ORIGINAL ARTICLE



Influence of prior contest experience and level of escalation on contest outcome

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Abstract

An individual's contest history can have a significant effect on their probability of winning a future contest. These winner-loser effects are likely to be mediated by the level of escalation in a contest, although this is rarely considered in the contest literature. We staged contests between sizematched male water skinks (Eulamprus quoyii) in a tournament design to investigate how prior contest success indirectly affected contest outcome through its effects on contest behavior. Moreover, we predicted that the effect of behavioral traits on contest outcome would depend on the level of escalation reached by contestants (non-escalated versus escalated contests). Contest initiation was the best predictor of contest outcome in both non-escalated and escalated contests, and whether an individual initiated a contest depended on prior contest experience. Prior winners were more likely to initiate subsequent aggressive encounters, and by doing so, initiators had an 88 % probability of winning compared to non-initiators in nonescalated contests. However, this effect was mediated by

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Fonti Kar fonti.kar@gmail.com the level of escalation. Initiators in escalated contests had only a 59 % probability of winning compared to non-initiators. These results suggest that the strength of the effect of prior contest experience on behavioral traits varies across contest stages and is consistent with the hypothesis that prior contest experience alters an individual's perception of its own fighting ability. Our study highlights the importance of considering the level of contest escalation when examining winner–loser effects in predicting contest outcome.

SIGNIFICANT STATEMENT

Our results show that the effect of prior contest experience on contest initiation varies depending on the level of escalation reached by the contestants. We emphasize the importance of considering the level of contest escalation when examining the influence of prior contest experience on contest outcome.

Keywords Contest history · Lizard · Contest initiation · Contest escalation · Bradley-Terry model · Tournament design

Introduction

The outcome of dyadic contests can be determined by asymmetries in multiple traits between contestants. For example, differences in rivals' morphology (e.g., body and head dimensions, Olsson 1992; Stuart-Fox et al. 2006), whole-organism performance (e.g., bite force, Husak et al. 2006), and behavior (e.g., aggressive displays, Molina-Borja et al. 1998; Osborne 2005; Martínez-Cotrina et al. 2014) are some factors that can influence an individual's probability of winning a contest. In addition to these intrinsic traits, prior contest experience has

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also been reported to affect contest outcome, where prior winners tend to have a higher probability of winning in subsequent contests, while prior losers have a decreased probability of winning in future contests (winner-loser effects, reviewed in Hsu et al. 2006). It has been hypothesized that prior contest experience affects outcome because it alters an individual's perception of its own fighting ability (Hsu et al. 2006). Perceived fighting ability may increase or decrease depending on whether a previous contest resulted in a win or loss and act by influencing an individual's fighting behavior in subsequent contests (Hsu and Wolf 2001). Behavioral modification, after having won or lost a prior contest, can therefore affect the probability of winning subsequent contests (Hsu et al. 2006). Despite this common view, the effects of prior contest experience are often considered as the direct cause for winner-loser effects, and the behavioral mechanisms that influence contest outcome are rarely discussed (Hsu and Wolf 2001; Garcia et al. 2012, 2014). Previous contest experience should indirectly affect contest outcome via changes to an individual's behavior (e.g., Fig. 1), as opposed to having a direct causal effect on contest outcome per se.

Animal contests are highly variable and often progress through stereotyped stages of display before escalating to physical fighting. For example, the Gallot's lizard (Gallotia galloti) compresses its body laterally and performs throat extensions and head bobs in the early stages of a contest. As the interaction escalates, individuals often chase, circle, and bite each other (Molina-Borja et al. 1998). Typically in non-escalated contests, rivals can resolve conflict without physical contact via displays that convey information about an individual's fighting ability (Smith and Parker 1976; Enquist and Leimar 1983). However, when rivals are similar in fighting ability, they often need to fight in order to resolve contests (Smith and Parker 1976; Enquist and Leimar 1983). Since the behavior exhibited by contestants varies with the level of contest escalation, the effects of prior contest experience on these behavioral traits and therefore contest outcome should also be context-dependent (Fig. 1). For example, male field crickets (Gyrllus bimaculatus) that lost a fight became more submissive and unresponsive to the threat displays of other males (Adamo and Hoy 1995). However, males that won in a previous fight were quicker to attack and thus were more likely to deter rivals (Adamo and Hoy 1995). These results suggest that prior contest experience could affect behavior in a context-dependent manner. This, in turn, could affect the outcome of a contest (Fig. 1) although this line of thinking has rarely been considered in the contest literature.

Lizards have been widely used as model species to test contest theory (Whiting et al. 2003; Baird 2013). Previous studies on the role of prior experience, however, have produced mixed results (Online Resource 1). Losing has been shown to decrease the probability of winning (Schuett 1997; Garcia et al. 2012, 2014), and prior winners of contests have been shown to have a higher probability of winning subsequent contests in some systems (Zucker and Murray 1996; Stuart-Fox and Johnston 2005; Stuart-Fox et al. 2006). However, there have also been a number of studies that have failed to show an effect of prior experience on contest outcome (Scott et al. 2013; McLean and Stuart-Fox 2014). Part of the reason why such disparate results exist may relate to the context-dependent effects of prior contest experience on behavioral traits (Fig. 1). In most lizard studies, previous contest experience is often assumed to directly influence the probability of winning, and only few studies have considered the importance of behavioral traits as determinants of contest outcome (Garcia et al. 2012, 2014). Even fewer studies directly investigate whether prior contest experience on behavior varies across different stages of a contest. Potential winner-loser effects may be difficult to detect, if prior contest experience has opposing effects on behavioral traits at different stages of a contest.

We investigated whether prior contest experience can influence contest outcome and the role of behavior at different levels of contest escalation in male eastern water skinks (Eulamprus quoyii). Male contests in this species follow a distinct sequence, where usually one male approaches his rival as an attempt to chase him away. Often, the rival will retreat immediately. In some instances, the pair will engage in stereotyped circling behavior before escalating to tail biting. However, contest duration and intensity can be highly variable (Online Resource 2). Contests were staged between size-matched lizards in a "tournament" design (Whiting et al. 2006), where males competed with multiple opponents. We followed a protocol where once a clear contest outcome was determined, opponents were immediately separated. No contests resulted in any injuries to a lizard. We recorded whether the contest escalated to physical biting by at least one individual, the initiator of the contest, and the number of times an individual bit his rival. We predicted that (1) contest initiation will be the best predictor of contest outcome in non-escalated contests because an individual's motivation to initiate may be telling of his aggressiveness, which could influence his probability of winning (Jackson 1991); (2) the total number of bites by a male will be an important predictor of contest outcome in escalated contests because the ability to inflict more damage than a rival may be an important determinant of contest outcome. Moreover, biting behavior may also be a cue used to assess an opponent's aggressiveness; and (3) winning a previous contest will increase the probability of initiating a contest and the number of times a



Fig 1 Previous contest experience should indirectly affect contest outcome via changes to an individual's behavior. However, the effect of prior contest experience should depend on the level of contest escalation. *Bold lines* indicate a strong effect of prior contest experience on behavior and therefore contest outcome; *thin lines* indicate a weak effect. In non-escalated contests, we predict that contest initiation will be an important predictor of contest outcome (*top*). Moreover, contest experience will

male bites his rival. (4) If contest initiation affects contest outcome, it should be more important in non-escalated contests.

Methods

Study species and collection

The eastern water skink (E. quoyii) occurs in close proximity to streams in southeast Australia (Law and Bradley 1990). Males and females are similar in appearance although males have slightly larger heads and weigh more than females of the same body length (Schwarzkopf 2005; Noble et al. 2014). The breeding season typically begins in late September and ends in October although males may be aggressive beyond the actual breeding period (Veron 1969; Noble et al. 2013a, b). To reduce the impact on local populations brought about by removing males for experiments and to control for familiarity between animals, 56 adult male lizards were collected from nine different sites across the Sydney region during 14-30 September 2014. Lizards were captured either by hand or by noosing and were placed in cloth bags. Individuals were transported in an ice cooler to Macquarie University within 2 h of capture. We recorded the following body dimensions to the nearest 1 mm: snout-to-vent length (SVL; from tip of snout to the beginning of the cloaca opening), total body length (from tip of snout to the distal tip of the tail), and body

affect an individual's propensity to initiate contests. In escalated contests, we predict that the total number of times an individual bites his rival will be an important predictor of contest outcome compared to contest initiation (*bottom*). Furthermore, we predict that prior contest experience influence the total number of times an individual bites his rival more strongly compared whether or not he initiates a contest

mass (g). We measured the following head dimensions to the nearest 0.01 mm using digital calipers: head width (widest point of head), head depth (maximum height of the occiput region), and head length (anterior edge of the tympanum to the tip of the snout). Lizards were kept individually in opaque plastic tubs measuring 350 (W) \times 487 (L) \times 280 (H) mm. We placed part of the tubs on heat cables in order to generate a thermal gradient for thermoregulation, and each tub had its own ultraviolet light. Males had access to a refuge, a water bowl, and were fed crickets or dog food three times a week.

Male contests

All lizards were acclimated to lab conditions for 8 days before contest trials took place. Male contests were carried out between 22 September and 12 October 2014 in a temperaturecontrolled room set at 28 °C. We used a tournament design instead of a random selection design (Beaugrand and Goulet 2000) because *E. quoyii* is a relatively long-lived species, and thus, we were unable to raise naïve individuals to sexual maturity (ca. 2 to 3 years) in captivity to ensure that they did not have any prior contest experience. Tournament designs have been criticized as a way to test for prior contest experience effects because differences in intrinsic fighting ability between contestants may be confounded with experience effects. However, we attempt to control for these potential intrinsic differences between contestants by size-matching each pair using SVL (mean size difference = 1.34 mm, range = 0–

5 mm) in our tournament design. The method with which to size-match individuals was based on other lizard studies (e.g., McLean and Stuart-Fox 2014; Stuart-Fox et al. 2006; Whiting et al. 2006). Individuals participated in on average 4.65 contests (range = 2-7 contests) with different opponents. Certain lizards were paired more often than others as not all lizards could be size-matched with opponents for more than two contests (Whiting et al. 2006). Contest trials took place in opaque plastic arenas measuring 470 (W) \times 690 (L) \times 455 (H) mm, partitioned in half using a wooden divider. Each male occupied half of the arena. The substrate of the arena was lined with newspaper, and males had access to a refuge and water. Males were left to habituate in the arena for 1.5 days for logistical reasons before contests took place. On the day of the contests, refuges, water bowls, and dividers were removed to allow males to interact without obstruction. Contests were usually resolved within 15 min of removing the divider. Contests were closely monitored so that once a clear outcome was reached, the opponents were immediately separated to avoid possible injury. A clear contest outcome occurred when one of the male lizards fled from his opponent following an aggressive behavior and the lizards were at least half a body length apart. Overall, contests were relatively short-lived, averaging 87 s. Given the short duration of contests, most lizards were unlikely to have experienced prolonged stress. After each contest, males were immediately placed in a new arena with a new opponent that had also fought in the previous round, separated by an opaque divider. All opponents were again size-matched. All arenas were cleaned and lined with new substrate before placing new pairs inside. Refuges and water bowls were returned to the males, and they were left to habituate for 1.5 days before the next contest. All contests were digitally recorded using CCTV cameras (digital video

recorder, model no. H.264, and dome security cameras, model no. NCDP).

Contest behavior

We scored the following from the video footage: (1) the frequency of head bobs, tongue flicks, and small and large tail waves during the 20-s period prior to and after the first interaction that led to a clear outcome (Table 1); (2) which male was the initiator of the interaction; (3) aggressive and submissive behavior that occurred during the interaction (Table 1); (4) whether the interaction took place in the eventual winner's or loser's half of the arena; (5) whether the contest escalated to physical biting by at least one individual; (6) the duration of the contest, recorded from the start of the first behavioral interaction that led to a contest outcome, until a clear outcome occurred; and (7) the winner and loser of the first interaction that led to a clear outcome. A winner was defined as an individual that consistently displayed aggressive behavior to his opponent, while a loser was defined as an individual that exhibited submissive behavior and moved away from his opponent. We coded whether a male won previously in the most recent contest. Males were assigned with a score of 1 for winning the previous contest and 0 for losing. The first fight of a given male was given a score of 0, as contestants did not have any prior wins yet (Stuart-Fox et al. 2006). All videos were scored blind, in order to minimize observer bias. To calculate repeatability of video scoring, we recorded the frequency of all behaviors on two occasions from a subset of 20 videos. Repeatability was defined as the percentage of videos, for each behavioral trait, that did not differ in recorded frequencies between the two occasions. Across all behaviors, the average repeatability score was 88 % (SE 3.54).

Table 1Contest behavior ofEulamprus quoyii recorded fromvideo footage

Behavior	Description
Aggressive	
Approach	Gradual, step-by-step movement toward opponent
Chase	Rapid movement toward opponent over a 1-s period
Nudge	Small push to the side of the body of opponent using snout
Tail bite	Bite to the tail of opponent
Flank bite	Bite to the side of the body of opponent
Head bite	Bite to the head of opponent
Submissive	
Retreat	Gradual, step-by-step movement away from opponent
Flee	Movement away from opponent over a 1-s period
Other	
Tongue flick	Extension and retraction of the tongue occurring within less than 1 s of each other
Head bob	Up and down head movement
Small tail wave	Rapid, side-to-side undulation of tail tip at approximately 20°
Large tail wave	Moderately slow, side-to-side undulation of tail approximately at 45°-60°

Statistical analyses

Fifty-six individuals were used in a total of 165 contests. Forty-two contests were discarded because males either failed to interact or there was no clear outcome. The Bradley-Terry (BT) model was used to investigate which male traits or behavior predicted the probability of winning a contest. For all continuous male-specific traits (SVL and body mass), we used standardized coefficients scaled to have unit standard deviation. We combined all biting during a contest into a "total number of bites" variable because bites were hardly ever directed at the head, neck, or flank region (Online Resource 2). The total number of bites was heavily right-skewed, and as a consequence, we log (x + 1) transformed this variable for our final analyses. We ran separate analyses using rank transformed and normalized total number of bites by calculating quantiles from a normal distribution with a mean = 0 and standard deviation = 1 to check if the underlying distribution of the variable was driving effects. Contest duration was also log-transformed to improve normality. All data were analyzed using R and the packages BradleyTerry2 and Ime4 (R Development Core Team 2010; Turner and Firth 2012; Bates et al. 2015).

The BT model is a logistic model for paired comparisons, and the standard equation can be expressed in a logit-linear form:

$$logit[pr(i \text{ beats } j)] = \lambda_i - \lambda_j$$

where *i* and *j* are the lizards in a contest and the probability of lizard *i* beating lizard *j* is a function of the difference in "fighting abilities" (λ) of each lizard. Fighting ability is calculated from differences in individual specific traits such as body dimensions as well as contest-specific traits (for more details, Stuart-Fox et al. 2006 and Turner and Firth 2012). Contestspecific traits are variables that vary between contests and can interact with the two players' probability of winning a contest. We incorporated a lizard's contest history and behavior such as contest initiation and total number of bites as contestspecific traits. We included standardized SVL and body mass, in our initial analyses to check if we had effectively sizematched the lizards. In these initial analyses, standardized SVL did not predict contest outcome; therefore, this was excluded in our final models. However, body mass appeared to be important in some analyses suggesting that we did not fully account for mass differences between our contestants. As a consequence, we included standardized body mass in all our models as a covariate and we predicted that small differences in body mass will result in longer contest duration, particularly in escalated contests. We assessed the following key predictors on the probability of winning for all contests (non-escalated and escalated): standardized body mass, contest history, and contest initiation. We predicted that the effect of contest

initiation would depend on whether the contest escalated or not (Fig. 1); therefore, we fitted an interaction term between these variables. Our overall model for all contests is thus given by

logit[pr(i beats j in contest k)]

$$= \beta(m_i - m_j) + \delta(z_{ik-l} - z_{jk-l}) + \gamma(g_{ik} - g_{jk})$$
$$+ \upsilon(g_i ck - g_j ck) + e_i - e_j$$

where *m* represents the body mass of lizard *i* or *j*, z_{ik-1} represents whether lizard *i* won the contest prior to contest *k* (same for lizard j i.e., z_{ik-1}), and g_{ik} indicates whether lizard i initiated contest k (same for lizard j i.e., g_{ik}). When $g_{ik} = 1$, lizard i has a contest initiation advantage over lizard *j* (Agresti 2002; Turner and Firth 2012). ck indicates whether the contest was escalated or not and is the same value for both lizards. e_i and e_i are the random effects for lizards *i* and *j*, respectively. Since both lizards have the same value for contest escalation (ck), it is not possible to estimate the main effect for contest escalation in the BT model as the effects are essentially canceled out. Nonetheless, the estimates and standard errors for the other parameters are still valid (H. Turner, pers. comm.) and can be used to test the prediction that the effects of contest initiation on contest outcome depend on escalation stage (i.e., escalated or not).

To explore whether biting influenced contest outcome, given that it only occurred in escalated contests, we ran a separate BT model for escalated contests including key predictors mentioned above in addition to total number of bites, $\tau(t_{ik}-t_{jk})$, where t_{ik} represents the total number bites from lizard *i* in contest *k*, whereas t_{jk} represents the total number bites from lizard *j* in contest *k*. To test the robustness of our results, we used the same predictors as the BT models in generalized linear mixed models (GLMMs) (Online Resource 3). We included fight and male ID as random effects to account for nonindependence given that males were repeated in multiple contests and similarities resulting from males being in the same contest. All GLMM analyses were similar to our BT model; thus, we present results from the BT models only.

We predicted that contest history could affect the probability of winning a contest indirectly through modification of male behavior (Fig. 1). We used a GLMM to assess whether contest history predicted the probability of initiating a contest (1 = initiated, 0 = not initiate) and the total number of bites in escalated contests. Standardized body mass was included as a covariate. We also used a GLMM to investigate whether residual body mass differences and prior contest experience influence the probability of a contest escalating.Data for this study is available from DOI:10.6084/m9.figshare.3444884.



Fig 2 Relationship between residual body mass differences and log duration of escalated contests. *Solid line* is the line of best fit as predicted by the model. *Dashed lines* indicate the upper and lower 95 % confidence intervals of the predicted mean

Results

We observed two distinct types of contest between rival male E. quovii. In non-escalated contests, conflict was resolved without physical contact between the contestants, while in escalated contests, the interaction escalated to physical biting by at least one individual (Online Resource 2). Eighty five of the 123 (69 %) contests were resolved without escalation, and the mean contest duration for non-escalated contests was 10.70 s (range = 0.40–473.20, SE = 5.84). Thirty eight of the 123 (31 %) contests escalated to physical biting, and the mean contest duration for escalated contests was 86 s (range = 1-818, SE = 23). As predicted, contest duration of escalated contests was longest when there was a small difference in standardized body mass between contestants (Fig. 2). Only 28 % (n = 35/123) of contests were resolved in the winner's area, suggesting that the time the lizards were in their experimental arenas was insufficient for any significant residency effect.

Behavioral predictors of contest outcome

Our overall BT model (including both non-escalated, n = 85, and escalated, n = 38, contests that resulted in a clear winner and loser) predicted 78/123 contests successfully when considering predicted probabilities of greater than or equal to 0.75 as sufficient to assign the winner of a contest. The median predicted probability that lizard *i* beats lizard *j* from our model was 0.83 (mean = 0.73, SE = 0.02, N = 123).

Winners initiated 97/123 (79 %) contests, and our BT model suggested that contest initiation was a significant predictor of the probability of winning a contest. However, this effect was dependent on whether a contest escalated or not (Table 2, Fig. 3). In non-escalated contests, a lizard that initiated a contest had an 88 % probability of winning (Fig. 3). In contrast, **Table 2** Bradley–Terry (BT) model examining the effects of contest initiation, contest escalation, prior contest history (i.e., whether a male won his last contest), and standardized body mass $[x-\overline{\mu}(x)/\overline{\sigma}(x)]$ on the log odds of winning a contest

Variable	Estimate	SE	Ζ	$P(\geq Z)$
Contest initiation (initiate)	1.7842	0.3561	5.011	5.42e-07
Escalate (escalated contest)	NA	NA	NA	NA
Previous win (won previous)	0.4322	0.4782	0.904	0.36618
Standardized body mass	1.0224	0.3591	2.847	0.00441
Contest initiation × escalate	-1.4228	0.5219	-2.726	0.00641

The main effect for "escalate" cannot be estimated in the BT model because lizard *i* and lizard *j* have the same value for escalate. The model includes both escalated and non-escalated contests (n = 123). Bolded estimates are significant

the effect of contest initiation on contest outcome was smaller for escalated contests (59 % of winning; Fig. 3).

Body mass appeared to be an important predictor of contest outcome (Tables 2 and 3). Our BT model predicted that a 1 standard deviation increase in the difference in mass, all else being equal, increases the estimated probability of winning by $\exp(1.0224) / (1 + \exp(1.0224)) = 0.74$ for the heavier male. Body mass, however, was not a significant predictor in the GLMM analyses (Online Resource 3, Tables 1 and 2).



Fig 3 Predicted probability of winning calculated from a BT model (Table 2) is dependent on whether a lizard initiated a contest and the type of contest (escalated versus non-escalated). Body mass was set at the mean, and contestants had won their previous contest. *Gray bars* represent non-escalated contests, while *white bars* represent escalated contests. *Error bars* represent standard error

Table 3 Bradley–Terry model examining the effects of contest initiation, log total number of bites, prior contest history (i.e., whether a male won his last contest), and standardized body mass $[x-\overline{\mu}(x)/\overline{\sigma}(x)]$ on the log odds of winning an escalated contest (n = 38)

Variable	Estimate	SE	Ζ	$P(\geq Z)$
Contest initiation (initiate)	0.1572	0.5220	0.301	0.7633
Log total bites	2.1490	0.9869	2.177	0.0294
Previous win (won previous)	-1.4822	1.1343	-1.307	0.1913
Standardized body mass	2.0584	0.8558	2.405	0.0162

Bolded estimates are significant

We predicted that the total number of times a male bit his rival would be important in determining contest outcome in escalated contests. The BT model using only escalated contests suggested that the log total number of bites was a significant predictor of contest outcome (Table 3). However, this effect was not significant in GLMM analyses (GLMM: estimate = 1.1136, SE = 0.6950, Z = 1.602, P = 0.109, N = 38). Given the highly skewed nature of this variable, we re-ran our GLMM using normalized quantiles of ranked total number of bites, which returned a nonsignificant result (estimate = 1.5137, SE = 0.8938, Z = 1.694, P = 0.0904, Online Resource 3, Table 2). Overall, there was no strong effect of the total number of times a lizard bit his rival on contest outcome in escalated contests, although there was a positive trend.

Prior contest experience on behavior and contest outcome

Winning experience (i.e., whether a male won his prior contest) did not directly affect the probability of a male winning a contest in all our models (Tables 2 and 3). If prior wins indirectly affect contest outcome through behavioral changes, we predicted that it might do so through motivational changes in subsequent contests (contest initiation). As predicted, prior winners had a higher probability of initiating their next contest (Table 4, Fig. 4). For an evenly matched pair, a lizard who had won his previous contest had an increase in the estimated probability of initiating by $\exp(0.7097) / (1 + (\exp(0.7097)) = 0.67$. Previous contest history and standardized body mass did not have an effect on the log-transformed total number of times a male bit his rival in escalated contests (GLMM; prior win: estimate = 0.0746, SE = 0.1598, t = 0.4670, P = 0.6436; standardized body mass: estimate = -0.0508, SE = 0.1068, t = -0.4758, P = 0.6367). Neither residual body mass differences nor previous winning experience were significant predictors of contest escalation (body mass difference: estimate 0.4238, SE = 1.1129, Z = 0.381, P = 0.703; prior win: estimate = 0.6352, SE = 1.7322, Z = 0.367, P = 0.714).

Table 4 Generalized linear mixed effects model (GLMM) examining the effects of prior contest history (i.e., whether a male won his last contest) and standardized body mass $[x-\overline{\mu}(x)/\overline{\sigma}(x)]$ on the log odds of initiating a contest

Variable	Estimate	SE	Ζ	$P(\geq Z)$
Intercept	-0.3168	0.1889	-1.677	0.0935
Previous win (Won previous)	0.7097	0.3075	2.308	0.0210
Standardized body mass	0.1226	0.1484	0.826	0.4088

The model includes both escalated and non-escalated contests (n = 123). Bolded estimates are significant

Discussion

Contest initiation in non-escalated contests strongly predicted contest outcome in *E. quoyii*, whereas there was a non-significant trend between the total number of bites and the probability of winning in escalated contests. As we predicted, previous winning experience did not influence contest outcome directly. Instead, contest experience acted indirectly on contest outcome by affecting the probability that a male initiated a contest. In accordance with contest theory (Enquist and Leimar 1983), we show that contests involving males that were similar in mass tended to be longer compared to contests involving males that were more asymmetric in mass.

Lizards that won their previous contest were more likely to initiate future contests, which increased their probability of winning. This supports the hypothesis that prior winning experience influences fighting behavior to indirectly affect contest outcome. Jackson (1991) proposed that individuals should only initiate when they are likely to win a contest. Previous



Fig 4 Predicted probability calculated from a GLMM (Table 3) examining the effects of prior contest experience on contest initiation. Body mass is set at the mean. *Error bars* represent standard error

contest experience may inflate an individual's estimation of his own fighting ability and thus increase his likelihood of initiating (Hsu et al. 2006). Motivation to fight may be an assessment cue used in contests because initiators of agonistic interactions may appear more aggressive and threatening to rivals. In support of this, Stuart-Fox et al. (2006) found that previous contest experience is one of the key predictors of contest outcome in dwarf chameleons. Winners tended to be more aggressive and initiated contests significantly more than losers (Stuart-Fox 2006). In green anoles (Anolis carolinensis), lizards that initiated contests, regardless of assigned prior contest experience, were more likely to win compared to noninitiators (Garcia et al. 2012, 2014). There is also the possibility that non-initiators may also be less motivated to initiate a fight due to prior losing experience. In male copperhead snakes (Agkistrodon contortix), prior winners did not initiate more via displaying compared to size-matched contestants; however, prior losers were less likely to initiate (Schuett 1997). Alternatively, prior winners may be more likely to initiate contests because they may be more intrinsically inclined to do so. Since we used a tournament design, we cannot remove intrinsic differences in motivation to fight between contestants with prior contest experience.

As predicted, the effect of prior contest experience on behavioral traits was context-dependent. We found that the effect of winning experience on initiation was most important in determining contest outcome in non-escalated contests. This result is in accordance with the hypothesis that contest experience influences an individuals' perception of its own fighting ability (Hsu et al. 2006). As interactions escalate to physical fighting, contestants may be more able to retrieve accurate estimates of their fighting ability; thus, the outcome of escalated contests should be largely governed by the intrinsic fighting abilities of contestants rather than display behavior (Hsu et al. 2006). Similar results were reported in mangrove killifish (Rivulus marmoratus); losing experience decreased an individual's probability of initiating subsequent contests (Hsu and Wolf 2001). Conversely, winning experience did not affect the probability of initiating, but prior winners are more likely to escalate by engaging a rival with attacks (Hsu and Wolf 2001). Our result highlights the importance of considering how prior contest experience could influence behavior at different contest stages because the effect of prior contest experience could vary across contest stages. We recommend that future studies assess a range of behaviors that could influence contest outcome and incorporate the effects of prior contest experience in different escalation stages separately.

In escalated contests, the total number of times a male bit his rival was not a strong predictor of contest outcome; however, body mass difference between contestants affected contest duration. Body mass appeared to play an important role even after we had size-matched contestants within 1.6 % of each other's SVL. This suggests that mass is an important assessment cue used to resolve conflict between rivals. Mass could act as a visual cue, or it may be correlated with other traits that may be important in escalated fighting, such as endurance (Robson and Miles 2000). In aggressive contests, E. quovii often circle and contact each other while biting each other's tails. Males that are heavier may be able to endure such energetically demanding behaviors longer than lighter males. Body size is known to predict contest outcome in many reptile systems (Tokarz 1985; Schuett 1997). For example, in tree lizards, body mass and prior contest experience were the best predictors of contest outcome (Zucker and Murray 1996). Zucker and Murray (1996) found that a prior loser must weigh at least 1 g more than his opponent in order to have an equal chance of winning when faced with a previous winner, whereas a previous winner can still have an equal chance of winning if it was disadvantaged in mass by ca. 1 g. The total number of times a male bit his rival during a contest did not predict contest outcome in escalated contests. Moreover, this was not influenced by prior winning experience. This suggests that a male's intrinsic fighting ability during escalated contests such as his endurance, bite force, or aggressiveness may be more important in determining contest outcome and could affect the total number of bites he exerts. Despite the importance of body mass and total number of bites, contest initiation appears to be a better predictor of contest outcome overall.

Conclusions

In summary, we found that previous contest experience directly influences contest initiation, which ultimately influences contest outcome between male *E. quoyii*. We show that an effect of previous contest experience is context-dependent, with contest initiation being more important only in nonescalated contests. This result highlights the need to explicitly consider contest escalation phase when examining winner– loser effects and when making predictions regarding the importance of particular traits in predicting contest outcome.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All protocols for this study were in accordance with the ethical standards of the Macquarie University Animal Ethics Committee (ARA 2014/036). A scientific permit for this study was granted by the New South Wales National Parks and Wildlife Service, Office of Environment and Heritage (SL100328).

References

- Adamo SA, Hoy RR (1995) Agonistic behaviour in male and female field crickets, *Gryllus bimaculatus*, and how behavioural context influences its expression. Anim Behav 49:1491–1501
- Agresti A (2002) Categorical data analysis, 2 edn. John Wiley and Sons, Hoboken
- Baird TA (2013) Lizards and other reptiles as model systems for the study of contest behaviour. In: ICW H, Briffa M (eds) Animal contests. Cambridge University Press, New York, pp. 258–286
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixedeffects models using lme4. J Stat Softw 67:1–48
- Beaugrand JP, Goulet C (2000) Distinguishing kinds of prior dominance and subordination experiences in males of green swordtail fish (*Xiphophorus helleri*). Behav Process 50:131–142
- Enquist M, Leimar O (1983) Evolution of fighting behaviour: decision rules and assessment of relative strength. J Theor Biol 102:387–410
- Garcia MJ, Murphree J, Wilson J, Earley RL (2014) Mechanisms of decision making during contests in green anole lizards: prior experience and assessment. Anim Behav 92:45–54
- Garcia MJ, Paiva L, Lennox M, Sivaraman B, Wong SC, Earley RL (2012) Assessment strategies and the effects of fighting experience on future contest performance in the green anole (*Anolis* carolinensis). Ethology 118:821–834
- Hsu Y, Earley RL, Wolf LL (2006) Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. Biol Rev 81:33–74
- Hsu Y, Wolf LL (2001) The winner and loser effect: what fighting behaviours are influenced? Anim Behav 61:777–786
- Husak JF, Lappin AK, Fox SF, Lemos-Espinal JA (2006) Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). Copeia 2:301–306
- Jackson WM (1991) Why do winners keep winning? Behav Ecol Sociobiol 28:271–276
- Law BS, Bradley R (1990) Habitat use and basking site selection in the water skink, *Eulamprus quoyii*. J Herpetol 24:235–240
- Martínez-Cotrina J, Bohórquez-Alonso ML, Molina-Borja M (2014) Morphological and behavioural correlates of contest success in male yellow-headed geckos, *Gonatodes albogularis*: sequential assessment or self-assessment? Behaviour 151:1535–1554
- McLean CA, Stuart-Fox DM (2014) Rival assessment and comparison of morphological and performance-based predictors of fighting ability in Lake Eyre dragon lizards, *Ctenophorus maculosus*. Behav Ecol Sociobiol 69:523–531
- Molina-Borja M, Padron-Fumero M, Alfonso-Martin T (1998) Morphological and behavioural traits affecting the intensity and

outcome of male contests in *Gallotia galloti galloti* (family Lacertidae). Ethology 104:314–322

- Noble DW, Fanson KV, Whiting MJ (2014) Sex, androgens, and wholeorganism performance in an Australian lizard. Biol J Linn Soc 111: 834–849
- Noble DWA, Keogh JS, Whiting MJ (2013b) Multiple mating in a lizard increases fecundity but provides no evidence for genetic benefits. Behav Ecol 24:1128–1137
- Noble DW, Wechmann K, Keogh JS, Whiting MJ (2013a) Behavioral and morphological traits interact to promote the evolution of alternative reproductive tactics in a lizard. Am Nat 182:726–742
- Olsson M (1992) Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*. Anim Behav 44:386–388
- Osborne L (2005) Information content of male agonistic displays in the territorial tawny dragon (*Ctenophorus decresii*). J Ethol 23:189–197
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://cran.r-project.org/
- Robson M, Miles D (2000) Locomotor performance and dominance in male tree lizards, *Urosaurus ornatus*. Funct Ecol 14:338–344
- Schuett GW (1997) Body size and agonistic experience affect dominance and mating success in male copperheads. Anim Behav 54:213–224
- Schwarzkopf L (2005) Sexual dimorphism in body shape without sexual dimorphism in body size in water skinks (*Eulamprus quoyii*). Herpetologica 61:116–123
- Scott ML, Whiting MJ, Webb JK, Shine R (2013) Chemosensory discrimination of social cues mediates space use in snakes, *Cryptophis* nigrescens (Elapidae). Anim Behav 85:1493–1500
- Smith JM, Parker GA (1976) The logic of asymmetric contests. Anim Behav 24:159–175
- Stuart-Fox DM (2006) Testing game theory models: fighting ability and decision rules in chameleon contests. Proc R Soc Lond B 273:1555–1561
- Stuart-Fox DM, Firth D, Moussalli A, Whiting MJ (2006) Multiple signals in chameleon contests: designing and analysing animal contests as a tournament. Anim Behav 71:1263–1271
- Stuart-Fox DM, Johnston GR (2005) Experience overrides colour in lizard contests. Behaviour 142:329–350
- Tokarz RR (1985) Body size as a factor determining dominance in staged agonistic encounters between male brown anoles *Anolis sagrei*. Anim Behav 33:746–753
- Turner H, Firth D (2012) Bradley-Terry models in R: the Bradley Terry2 package. J Stat Softw 48:1–21
- Veron J (1969) The reproductive cycle of the water skink, Sphenomorphus quoyii. J Herpetol 3:55–63
- Whiting MJ, Nagy KA, Bateman PW (2003) Evolution and maintenance of social status-signaling badges. In: Fox S, McCoy J, Baird T (eds) Lizard social behaviour. The John Hopkins University Press, Baltimore, Maryland, pp. 47–82
- Whiting MJ, Stuart-Fox DM, O'Connor D, Firth D, Bennett NC, Blomberg SP (2006) Ultraviolet signals ultra-aggression in a lizard. Anim Behav 72:353–363
- Zucker N, Murray L (1996) Determinants of dominance in the tree lizard Urosaurus ornatus: the relative importance of mass, previous experience and coloration. Ethology 102:812–825