) of aggressive behaviour patterns shown by winner and loser geckos during the contests * $p < 0.05$, ** $p \leq 0.01$ (Wilcoxon tests).

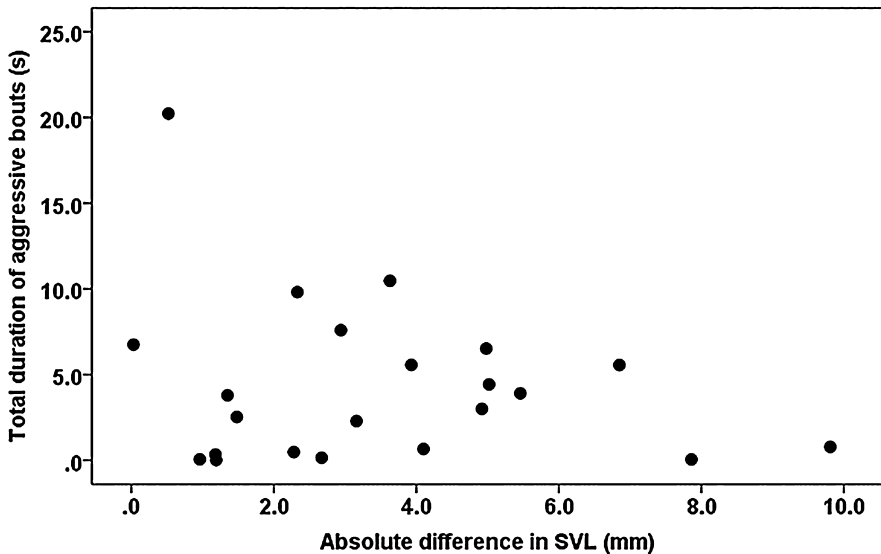


Figure 2. Relationship between total duration of aggressive bouts and absolute difference in SVL between winner and loser geckos.

were not statistically significant ($R^2 = 0.04$, $F_{1,20} = 0.084$, $p = 0.77$ and $R^2 = 0.08$, $F_{1,20} = 0.161$, $p = 0.69$, respectively for durations and frequencies of aggressive patterns). Post-hoc analysis showed that powers of the regressions were 0.262 and 0.145, respectively. Simple linear regressions applied separately to winner and loser data showed that the only trait that significantly predicted the aggressive intensity of the contest was winner SVL ($R^2 = 0.25$, $F_{1,20} = 6.61$, $p = 0.018$) but not loser SVL ($R^2 = 0.03$, $F_{1,20} = 2.27$, $p = 0.14$). When we entered simultaneously winner and loser traits and an interaction term (winner trait \times loser trait), no variable significantly ($p > 0.05$ in all cases) predicted the aggressive intensity of the contest.

3.4.2. Behavioural traits

The result of logistic regression of all behaviour pattern frequencies on individual status (winners or losers) showed that the only trait significantly affecting individual's status was the frequency of 'throat depression' (Wald = 2.99, $df = 1$, $p = 0.012$). On the other hand, logistic regression using as independent variables durations of agonistic patterns, showed that the only trait affecting an individual's status (winner or loser) was the duration of 'whole body waving' (marginally significant, Wald = 3.75, $df = 1$, $p = 0.053$).

4. Discussion

4.1. Agonistic behaviours and sequence during contests

We have shown that agonistic behaviours of male *G. albogularis* include a variety of patterns, all of them imply the use of stereotyped movements and postures such as in ‘throat depression’, ‘push-ups’, ‘whole body waving’ or ‘tail displays’; some of these behaviours are performed in a similar way to that described previously for other gekkonids in several contexts (Marcellini, 1977; Demeter & Marcellini, 1981; Regalado, 2003a, b). For example, tail displays are used in social or aggressive interactions and the extent of lateral tail movement varies in different species and contexts (several gekkonids, Marcellini, 1977; *Gonatodes vittatus*, Demeter & Marcellini, 1981; *Sphaerodactylus clenchi*, Leuck et al., 1990). The agonistic type-3 tail-display of *G. albogularis*, initially raising and then waving the tail, shows a similar pattern to that of tail displays performed by geckos during intrasexual encounters (several Australian species, Bustard, 1965) or as an antipredatory behaviour (*Coleonyx variegatus*, Johnson & Brodie, 1974; *G. albogularis*, Bohórquez-Alonso et al., 2010). ‘Whole body waving’ and ‘push-ups’ were important patterns in contests of *G. albogularis* since geckos performed them during relatively long times and were those that most differed between winners and losers (see below). On the other hand, ‘head shaking’ includes up and down head movements that are frequently described as ‘headbobbing’ in several lizard taxa (Carpenter & Ferguson, 1977; Jenssen, 1977; Labra et al., 2007); though this pattern was not described for the close *G. vittatus* (Demeter & Marcellini, 1981), three types of head bobs were described for *Sphaerodactylus nicholsi* (Regalado, 2003).

During the sequence of agonistic behaviour patterns, male geckos initially used displays involving low-amplitude movement of only a body part (‘throat depression’) and later on (if contest escalates) those involving more intense movements of several body elements, as ‘push-ups’ or ‘tail displays’, ‘whole body waving’ or ‘bite’. This agrees with the increasing cost as fights escalate that has been found in other taxa (Briffa & Elwood, 2001; De Carvalho et al., 2004).

The complex repertoire of behaviour patterns shown in the agonistic encounters between *G. albogularis* males suggests that intrasexual selection in this species is an important factor (Ellingson, 1994). In several lizard species (excluding gekkonids), a significant evolutionary relationship has been found

between signal complexity and intrasexual selection: species with higher sexual dimorphism (in SVL) also have a higher repertoire of display patterns involved in male intrasexual competition (Ord et al., 2001).

4.2. Morphological and behavioural differences between winner and loser lizards

4.2.1. Body traits

Winner geckos had marginal significant larger SVL than losers and they did not differ significantly in other biometric traits. However, a common finding in analyses of lizard contests is that winners usually have larger bodies, are heavier than losers or have larger heads (Tokarz, 1985; Edsman, 1990; Hews, 1990; Olsson, 1992; Carpenter, 1995; Molina-Borja et al., 1998); head size clearly affects lizard contest outcome and it has been considered an intrasexually selected trait (Carothers, 1981, 1984; Anderson & Vitt, 1990; Hews, 1990). Therefore, SVL and other body traits may be cues related to fighting ability (Maynard Smith & Harper, 1976). In our case, the absence of a significant difference between the two types of individuals in the remaining traits could be due to a small sample size (small powers in post-hoc analysis).

The statistical comparison of GPA from winners and losers did not provide a significant difference; Ellingson (1994) found that geckos winning contests had more commonly a yellowish gular patch than losers (more orange patch). Patch coloration may have some communicative value during fighting and in some lizard species coloured patches or chin signal status (Thompson & Moore, 1991; Zucker, 1994) are related to fighting ability (*Lacerta agilis*, Olsson, 1994) and affect dominance relationships (*Sceloporus undulatus erythrocheilus*, Rand, 1991).

4.2.2. Behavioural traits

The higher values of PC1 and PC2 factor scores (from frequency and duration analyses) for winner than for loser geckos were mainly due to the contributions of ‘throat depression’, ‘push-ups’, ‘tail displays’, ‘body-tail waving’ and ‘bite’; these behaviours could be interpreted as indicators of higher fighting ability in winners than in losers, probably due to several underlying factors (genetic and metabolic ones, for example). Some theoretical models predict that contestants may persist until the loser reaches a threshold of the cost that it is prepared to pay in its attempt to win (Mesterton-Gibbons et al., 1996). This means that contest outcome could result from loser self-assessment more than contestant’s mutual assessment as considered in older models of intrasexual conflict (see below, Taylor & Elwood, 2003).

4.3. Relationship between aggressive intensity and male traits

Earlier studies of male contests have shown assessment of body size (in scorpion flies, Thornhill, 1984), dominant song frequency (in cricket frogs, Wagner, 1989), body area (in fishes, Enquist et al., 1990) and body size and songs (in toads, Davies & Halliday, 1978), for example; however, in these cases separate analyses for winner and loser RHP relationship to contest duration were not performed (see Taylor & Elwood, 2003).

In *G. albogularis* the relationship between the rate or duration of aggressive behaviour patterns and differences in SVL of opponent geckos was negative but not significant. Enquist & Leimar's prediction (1983) was that aggression will be more intense when contestants are more similar in size. Our non-significant result again may not be so surprising taking into account that contestants did not differ significantly in most biometric traits. However, a small sample size could also explain the lack of significance; in fact, post-hoc analysis showed that powers of the above-mentioned regressions were 0.262 and 0.145, respectively.

Aggressive intensity of geckos increased with both winner and loser SVL, but the relationship was only significant for winners, suggesting that this trait influences (more than the loser one) the intensity of aggressiveness during the contests. Even so, this result agrees more with the 'self-assessment only' model than to the 'mutual assessment' model (Taylor & Elwood, 2003). The self-assessment model predicts that contest duration should increase with loser and winner (more and less steeply, respectively) resource-holding potentials (SVL is a trait related to RHP); in our case this was true for winner SVL but not for loser SVL. In the 'mutual assessment' model the relationship between contest duration and RHP should be positive for losers and negative for winners (Taylor & Elwood, 2003). This is not shown in our data and, moreover, the interaction term between winner and loser SVL in the multiple regression analysis was not significant. These results support the idea that there is no mutual assessment in *G. albogularis* contests. Males of this species are territorial in the wild (Rivero-Blanco, 1979; Ellingson, 1994) and probably large males are more aggressive (older and more experienced) than small ones. In spider contests, Elias et al. (2008) showed that the relationship between contest duration and RHP of winner and loser spiders adjusted more to the self-assessment than to the mutual assessment model (see also Taylor et al., 2000). However, some authors think that mutual assessment and self-assessment mechanisms may be part of continuum of assessment

strategies, males could shift between self-assessment and mutual assessment as more information becomes available or as information becomes more reliable (Prenter et al., 2006).

To our knowledge, no previous study in a gecko had undertaken this type of analysis and, overall, we have shown that behavioural asymmetries of contestant geckos do affect the outcome of the fights and that the relationship of individual traits to aggressive intensity adjusted more to the self-assessment than to the mutual assessment model of animal contests. As *G. albogularis* is territorial (Ellingson, 1994), further behavioural observations should provide insights into the influence on male contest outcome of combined factors like body size, intensity of gular patch coloration, behaviour and previous residence on a territory. Future analysis of morphological and behavioural factors affecting male contests in other diurnal geckos will provide a comparative view of the development and importance of visual signals within this animal group.

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