

Rival assessment and comparison of morphological and performance-based predictors of fighting ability in Lake Eyre dragon lizards, *Ctenophorus maculosus*

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Abstract Although the outcome of contests is often critical to fitness, we still have much to learn regarding the reliability of different predictors of fighting ability (e.g. morphological traits versus performance measures) and the strategies individuals use to decide when to withdraw. We examined predictors of contest success and assessment strategies in staged contests between male Lake Eyre dragon lizards, *Ctenophorus maculosus*, in which males engage in escalated contests. Bite force was the only significant predictor of contest success. Although head width and depth predicted the number and duration of bites during contests, neither of these traits predicted contest outcome, nor did body size or experience in the prior two contests. These results support the view that measures of physical performance may be more reliable indicators of male fighting ability in escalated contests than morphological traits, because performance is more directly linked to the quality being signalled (i.e. fighting ability). Contest intensity was positively associated with the resource holding potential (RHP) of the loser, but not that of the winner or RHP asymmetry, indicating that individuals base their decision to withdraw on assessment of their own cost threshold (self-assessment) rather than assessment of their opponent's ability (mutual assessment). Lastly, the number of displays (head bobs and push-ups) was also correlated with the RHP of losers

(but not winners or RHP asymmetry), consistent with the recently proposed 'information conflict hypothesis', which predicts that weaker individuals should limit information transfer about their ability by performing fewer displays.

Keywords Resource holding potential · Game theory · Intra-sexual selection · Contests · Performance · Display

Introduction

The study of animal contests has a rich history because the outcome of contests is often critical to fitness. Although we know a great deal about the dynamics and predictors of contest success for many taxa, several topics remain debated and are the focus of current research. With respect to contest dynamics, a significant focus has been to understand the assessment strategies individuals use to decide whether or not to persist in a contest (Arnott and Elwood 2008, 2009; Mesterton-Gibbons and Heap 2014). In terms of predictors of fighting ability or contest outcome, a current focus is whether morphological traits such as ornament size or quality or, alternatively, measures of physical performance (e.g. endurance, locomotor performance, bite force) better predict the outcome of contests (Lailvaux and Irschick 2007; Henningsen and Irschick 2012). Assessing the reliability of predictors of contest success in a broad range of taxa is important because morphological traits (e.g. body size, ornament size) are often used as proxies for the strength of intra-sexual selection (e.g. Stuart-Fox and Ord 2004; Chen et al. 2012).

An individual's absolute fighting ability, or 'resource holding potential' (RHP; Parker 1974) is related to multiple factors. These commonly include body size, mass and energy

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stores (Hsu et al. 2006; Arnott and Elwood 2009) because these often dictate an individual's ability to inflict or bear damage or to persist in a contest. Although ornament size can also reliably signal fighting ability (Stuart-Fox et al. 2006; Lailvaux and Irschick 2007; Hamilton et al. 2013), mechanisms linking the two are often unclear. Measures of performance, such as endurance capacity or bite force, potentially provide a more direct and therefore reliable indicator of fighting ability (Robson and Miles 2000; Sneddon et al. 2000; Perry et al. 2004; Huyghe et al. 2005; Lappin and Husak 2005; Henningsen and Irschick 2012). For example, in species that engage in escalated contests that frequently involve biting, bite force is expected to be a strong predictor of fighting ability, whereas this is not the case for species in which contests rarely escalate to physical aggression. Similarly, in species that engage in extended bouts of energetically costly displays (e.g. energetic wars of attrition; Payne and Pagel 1996a, 1997), energy stores and endurance capacity are likely to be critical. Although available evidence supports the view that relevant performance measures are more reliable predictors of RHP than morphological traits such as body size or ornament size (Sneddon et al. 2000; Henningsen and Irschick 2012), the generality of this pattern remains unclear.

The outcome of a contest is decided when one individual chooses to withdraw (Arnott and Elwood 2008, 2009). This decision can be based on an individual's assessment of its own ability to persist in, or pay the costs of, a contest over resource ownership (RHP; Parker 1974; Parker and Rubenstein 1981) relative to that of its opponent (termed mutual assessment). Alternatively, an individual may decide to withdraw once it has reached a threshold of costs that it can endure (termed self-assessment; Payne and Pagel 1996b, 1997; Payne 1998). Although mutual assessment may reduce the probability of making strategic errors during contests (i.e. withdrawing when it would be better to persist or vice versa; Enquist and Leimar 1983), the process of assessing an opponent's RHP can be costly and potentially requires more sophisticated cognitive abilities (Taylor and Elwood 2003; Prenter et al. 2006; Elias et al. 2008; Arnott and Elwood 2009; Wilczynski and Ryan 2010; Mesterton-Gibbons and Heap 2014). Therefore, mutual assessment strategies may be rare as such complex abilities may be beyond many animals, and selection is expected to favour simple decision-making processes (Elwood and Arnott 2012, 2013). Nevertheless, the assessment strategy employed will depend on the trade-off between the cost of strategic error and the cost of mutual assessment (Mesterton-Gibbons and Heap 2014). Consequently, more recent game theoretic models (Prenter et al. 2006; Mesterton-Gibbons and Heap 2014) predict that the assessment strategy should shift from mutual assessment to self-assessment with increasing value of the contested resources, increasing costs of escalation (when resource value is high) and decreasing cost-effectiveness of assessment (Mesterton-

Gibbons and Heap 2014). A critical assumption of this view is that only weak individuals benefit from their opponent making a strategic error; therefore, weaker individuals should limit information transfer by performing fewer displays (Mesterton-Gibbons and Heap 2014). Consequently, the first step to understanding the nature of assessment strategies in animal contests is to determine whether contest intensity or duration, or the number/duration of displays, is associated with the RHP of winners, losers or the difference between them (Taylor and Elwood 2003; Mesterton-Gibbons and Heap 2014).

Lake Eyre dragon lizards, *Ctenophorus maculosus*, defend non-overlapping, two-dimensional territories and engage in escalated contests in the wild (Mitchell 1973; Olsson 1995b). The species exclusively inhabits large arid salt pans in Australia's southern interior, where their main food source consists of wind-blown arthropods and, to a lesser degree, ants (Mitchell 1973; Olsson 1995b). As their primary food source is ephemeral and unpredictable, males do not defend trophic resources (Olsson 1995b); instead, territories provide males with access to females, with larger territories overlapping the home ranges of more females (Olsson 1995b). Both sexes are promiscuous, and females can produce multiple clutches within a breeding season; however, male territories do not provide females with resources (e.g. oviposition sites), and neither sex provides parental care. Males persistently court and harass females and often attempt forced copulation, which can result in injury or death from the male's mating grasp (Mitchell 1973; Olsson 1995a). Receptive females will generally mate with courting males, while non-receptive and gravid females perform rejection behaviours to deter superfluous courtship and copulation (Chan et al. 2009; McLean and Stuart-Fox 2010). Thus, competition for mates is intense in the relatively brief breeding season (August–October), and contest outcome is likely to be critical for male reproductive success.

We staged contests between male *C. maculosus* and tested whether morphological traits (body size, relative head size) or 'weapon performance' (bite force) predicted the outcome of contests or the number of specific aggressive behaviours. The experiments were done in a 'tournament' design such that each male encountered several other opponents. We therefore explicitly tested for an effect of prior experience on subsequent probability of winning or losing. We derived estimates of fighting ability (RHP) from structured Bradley–Terry models of the tournament (Firth 2005; Stuart-Fox et al. 2006) and used these measures of fighting ability to assess the nature of opponent assessment in this species. Specifically, we tested some predictions of mutual assessment and self-assessment models by investigating the relationships between contest intensity and loser RHP, winner RHP and a measure of RHP asymmetry (Taylor and Elwood 2003; Briffa and Elwood 2009). Lastly, we tested whether the number of

communicative behaviours (displays) performed by males is associated with the absolute RHP of individuals, rather than RHP asymmetry between contestants, to determine whether weaker individuals may limit the transfer of information on RHP by performing fewer displays (Mesterton-Gibbons and Heap 2014).

Methods

Animal capture and husbandry

We captured 32 males by hand from Lake Eyre, South Australia (28.95–29.05° S, 137.65–137.76° E), between 22 August and 7 September 2007, shortly after emergence from hibernation, and maintained them in captivity at The University of Melbourne, Victoria, Australia. Lizards were housed individually in 61×30×30 cm (length×width×height) glass tanks containing a layer of sand and salt crust to mimic natural habitat, separated by opaque partitions to avoid visual contact. The room was maintained at an average temperature of 28 °C on a 12:12 day–night light cycle, and a heat lamp was suspended above each tank to provide a heat gradient (approximately 28–38 °C) to allow animals to attain their preferred body temperatures (32 °C; Mitchell 1973). Lizards were sprayed with water for hydration and fed live crickets (*Anchieta domesticus*) and mealworms (*Tenbrio* spp. larvae) dusted in calcium and multivitamins three times a week.

Morphology and bite force

Just prior to conducting behavioural trials (October 2007, see below), we measured several morphological traits chosen for their importance in determining contest success in other lizards (Tokarz 1985; Hews 1990; Perry et al. 2004; Pratt et al. 2004). These were body size (snout–vent length, SVL, to the nearest 0.1 mm), mass, head depth (maximum), head width (maximum) and jaw length (horizontal distance from the tip of the snout to the posterior edge of the jaw bone). We measured mass to the nearest gram and head dimensions to the nearest 0.01 mm. The males used in this study had a mean (\pm SD) body size of 65.9 \pm 3.0 mm (range 60.2–70.2 mm) and were all larger than the minimum size at sexual maturity (54 mm; Mitchell 1973; Table 1).

We determined the maximal bite force of lizards using a purposely built measuring device as per Herrel et al. (2001), consisting of a mounted isometric Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland) connected to a Kistler charge amplifier (type 5995A, Kistler Inc., Winterthur, Switzerland). Lizards were induced to bite on two foam-covered metal plates, which exert a pull on the piezoelectric force transducer. The foam coverings protected the lizards' teeth and standardised the point at which the force was

Table 1 Descriptive statistics of morphological and performance (bite force) variables measured for male Lake Eyre dragons in this study ($N=32$)

Variable	Mean	SD	Minimum	Maximum
Snout–vent length (mm)	65.87	2.97	60.19	70.21
Mass (g)	10.46	1.42	7.40	12.50
Jaw length (mm)	18.80	0.78	17.38	20.14
Head width (mm)	14.37	0.66	12.90	15.55
Head depth (mm)	9.39	0.47	8.34	10.15
Bite force (N)	8.91	2.98	3.00	14.00

applied. Prior to biting, we measured cloacal temperature using a thermocouple. If required, lizards were warmed under a heat lamp to ensure that they were at close to their preferred body temperature (32 °C; Mitchell 1973) when bite force was measured. The bite force of each lizard was measured five times, with at least 1 h between measurements, and the highest recorded value was considered to be the maximal bite force for that individual.

Behavioural trials

We staged contests in a neutral 61×30×30 cm arena, under the same conditions as where lizards were housed. Contests were video-taped and lasted approximately 15 min, which a pilot study had shown to be sufficient time to establish a clear winner and loser. The loser was the male that withdrew from the contest and/or fled from their opponent, thus ending the trial. We employed a tournament design with each male used in four to seven contests separated by at least two days.

In the first trial, we used pairs of males that were size-matched as closely as possible (to within 2.57% \pm 0.25 SE for SVL). Subsequent opponents were chosen based on both size and contest history. Specifically, we chose the opponent that was next closest in size and had the same contest history (e.g. had both won their previous encounter or both lost it). However, it becomes increasingly difficult to match opponents for contest history. A lizard that has been in three contests, for instance, has eight potential contest histories (000, 011, 010, 001, 111, 100, 101, 110 where 0 represents a loss and 1 represents a win). Consequently, we matched opponents for the outcome of their previous one or usually two contests. The entire tournament consisted of 78 contests involving 32 lizards. Contests in which there was no interaction between males were excluded from the analysis, and there was no difference in size (SVL; $t=-0.518$, $df=76$, $P=0.606$) or bite force ($t=0.270$, $df=76$, $P=0.788$) asymmetry between trials with or without an interaction. This resulted in 58 usable contests with each male participating in two to five contests.

From the videos, we recorded the number of approaches, retreats, chases and times a lizard fled from his opponent. We

also recorded the number of head bobs, number and duration of bites and push-ups and the duration of tail lashes. Retreating and fleeing were submissive behaviours, while all other behaviours were aggressive (Table 2). Behavioural variables were converted to measures per minute to account for differences in trial duration and then square-root-transformed to meet model assumptions of normality. Based on aggressive behaviours, we calculated a weighted aggression score (per minute) for each contest as: aggression score = $(1 \times \text{number of head bobs and duration of push-ups}) + (2 \times \text{number of chases and duration of tail lashes and bites})$, reflecting increasing levels of intensity, consistent with the likely associated costs of these behaviours (Losos 1985; Whiting 1999; O'Connor and Shine 2004; Stuart-Fox and Johnston 2005). The aggression score for a contest was square-root-transformed and used as a measure of contest intensity.

Statistical analysis

We first examined the inter-correlation among male traits using Pearson correlations (PROC CORR SAS ver. 9.3). Next, we examined which male traits predict fighting ability using the structured Bradley–Terry (B–T) model for paired comparisons (Bradley and Terry 1952; Firth 2005), fitted using the BradleyTerry2 package (Turner and Firth 2012) in R ver. 3.0.3 (R Development Core Team 2010). Fighting ability is a relative score which is calculated for each male based on the outcome of contests in a tournament design (where each male encounters multiple others). For example, consider a tournament between three males (A, B and C) where A loses to C, B beats A and C loses to B. According to these contest outcomes, B has the highest fighting ability, followed by C and then A. A discussion of the application of the B–T model to contest data can be found in Firth (2005) and Stuart-Fox et al. (2006). Briefly, the structured B–T model is a form of generalised linear model that relates fighting

abilities (derived from the binary contest outcomes) to a series of predictors (in this case, male traits) and estimates the probability of individual i beating individual j (Firth 2005). As each male is paired with several different opponents, the model we employed incorporates an additional term that allows for the potential effect of prior experience, where the extra predictor z_{ik} summarises the contest history of individual i at the time of contest k . Thus, the full model can be expressed as:

$$\text{logit}[\text{probability}(i \text{ beats } j \text{ in contest } k)] = \lambda_i - \lambda_j + \delta(z_{ik} - z_{jk})$$

where λ_i and λ_j represent the abilities of the two individuals.

To account for prior experience, each contestant was given a score ranging between 0 and 2 for ‘prior wins’ (0=no wins, 1=one win, 2=two wins) based on up to two previous interactions. As the effect of prior wins and losses on behaviour may differ (Hsu et al. 2006), we also gave each contestant a score for ‘prior losses’ (0=no losses, 1=one loss, 2=two losses). We chose to incorporate an experience effect for (up to) the previous two contests rather than only the most recent contest, or the entire contest history, as Stuart-Fox et al. (2006) showed that the previous two contest outcomes had the strongest influence on subsequent fighting ability in male chameleons.

We assessed the following potential predictors of fighting ability: ‘prior wins’, ‘prior losses’ (in up to two previous contests), SVL, mass, head depth, head width, jaw length and maximal bite force. To choose the most parsimonious model, we employed a standard stepwise procedure, examining reduction of model Akaike Information Criterion as well as the significance of variables.

We also examined which male traits predicted the behaviours performed during contests. For this analysis, we used a multivariate generalised linear mixed model (PROC MIXED, SAS ver. 9.3) with two random factors identifying trial number and male ID to account for non-independence of males within the same trial and repeated use of the same male, respectively. We derived five separate models, one for each of the following dependent variables: (1) number of head bobs, (2) duration of push-ups, (3) duration of tail lashes, (4) number of bites and (5) duration of bites (all behaviours were measured per minute). We chose these variables because they represented the most common aggressive behaviours performed during contests. For each model, the independent variables (predictors) were SVL, mass, head depth, head width, jaw length and maximal bite force.

Contest characteristics and models of rival assessment

We examined whether contests were initiated by eventual winner or losers using a binomial test (PROC FREQ, SAS ver. 9.3) and tested whether contest winners and losers

Table 2 Contest behaviour scored from video footage

Behaviour	Description
Aggressive	
Approach	Moves slowly towards opponent
Bite	Bites any body part on opponent
Chase	Runs towards and pursues opponent
Head bob	Pronounced up and down ‘nodding’ movement of the head
Push-up	Lateral compression of the body and a raised stance
Tail lash	Tail lashed at opponent
Submissive	
Flee	Runs away from opponent
Retreat	Moves slowly away from opponent

differed in the number and/or duration of aggressive behaviours, and the number of behavioural elements performed, using paired *t* tests (t.test, R ver. 3.1.0). To investigate whether more aggressive encounters began more quickly, we performed a simple regression analysis (PROC REG, SAS ver. 9.3) between contest intensity (aggression score) and contest latency (time taken for males to engage in the contest).

The main game theoretic models applicable to escalated contests have some key predictions which can be tested by examining the relationship between contestant RHP and contest duration and/or intensity (Taylor and Elwood 2003; Elwood and Arnott 2012). These models can be separated into two categories: self-assessment, where individuals base their decisions on their own ability, and mutual assessment, where individuals know their own ability and compare this to information gathered on the ability of their opponent. Under a model of pure self-assessment (war of attrition without assessment, WOA-WA; Mesterton-Gibbons et al. 1996; energetic war of attrition, E-WOA; Payne and Pagel 1996a, 1997), contestants have individual time or energy thresholds set according to their ability and the value of the resource, and the weaker contestant will reach their threshold first. Therefore, if contestants are using pure self-assessment, contest duration/intensity will have a strong positive relationship with loser RHP and a weak positive relationship or no relationship with winner RHP (Taylor and Elwood 2003; Elwood and Arnott 2012). Similarly, the cumulative assessment model (CAM; Payne 1998) is a self-assessment model; however, under the CAM, opponents inflict costs upon each other, and therefore contest duration/intensity will have a strong positive relationship with loser RHP and an equally strong negative relationship with winner RHP. Conversely, an example of mutual assessment is the sequential assessment model (Enquist and Leimar 1983). Under this model, contest duration/intensity depends on the difference in abilities between contestants (RHP asymmetry). As with the CAM, this results in contest duration/intensity having a strong positive relationship with loser RHP and a strong negative relationship with winner RHP; thus, it is not possible to distinguish these two models based on these comparisons alone (Taylor and Elwood 2003).

As all contests in this study were stopped after 15 min, we use contest intensity (aggression score) to test model predictions. We performed simple regression analyses (PROC REG, SAS ver. 9.3) between the aggression score of contests (contest intensity) and the RHP (fighting ability based on contest outcomes) of winners and losers and RHP asymmetry (fighting ability of winner – fighting ability of loser). Lastly, we tested whether the total number of communicative behaviours (displays; number of head bobs and push-ups combined) are associated with absolute RHP of winners or losers or RHP asymmetry (PROC REG, SAS ver. 9.3).

Results

Predictors of fighting ability and aggressive behaviour

We detected positive relationships among all male traits (Table S2). The best model for predicting male fighting ability incorporated bite force and jaw length, and bite force was a significant predictor in the model (standardised coefficient = 0.679, $P=0.027$; Table 3). The relationship was such that males with stronger bites and shorter jaws had higher fighting abilities. Notably, experience in the previous two encounters was not a strong predictor of fighting ability and was not included in the final model. For males that differ by two standard deviations in bite force, and all else being equal, the probability that male A (with higher bite force) defeats male B is estimated to be $\exp(2 \times 0.679) / [1 + \exp(2 \times 0.679)] = 0.80$. For males that differ by two standard deviations in jaw length, and all else equal, the probability that male A (with relatively shorter jaw length) defeats male B is estimated to be $\exp(2 \times 0.374) / [1 + \exp(2 \times 0.374)] = 0.72$. Furthermore, the final model correctly predicted the winner of only 32 of the 58 contests (55 %), suggesting that it was a relatively weak overall predictor of fighting ability.

Two male traits, head depth and head width, were significant predictors of the number of bites per minute (head depth: $F_{1,27}=5.11$, $P=0.032$; head width: $F_{1,27}=6.92$, $P=0.014$), with males with deeper and narrower heads biting their opponent more frequently. Head width was also a significant predictor of bite duration per minute ($F_{1,27}=5.66$, $P=0.025$), with males with narrower heads biting for longer. No other male traits were significant predictors of any other behaviour (Table 4).

Contest characteristics and models of rival assessment

Winners initiated 43 of 58 contests which was significantly more than predicted by chance ($z=-3.68$, $P<0.0001$), and contests with higher aggression indices had shorter latencies (i.e. males engaged in contests more quickly; standardised estimate = -0.281 , $P=0.033$, $R^2=0.079$). Winners performed significantly more behavioural elements during contests ($t=3.623$, $df=57$, $P=0.0006$). Furthermore, contest winners chased more ($t=3.890$, $df=57$, $P=0.0002$) and performed

Table 3 Bradley–Terry model showing best predictors of fighting ability in male Lake Eyre dragon contests. The standardized coefficient allows assessment of the relative strength (slope) of each variable

Variable	Coefficient	SE	Z	$P(> Z)$	Standardised coefficient
Bite force	0.343	0.155	2.22	0.027	0.679
Jaw length	-1.072	0.618	-1.73	0.083	-0.474

Table 4 Results of generalised linear mixed models investigating which traits are predictors of aggressive behaviour in male Lake Eyre dragon contests. Behaviours were converted to measures per minute to account for differences in trial length. Statistically significant relationships are in italics

Behaviour	Variable	Estimate	$F_{1,27}$	P
Number of head bobs	SVL	−0.006	0.02	0.903
	Mass	0.024	0.04	0.845
	Head depth	−0.009	0.00	0.987
	Head width	−0.475	2.14	0.155
	Jaw length	0.071	0.06	0.801
	Bite force	0.097	3.87	0.060
Duration of push-ups	SVL	−0.007	0.04	0.843
	Mass	0.022	0.06	0.810
	Head depth	0.095	0.05	0.823
	Head width	0.320	1.80	0.191
	Jaw length	−0.119	0.36	0.555
	Bite force	−0.035	0.99	0.330
Duration of tail lashes	SVL	0.044	1.13	0.298
	Mass	−0.005	0.00	0.966
	Head depth	−0.330	0.39	0.539
	Head width	0.098	0.11	0.745
	Jaw length	0.010	0.00	0.969
	Bite force	0.018	0.16	0.693
Number of bites	SVL	−0.017	2.68	0.114
	Mass	−0.001	0.00	0.988
	Head depth	0.308	5.11	<i>0.033</i>
	Head width	−0.203	6.92	<i>0.014</i>
	Jaw length	0.021	0.11	0.748
	Bite force	0.009	0.57	0.458
Duration of bites	SVL	−0.018	0.56	0.462
	Mass	0.027	0.16	0.692
	Head depth	0.268	0.77	0.389
	Head width	−0.414	5.66	<i>0.025</i>
	Jaw length	0.008	0.00	0.956
	Bite force	0.033	1.62	0.214

more head bobs per minute ($t=5.698$, $df=57$, $P<0.0001$) than their opponent, while there was no significant difference in the number of bites ($t=0.664$, $df=57$, $P=0.509$) or duration of bites ($t=0.906$, $df=57$, $P=0.369$), push-ups ($t=0.985$, $df=57$, $P=0.329$) or tail lashes per minute ($t=1.762$, $df=57$, $P=0.083$).

Given the relatively weak predictive capacity of our model incorporating bite force and jaw length, we used fighting abilities, estimated from the outcome of contests in the tournament (i.e. a relative score based on which males beat and were beaten by which other males), as measures of individual RHP (BTabilities; Turner and Firth 2012). There was a significant positive relationship between contest aggression score (intensity) and loser RHP (standardised estimate=0.388, $P=$

0.003, $R^2=0.15$), while the relationships between contest intensity and winner RHP was positive and non-significant (standardised estimate=0.170, $P=0.202$, $R^2=0.029$). Furthermore, the relationship between contest intensity and the measure of RHP asymmetry between opponents was negative and non-significant (RHP asymmetry: standardised estimate=−0.087, $P=0.078$, $R^2=0.054$). This pattern suggests a pure self-assessment model (e.g. E-WOA or WOA-WA). The number of displays per minute (head bobs and push-ups) performed during contests was significantly positively correlated with loser RHP (standardised estimate=0.274, $P=0.038$, $R^2=0.075$), but not with winner RHP or RHP asymmetry (winner RHP: standardised estimate=0.076, $P=0.304$, $R^2=0.018$; RHP asymmetry: standardised estimate=−0.087, $P=0.274$, $R^2=0.021$).

Discussion

Staged contests between male Lake Eyre dragon lizards, *C. maculosus*, involved both displays (head bobs and push-ups) and physical aggression (biting and chasing), and bite force, a measure of ‘weapon performance’, was the only significant predictor of fighting ability. Neither body size nor prior experience (winning or losing in the previous two encounters) were significant predictors of fighting ability. Furthermore, size did not predict the number or duration of specific aggressive behaviours. Instead, the only behaviours predicted by morphological traits were the number and duration of bites (per minute): males with relatively deeper and narrower heads bit their opponents more frequently, and males with narrower heads bit for longer. We found no relationship between contest intensity and RHP asymmetry between contestants or RHP of the winner but a significant relationship with the RHP of the loser. This is consistent with pure self-assessment as the basis for the decision to withdraw from a contest. We also found that the number of displays (head bobs and push-ups) per minute were significantly positively correlated with the RHP of the contest loser, suggesting that weaker individuals may limit the ability of opponents to accurately assess RHP by performing fewer communicative behaviours (Mesterton-Gibbons and Heap 2014).

Our results are consistent with the general prediction that weapon performance may be a better predictor of fighting ability than morphological traits (size, condition, ornamentation) in contests that frequently escalate to physical aggression. Bite force is a common measure of weapon performance in lizards and is an important determinant of contest outcome in multiple species (Lailvaux et al. 2004; Huyghe et al. 2005; Husak et al. 2006; Lailvaux and Irschick 2007; Henningsen and Irschick 2012). Furthermore, bite force appears to better predict contest outcome than ornament size or morphological

traits within and between species when contests are more likely to escalate. In species where bite force predicts contest outcome, contests regularly escalate to biting (Lailvaux et al. 2004; Huyghe et al. 2005; Husak et al. 2006; Lailvaux and Irschick 2007; Henningsen and Irschick 2012), whereas in species where bite force does not predict contest outcome (which is instead predicted by ornament size or quality), contests do not escalate to physical aggression (e.g. Hamilton et al. 2013). Further indirect evidence comes from Caribbean *Anolis* lizards in which bite force predicts male contest success in species that are more sexually dimorphic and territorial, whereas dewlap size predicts contest success in species that are less dimorphic and territorial (Lailvaux and Irschick 2007). This pattern is also evident within species, for example, in *Anolis carolinensis*, there appears to be two male ‘life stages’ that differ in age and fighting tactics. Contests between ‘lightweight males’, which have smaller heads, lower bite forces and higher display rates, did not escalate to biting, and contest outcome was predicted by which male was the first to occupy and retain the perch. Conversely, contests between ‘heavyweight males’, which have larger heads, higher bite forces and lower display rates, frequently escalated to biting, and contest outcome was best predicted by bite force (Lailvaux et al. 2004). Overall, therefore, the relationship between male traits and RHP appears to differ depending on the propensity for contests to escalate, which in turn will depend on numerous factors such as resource value and costs of escalation.

The value of contested resources and costs of escalation also have direct bearing on the assessment strategy that individuals should use to decide when to withdraw from a contest. Specifically, assessment strategies are expected to shift from mutual to self-assessment with increasing value of the contested resources and with increasing cost of escalation when resource value is high (Mesterton-Gibbons and Heap 2014). This pattern appears to hold among species of fig wasps (Mesterton-Gibbons and Heap 2014) and within several species where individuals switch from mutual assessment during display-only phases of a contest to self-assessment during more costly phases involving physical aggression (Morrell et al. 2005; Elias et al. 2008; Hsu et al. 2008; Kasumovic et al. 2011). The use of self-assessment by *C. maculosus* is consistent with these general predictions. In this species, the costs of escalation are likely to be high not only due to potential injury inflicted during contests but also the high cost of energy expenditure in the extreme environment inhabited by the species. The dry salt lakes may reach temperatures of >60 °C in the shade, which is only provided by small pieces of driftwood deposited in floods and buckling of the salt crust. There is no free water, their food contains almost no moisture and lizards must conserve water by retreating to burrows in moist sand beneath the crust. Therefore, energy expenditure for contests is likely to be costly in

terms of thermal and hydro-regulation. Furthermore, resource value is likely to be high because territorial males may gain exclusive access to females (Mesterton-Gibbons and Heap 2014), and a relatively small proportion of males appear to be able to defend territories in *C. maculosus* (16 % estimated by Olsson 1995b).

Self-assessment is also expected when the cost effectiveness of opponent assessment decreases, regardless of resource value and contest costs (Mesterton-Gibbons and Heap 2014). This view assumes that only weak individuals benefit from their opponent making a strategic error (i.e. the stronger individual deciding to withdraw when it would have won the contest had it persisted). Strong individuals are not expected to benefit by their opponent making a strategic error because they do not benefit if a weaker opponent persists when it should have withdrawn; the stronger individual will ultimately win regardless. Mesterton-Gibbons and Heap (2014) term this the ‘information-conflict hypothesis’, which predicts that weak individuals will attempt to limit information transfer by performing fewer or less informative communicative behaviours (displays) and therefore that these behaviours will be associated with the absolute RHP of individuals rather than the relative RHP of contestants. Our data support this hypothesis because the number of communicative behaviours (head bobs and push-ups) performed per minute was positively associated with the RHP of losers rather than that of winners or the RHP difference between contestants. Furthermore, winners performed more behavioural elements during contests, consistent with the view that winners are more willing to communicate information about their ability than losers.

Although our data identified bite force as the best predictor of contest success, the model had weak predictive power, suggesting that other unmeasured factors were affecting the outcome of contests. This may in part be due to the artificial setting of experiments, affecting intrinsic individual motivation to interact. Low motivation to interact in a laboratory setting is also indicated by the relatively high proportion of trials in which there was no interaction; however, this may also be due to personality differences between males or due to males adopting different behavioural strategies (territorial versus floater males; Olsson 1995b). Thus, the results of these experiments, although consistent with expectations based on the biology and natural history of the species, must be treated with caution. More generally, it is invariably difficult to know how behaviour in a laboratory setting translates to behaviour in the wild. Nevertheless, the effect size of bite force was comparable, if not higher than the effect size of morphological traits in other lizard contests (e.g. Stuart-Fox and Johnston 2005; Stuart-Fox et al. 2006); a male with a bite force two standard deviations greater than his opponent would have an 80 % chance of winning the contest, all else being equal.

Overall, our results suggest that bite force is a moderate predictor of fighting ability in staged contests between *C. maculosus* males in a laboratory setting and that it is a stronger predictor of contest outcome than body size or head shape. Additionally, in contrast to staged encounters in many other species, including closely related species such as the tawny dragon, *Ctenophorus decresii* (Stuart-Fox and Johnston 2005), we found no effect of prior experience on fighting ability despite a relatively short period between consecutive contests for individual males (1–2 days). Instead, our results support the view that measures of physical performance may be more reliable indicators of male fighting ability than morphological traits in escalated contests, irrespective of prior experience. This may be because performance measures are more directly linked to the quality being signalled (i.e. fighting ability) and perhaps also because they implicitly incorporate differences in motivation between contestants. Our study is also among a growing number that suggest that individuals base their decision to withdraw from a contest on assessment of their own cost threshold (i.e. self-assessment) rather than assessment of their opponent's ability (mutual assessment). Self-assessment is expected when both resource value and the cost of escalation are high, as likely to be the case in *C. maculosus*. Lastly, our results are consistent with the recently proposed 'information conflict hypothesis' because the RHP of losers (but not winners or RHP asymmetry) was correlated with the number of communicative behaviours (head bobs and push-ups) performed during the contest, suggesting that weaker individuals limit information transfer about their ability by performing fewer displays.

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