

PREDICTORS OF SOCIAL DOMINANCE AND ITS ROLE IN SOCIAL INFORMATION USE



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ANIMAL RESEARCH AUTHORITY (ARA)

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or Animal Welfare Officer - 9850 7758 / 0439 497 383*

The above-named are authorised by MACQUARIE UNIVERSITY ANIMAL ETHICS COMMITTEE to conduct the following research:
Title of the project: Predictors of contest outcome and the effects of social dominance on social learning in the Eastern Water Skink (*Eulamprus quoyii*)

Purpose: 4 - Research: Human or Animal Biology

Aims: 1) Determine the sequence of agnostic behaviour in male *E. quoyii*

2) Determine the predictors of male to male contests in *E. quoyii*

3) Investigate whether social dominance affects social learning in *E. quoyii*

Surgical Procedures category: 1 - Observation Involving Minor Interference

All procedures must be performed as per the AEC-approved protocol, unless stated otherwise by the AEC and/or AWO.

Maximum numbers approved (for the Full Approval Duration):

Species	Strain	Age/Sex/Weight	Total	Supplier/Source
27 Lacertilia	<i>Eulamprus quoyii</i>	Age from 2 years - 5 years/ Male	60	Macquarie University Campus, Lane Cove National Park, Sydney Olympic Park
		Total	60	

Location of research:

Location	Full street address
Macquarie University, Sydney Olympic Park, Elanora Golf Club, Narabeen	NSW, Australia

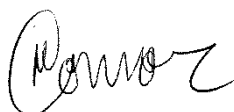
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- Amendment #1 – Addition of Pierre - Alexis Billa as Volunteer intern (Exec approved, ratified 16 October 2014)
- Amendment #2 – Addition of James Baxter - Gilbert as Volunteer (Exec approved, ratified 16 October 2014)
- Amendment #3 – Addition of Aloys Tack as Volunteer Intern (Exec approved, ratified 16 October 2014)
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- Amendment #5 – Addition of Marie Favre as Volunteer Intern (Exec approved, ratified 16 October 2014)
- Amendment #6 – Addition of Lorene Chieze as Volunteer Intern (Exec approved, ratified 16 October 2014)
- Amendment #7 – Amend experimental design (Approved by AEC 16 October 2014)

Conditions of Approval:

- Amendment #1,3,&5 - Volunteer/Volunteer Interns are supervised until competent in all procedures by the investigators nominated on the amendment
- Amendment #6 – Volunteer Inter is to be supervised until competent in all procedures by the investigators nominated on the amendment as well as attending the next WWRAW if she still at Macquarie University.

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.



Professor Mark Connor (Chair, Animal Ethics Committee)

Approval Date: 16 October 2014

DECLARATION

This thesis is written as a ‘thesis by publication’ and both my chapters are written and formatted for the journal Animal Behaviour.

I wish to acknowledge the following assistance in the research detailed in this report:

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All other research described in this report is my own original work.

Fonti Shuk Ming Kar (Student ID: 43538126)

9/10/2015

All protocols in this study were approved by the Macquarie University Animal Ethics Committee (ARA 2014/036) and collection of lizards was approved by the New South Wales National Parks and Wildlife Service, Office of Environment and Heritage (SL100328)

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SUMMARY

Social dominance is often determined through contest competition (physical combat). There are many factors that can influence the outcome of a contest, however very little is known about how prior contest experience can result in winner-loser effects. An individual's dominance status can have profound effects on its fitness and behaviour but the effects of dominance on the ability to learn from others remain poorly understood. I use male Eastern Water skinks (*Eulamprus quoyii*) to understand 1) how prior contest experience influences contest outcome and test whether this depended on assessment stage and 2) the role dominance plays on social information use. I begin by exploring how contest experience influences behavioural traits under different levels of escalation. I show that prior winners were more likely to initiate contests and by doing so, initiators were much more likely to win in non-escalated contests. I then tested the effects of an observer's dominance status of social information use in two association tasks. Contrary to my predictions, social dominance did not drive differences in social information use. Interestingly, lizards that viewed a demonstrator did not learn faster than the control group. My results, in light of a previous study on this species, seem to suggest that individuals may ignore social information from a demonstrator that may be similar in age or size. To the best of my knowledge, this study is the first to explore the effects on prior contest experience on behaviours in a context-dependent manner and to examine the effects of the outcome of these contests (i.e. dominance status) on social learning in a lizard.

INTRODUCTION

Contest competition, in which individuals of the same sex physically compete in aggressive interactions, is incredibly widespread. Contests play an important role in determining social dominance, where winners of fights tend to consistently dominate over losers for priority of access to limited resources (Drews, 1993). Contest competition is a strong selective force because winning fights leads to priority access to limited resources (Andersson, 1994). Thus, selection favours the evolution of physical traits such as large body size (Tokarz, 1985), weaponry (Emlen, 2008) and performance capacities (Briffa & Sneddon, 2007) that are advantageous for winning fights. However, evidence also shows prior contest experience playing an even more crucial role in determining the outcome of contests (Hsu, Earley, & Wolf, 2006; Stuart-Fox & Johnston, 2005; Zucker & Murray, 1996). Some studies have shown that experience can ‘override’ the effect of morphological traits. For example, in tree lizards (*Urosauria oranatus*), individuals that have won a previous contest are more likely to win against an opponent that is heavier (Zucker & Murray, 1996).

An animal’s previous contest history can influence its future probability of winning. Generally, an animal that loses a contest is more likely to lose his next bout, while a winner is more likely to continue winning (winner-loser effects). Despite the prevalence of winner-loser effects, how exactly contest experience influences contest outcome is not entirely clear. Prior contest experience has been postulated to affect contestants’ fighting behaviour by altering an individual’s perception of its own fighting ability (Hsu et al., 2006). Changes to behaviour after winning or losing a fight can subsequently influence the outcome of future contests. Despite this common view, prior contest experience is often considered as the direct cause for winner-loser effects and behavioural mechanisms that influence contest outcome are rarely discussed (Garcia, Murphree, Wilson, & Earley, 2014; Garcia et al., 2012; Hsu & Wolf, 2001). Moreover, the adaptive function of winner loser effects remains poorly understood. It has been suggested that prior contest experience may be used as a cue to optimise decisions about whether to engage in a fight or not (Rutte, Taborsky, & Brinkhof, 2006). The ‘social-cue’ hypothesis states that animals can detect whether an opponent has lost or won previously by signs of fatigue, chemical cues or by eavesdropping (Rutte et al., 2006; Valone, 2007). Thus, individuals can avoid engaging in costly fights by assessing their probability of winning. Multiple species have been shown to social cues in a competitive context. In Siamese fighting

fish (*Betta splendens*), an individual that viewed a contest between two opponents is more wary to approach the winner (Oliveira, McGregor, & Latruffe, 1998). Snapping shrimps (*Alpheus heterochae*) can recognise prior contest experience by the odour cues emitted by an opponent (Obermeier & Schmitz, 2003). As a consequence, prior losers are less likely to engage with winners, but would readily engage with an individual that has had no recent prior contest experience (Obermeier & Schmitz, 2003). Understanding the mechanisms of contest experience on contest outcome is crucial because theoretical analyses have shown that winner-loser effects play an important role in the formation of dominance hierarchies (Dugatkin & Druen, 2004; Dugatkin & Earley, 2003, 2004). Additionally, an individual's status within these hierarchies can have important fitness consequences (Ellis, 1995).

Different selective pressures on dominant and subordinate individuals can drive variation in fitness, physiology and behaviour. Generally, dominant individuals are more able to monopolise resources and tend to have a much higher reproductive success, however a high social status does not come without its costs (Côté & Festa-Bianchet, 2001; Cowlshaw & Dunbar, 1991; von Holst et al., 2002). For example, López and Martín (2002) found that dominant Iberian rock lizards (*Lacerta monticola*) had significantly larger heads compared to subordinates and thus were more successful in contests. However this was at the expense of the ability to escape from predators, dominant males suffered from decreased escape speeds due to asymmetries in limb length (López & Martín, 2002). Another study found that high-ranking savannah baboons (*Papio cynocephalus*) have higher reproductive fitness but experience greater amounts of stress compared to low-ranking individuals (Gesquiere et al., 2011). This maybe due to high levels of aggressive interactions and mate guarding activities. Since subordinate individuals live within the constraints of dominant individuals, selection should favour traits to compensate such costs. For example, subordinate mountain chickadees (*Poecile gambeli*) tend to be more exploratory and neophilic compared to dominant individuals. This could perhaps be a behavioural strategy to deal with being excluded from resources (Fox, Ladage, Roth, & Pravosudov, 2009). Western scrub jays (*Aphelocoma californica*) recovered cached food more often when being watched by a dominant individual, possibly an adaptation to reduce pilfering (Dally, Emery, & Clayton, 2005).

The effects of dominance on learning abilities have received considerably less attention. The 'cognitive disadvantage hypothesis' posits that individuals of different social

status have intrinsically different cognitive abilities, such that advanced cognitive abilities translates to social superiority (Drea & Wallen, 1999). This hypothesis predicts that subordinate individuals have poor cognitive abilities regardless of the presence of higher status individuals (Drea & Wallen, 1999). In support of this hypothesis, studies have indeed found that dominant individuals perform better than subordinate individuals in a variety of individual learning tasks (Barnard & Luo, 2002; Boogert, Reader, & Laland, 2006; Fitchett, Collins, Barnard, & Cassaday, 2005). However the effects of social dominance on social learning are more complex and the ‘cognitive disadvantage’ hypothesis does not seem to apply. Furthermore, it may be difficult to make substantial conclusions about the role of dominance because dominance is often confounded with age and sex (Drea & Wallen, 1999; Nicol & Pope, 1999).

Learning from the behaviour and interactions of conspecifics (social learning) is considered adaptive, because individuals can avoid trial and error learning (Rieucou & Giraldeau, 2011). Social dynamics such as dominance-subordinate relationships can influence the likelihood of learning from others (Coussi-Korbel & Frigaszy, 1995). However, there is currently no consensus on whether dominant or subordinate individuals are more likely to use social information (Aplin, Sheldon, & Morand-Ferron, 2013; Stahl, Tolsma, Loonen, & Drent, 2001). Dominant individuals may watch other conspecifics for opportunities to scrounge from (Stahl et al., 2001). In contrast, subordinate individuals may exploit information to maximise foraging opportunities and alleviate the costs of living as a subordinate individual. Distinguishing the drivers of social learning is essential to understanding the cultural transmission and the development of traditions in a population (Heye, 1993; Heyes & Galef Jr, 1996; Laland, 2004; Rendell et al., 2011).

My thesis explores two main questions using Eastern Water Skinks (*Eulamprus quoyii*) as a model system: 1) how does contest experience and behaviour influence contest outcome and 2) how does an individual’s dominance status influence its ability to learn from others? *Eulamprus quoyii* is a territorial species and occurs in relatively high densities in the wild. As a result, males often encounter each other and engage in fights and it has been shown that they are capable of forming dominance hierarchies (Done & Heatwole, 1977). *Eulamprus quoyii* have also been shown to perform well on a multitude of cognitive tasks and a previous study has also shown that young lizards are capable of using social information to learn an

association task within a novel foraging paradigm (Noble, Byrne, & Whiting, 2014). This species responds well in captivity, making it a suitable system to address questions about contest competition and the effects of social dominance on behaviour and learning. My thesis is structured into two chapters and below I provide brief summaries of each.

Chapter 1: Context dependent effects of prior contest experience on contest outcome in water skinks

Winner-loser effects have been documented in a wide range of species, however it is poorly understood in reptiles. Contest experience is often assumed to have a direct effect on contest outcome and behavioural mechanisms are usually not considered. For this chapter, I examined the effects of prior contest experience on two key contest behaviours during different assessment stages. I used a tournament design, where lizards competed with multiple contestants, and explored how prior contest experience influenced the propensity to initiate contests and how prior experience effects vary depending on the assessment stage of a given contest. My supervisors, Daniel Noble and Martin Whiting are co-authors on this manuscript (my contributions to experimental design: 70%; data collection: 80%; data analysis: 100%; writing: 95%).

Chapter 2: Dominance relationships and social information use in a lizard

Social learning has previously been thought to be limited to group-living species (Lefebvre, 2010). However, recently the use of social information to solve novel tasks has been reported in several reptilian species (Davis & Burghardt, 2011; Kis, Huber, & Wilkinson, 2014; Wilkinson, Kuenstner, Mueller, & Huber, 2010). Nonetheless, there is very little knowledge on the drivers of social information use in reptiles. There is evidence to suggest that social learning is dependent on age in *E. quoyii* (Noble et al., 2014). However lizards exhibit indeterminate growth, therefore age and dominance are tightly correlated, making it difficult to disassociate these effects (Halliday & Verrell, 1988). For this chapter, I attempt to account for age of lizards and using contest data from Chapter 1, test the effects of a lizard's dominance status (relative to a demonstrator) on social learning. My supervisors, Daniel Noble and Martin Whiting are co-authors on this manuscript (my contributions to experimental design: 70%; data collection: 80%; data analysis: 100%; writing: 95%).

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CHAPER 1: Context dependent effects of prior contest experience on contest outcome in water skinks

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ABSTRACT

An individual's recent 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 size-matched male water skinks (*Eulamprus quoyii*) in a tournament design to investigate whether prior contest experience influenced contest outcome. For each contest we noted the initiator, any aggressive behaviours, and the level of escalation. Contest initiation was the best predictor of contest outcome across all contests and this was influenced by an individual's contest history. Prior winners were more likely to initiate subsequent aggressive encounters and by doing so, initiators had an 88% probability of winning in non-escalated contests. In contrast, initiators had only 33-55% probability of winning in escalated contests. 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 a contests assessment stage when examining winner-loser effects.

HIGHLIGHTS

- Contest initiation was the strongest predictor of contest outcome in male Eastern Water Skinks
- Prior contest experience influenced contest initiation; prior winners had a much higher probability of initiating subsequent contests
- Initiators had an 88% probability of winning in non-escalated contests, whereas in escalated contest, initiators had only 33-55% probability of winning in escalate contests.
- The strength of the effect of prior contest experience is dependent on the level on escalation

KEYWORDS

Winner-loser effects, contests, game theory, resource holding potential

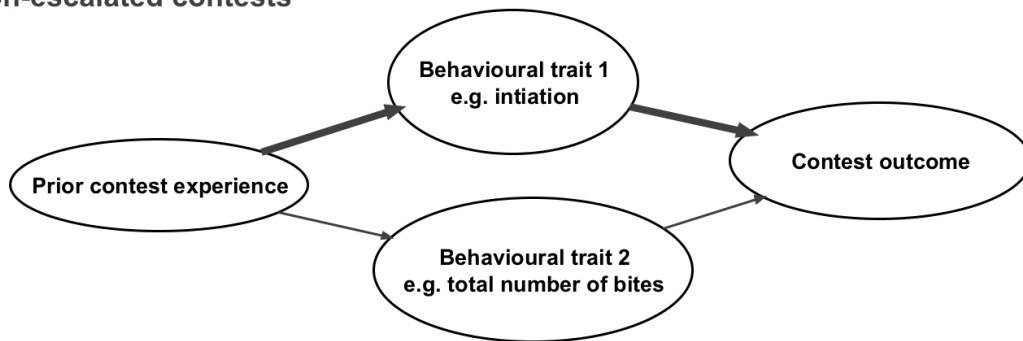
INTRODUCTION

Conflict between individuals is resolved by assessing differences in resource holding potential (RHP, Parker, 1974). The cues used to assess RHP are varied, but include a rival's morphology (e.g. body and head dimensions, Olsson, 1992; Stuart-Fox, Firth, Moussalli, & Whiting, 2006), whole-organism performance (e.g. bite force, Husak, Lappin, Fox, & Lemos-Espinal, 2006) and behaviour (e.g. aggressive displays, Martínez-Cotrina, Bohórquez-Alonso, & Molina-Borja, 2014; Molina-Borja, Padron-Fumero, & Alfonso-Martin, 1998; Osborne, 2005). In addition to these intrinsic traits, prior contest experience has been postulated to affect contestants' fighting behaviour by altering an individual's perception of its own RHP (Hsu, Earley, & Wolf, 2006; Hsu & Wolf, 2001). Behavioural modification after having won or lost a prior contest can increase or decrease the probability of winning (winner—loser effects, reviewed in Hsu et al., 2006). Under the 'perceived ability' hypothesis, prior contest experience should affect the outcome of non-escalated contests more because contestants are better able to estimate their true RHP during direct physical combat in escalated contests (Hsu et al., 2006). Moreover, theoretical analyses have also shown that as individuals become older and have accumulated more fighting experiences, their perceived ability approaches their true RHP (Fawcett & Johnstone, 2010). Despite this common view that fighting experience influences perceived RHP, the behavioural mechanisms that influence contest outcome and winner–loser effects are rarely discussed (Garcia, Murphree, Wilson, & Earley, 2014; Garcia et al., 2012; Hsu & Wolf, 2001). Previous contest experience should directly act on contest behaviour to influence rival assessment and contest outcome (e.g. Fig.1). Winning experience is thus predicted to increase the likelihood of exhibiting certain contest behaviours and as a consequence, increase an individual's probability of winning.

Contests are highly variable and generally progress through phases of display before escalating to physical fighting. Short, low intensity contests occur when large differences in RHP are detected, while long, high intensity contests occur when differences in RHP are small and rival assessment is less accurate (Enquist & Leimar, 1983; Enquist, Leimar, Ljungberg, Mallner, & Segerdahl, 1990). Rival assessment models implicitly assume that animals use one assessment strategy throughout an entire contest; however, recent evidence suggests that animals are capable of employing different assessment strategies at different stages of a contest (Arnott & Elwood, 2009). Rival assessment in anole lizards appear to be flexible, such

that designated winners used mutual assessment, while designated losers used self-assessment (Garcia et al., 2012). Another study found that mangrove killifish, a species known to exhibit winner-loser effects, uses mutual assessment during the early display stages of a contest (Hsu, Lee, Chen, Yang, & Cheng, 2008). Once the contest escalates to physical attacks, losers appear to use self-assessment to make decisions about when to retreat (Hsu et al., 2008). These results suggest that there may be context-dependency in how animals assess their own RHP relative to their rivals. If prior contest experience affects how an individual perceives his own RHP, then the effects of prior contest experience on behavioural traits and contest outcome should also depend on the stage of a contest (Fig. 1).

Non-escalated contests



Escalated contests

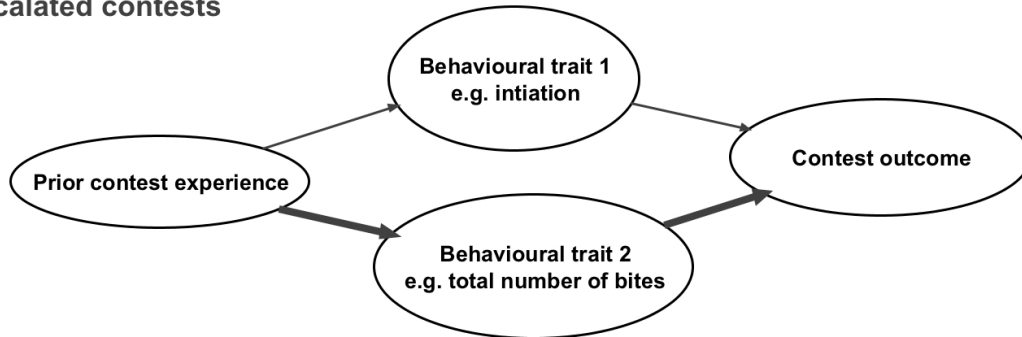


Figure 1 - The effect of prior contest experience on contest outcome is mediated via behavioural traits such as contest initiation or the total number of bites. Bold lines indicate a strong effect of prior contest experience on behaviors and therefore contest outcome; thin lines indicate a weak effect. Top: We predict that in non-escalated contests, contest initiation is affected more strongly by prior contest experience compared to total number of bites. Bottom: We predict that in escalated contests, total

number of bites is affected more strongly by prior contest experience compared to contest initiation

Lizards have been widely used as model species in empirical tests of contest theory (Baird, 2013; Whiting, Nagy, & Bateman, 2003). However, previous studies on the role of prior experience have shown mixed results (Table 1). In some studies, losing has been shown to decrease the probability of winning in some species (Garcia et al., 2014; Garcia et al., 2012; Schuett, 1997). In contrast, prior winners of contests have been shown to increase the probability of winning subsequent contests in other systems (Stuart-Fox et al., 2006; Stuart-Fox & Johnston, 2005; Zucker & Murray, 1996) and there have also been a number of studies that have shown no effect of prior contest experiences on the outcome of contests (McLean & Stuart-Fox, 2014; Scott, Whiting, Webb, & Shine, 2013). Part of the reason why such disparate results exist may relate to the context-dependent effects of prior contest experience on behavioural traits (Fig. 1). In most lizard studies, the importance of prior contest experience on behavioural traits as determinants of contest outcome are rarely discussed (Garcia et al., 2014; Garcia et al., 2012). Even fewer studies directly investigate how experience can influence behavioural traits in a contest (Garcia et al., 2014; Garcia et al., 2012). Moreover, no studies have considered the effects of prior contest experience on behaviours that vary across different stages of a contest. Potential winner-loser effects may be difficult to detect, if prior contest experience has opposing effects on behavioural traits at different stages of a contest.

Table 1. Studies that used squamate reptiles to investigate the effects of prior contest experiences on contest outcome and or contest behaviours. The table is arranged in alphabetical order by species name. Methodological details are provided, including sample size of contests (when provided), the type of contest experience used (previous encounter, previous two encounters) and other details including procedures used to test experience effects. The effects of 1) prior experience on contest outcome; 2) behaviour on contest outcome; 3) prior experience on behaviour are summarized when available. W = Winner, L = Loser, Y = Yes, N = No.

Species and sample size of contests	Type of experience	Effect of experience on contest outcome	Examined behaviours as determinants of contest outcome?	Examined experience effects on behaviours?	Other details	Reference
Copperhead snake ¹ <i>Agkistrodon contortrix</i> n = 10	Previous encounter	<ul style="list-style-type: none"> • L challenged significantly less than an opponent with no prior experience • L lost all contests without interactions escalating to physical fighting 	N	Y L were never first to display	Used naïve individual as opponents	Schuett (1997)
Green anole lizard ² <i>Anolis carolinensis</i> n = 102	Previous encounter	<ul style="list-style-type: none"> • No effect of experience on W's probability of winning overall • L were more likely to lose in non-escalated contests 	Y <ul style="list-style-type: none"> • Initiators were more likely to win in primary contests • Initiation did not affect probability of winning in secondary contests 	Y <ul style="list-style-type: none"> • No effect of primary contest experience on initiating in secondary contests • L that were more likely to escalate in primary contests, won significantly more secondary contests 	<ul style="list-style-type: none"> • Used naïve individual as opponents • Primary contests and secondary contests • Designated status and actual status 	Garcia et al. (2012)

Green anole lizard ² <i>Anolis carolinensis</i> n = 146	Previous encounter	<ul style="list-style-type: none"> • No effect on W's probability of winning overall • L were more likely to lose in non-escalated contest • No effect on W's probability of winning in escalated contests 	Y <ul style="list-style-type: none"> • Initiators were more likely to win in primary contests 	Y <ul style="list-style-type: none"> • Experience has no effect on initiating in secondary contests • Primary contest winners were more likely to escalate in secondary contests 	<ul style="list-style-type: none"> • Used naïve individual as opponents • Primary contests and secondary contests • Designated status and actual status 	Garcia et al. (2014)
Dwarf Chameleon ¹ <i>Bradpodion pumilum</i> n = 107	Previous two encounters	<ul style="list-style-type: none"> • W are more likely to win in future contests 	N but see Stuart-Fox (2006)	N	<ul style="list-style-type: none"> • Tournament design 	Stuart-Fox et al. (2006)
Lake Eyre dragon lizard ¹ <i>Ctenophorus maculosus</i> n = 58	Previous two encounters	<ul style="list-style-type: none"> • No effect of experience 	N	N	<ul style="list-style-type: none"> • Tournament design 	McLean and Stuart-Fox (2014)
Red-barred crevice dragon lizard ¹ <i>Ctenophorus vadrappa</i> n = 14	NA	<ul style="list-style-type: none"> • W won subsequent contests 	N	N	<ul style="list-style-type: none"> • Same individuals in subsequent contests 	Stuart-Fox and Johnston (2005)

Small-eyed snake ² <i>Cryptophis nigriscens</i> n = 24	Previous encounter	<ul style="list-style-type: none"> *The study's focus was on chemosensory site selection based on chemical cues from previous opponent, not predictors of contest outcome 	*The study's focus was on chemosensory site selection based on chemical cues from previous opponent, not predictors of contest outcome	No effect of experience on site selection	<ul style="list-style-type: none"> Same individuals used for subsequent scent trials 	Scott et al. (2013)
Velvet Gecko ¹ <i>Oedura lesueurii</i> n = 30	Previous encounter	<ul style="list-style-type: none"> *The study's focus was on chemosensory site selection based on chemical cues from previous opponent, not predictors of contest outcome 	*The study's focus was on chemosensory site selection based on chemical cues from previous opponent, not predictors of contest outcome	<p>Y</p> <ul style="list-style-type: none"> L chose sites covered with the scent of unknown male conspecific more than those covered with scent of previous opponent defeated them. No differences in site selection in W <p>L were more active and mobile and spent less time in the half of the tub containing retreat site covered in opponents scent.</p>	<ul style="list-style-type: none"> Same individuals used for subsequent scent trials 	Kondo, Downes, and Keogh (2007)
Tree lizard ¹ <i>Urosaurus ornatus</i> n = 29	Previous encounter	<ul style="list-style-type: none"> W are more likely to win in future contests 	N	N	<ul style="list-style-type: none"> Opponents spent 3 days in same arena 	Zucker and Murray (1996)

¹Used self-selected procedures where contestants were closely size matched and allowed to interact. Winner is treated with winning experience, losers is treated with losing experience.

²Used random selection procedures where focal individuals were matched with smaller opponents to create winning experiences and larger opponents to create losing experience.

Our study investigated whether prior contest experience can influence contest outcome and the role of behaviour at different stages of contest escalation in male Eastern Water Skinks (*Eulamprus quoyii*). Male contests in this species follow a distinct sequence; however, contest duration and intensity can be highly variable (see supplementary materials). In some cases, as soon as a lizard begins to move towards a rival, the rival flees, suggesting assessment is prior to any physical interactions (FK, personal observation). Contests were staged between size-matched lizards in a ‘tournament’ design, where males competed with multiple opponents. 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: 1) contest initiation will best predict 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) winning increases the probability of initiating a contest and the number of times a male bit his rival; 3) 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.

METHODS

Study Species, Collection and Husbandry

The Eastern Water Skink (*Eulamprus quoyii*) occurs in close proximity to creeks and streams in southeast Australia (Law & 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 (Noble, Fanson, & Whiting, 2014; Schwarzkopf, 2005). The breeding season typically begins in late September and ends in October although males may be aggressive beyond the actual breeding period (Noble, Keogh, & Whiting, 2013; Veron, 1969). We collected 56 adult male *E. quoyii* from nine sites in the Sydney region during 14 - 30 September 2014 and brought them back to Macquarie University for behavioural trials. 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 mass (g). We measured the following head dimensions to the nearest 0.01 mm: head width (widest point of head), head depth (maximum height of the occiput region), head length (anterior edge of the tympanum to the tip of the snout). Lizards were kept individually in opaque plastic tubs measuring 350 (W) x 487 (L) x 280 (H) mm in a temperature controlled room set at 28°C. 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 every second day.

Male contests

Male contests were carried out between 22 September and 12 October 2014 in a temperature controlled room set at 28°C. Males were sized matched based on SVL (mean size difference = 1.34 mm, range = 0 – 5mm). We used a tournament design where individuals participated between two to seven different contests with different opponents (Whiting et al., 2006). Contest trials took place in opaque plastic arenas measuring 470 (W) x 690 (L) x 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 before contests took place. On the day of the contests, refuges, water bowls and dividers were removed to allow males to interact. Males were given a maximum of 1.5 hrs to interact, but contests were usually resolved within 15 minutes 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 behaviour and the lizards were at least half a body length apart (except if the losing male was constrained by the corners of the arena). After each contest, males were immediately placed in a new arena with a new opponent, separated by an opaque divider. 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 behaviour

We scored the following from the video footage: 1) the frequency of headbobs, tongue-flicks, small and large tail waves during the 20 s period prior to and after the first interaction that led to a clear outcome (Table. 2); 2) which male was the initiator of the interaction; 3) aggressive and submissive behaviours that occurred during the interaction (Table. 2); 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 behavioural interaction that led to a contest outcome, until a clear outcome has occurred; 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 behaviours to his opponent, while a loser was defined as an individual that exhibited submissive behaviours and moved away from his opponent. To calculate repeatability of video scoring, we recorded the frequency of all behaviours on two occasions from a subset of 20 videos. Repeatability was defined as the percentage of videos, for each behavioural trait, that did not differ in recorded frequencies between the two occasions. Across all behaviours, the average repeatability score was 88% (SE = 3.54

Table 2 - Contest behaviours of *E. quoyii* recorded from video footage.

Behaviour	Description
<i>Aggressive</i>	
Approach	Gradual, step-by step movement towards opponent
Chase	Rapid movement towards opponent over a one second 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
<i>Submissive</i>	
Retreat	Gradual, step-by step movement away from opponent
Flee	Movement away from opponent over a one second period
<i>Other</i>	
Tongue flick	Extension and retraction of the tongue occurring within less than once second of each other
Head bob	Up and down head movement
Small tail wave	Rapid, side to side undulation of tail tip at approximately 20° angles
Large tail wave	Moderately slow, side to side undulation of tail approximately at 45° – 60° angles

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 behaviours 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 (See supplementary material). 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 lme4 (Bates, Mächler, Bolker, & Walker, 2015; R Development Core Team, 2010; Turner & Firth, 2012).

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

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

where i and j are 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., 2006a and Turner and Firth, 2012). Contest-specific 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 behaviours such as contest intitation and total number of bites as contest-specific traits. We included standardized SVL, body mass and head dimensions in our initial analyses to check if we had effectively size-matched the lizards. In these initial analyses, both standardized SVL and head dimensions did not predict contest outcome therefore these were 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 contest initiation might depend on whether the contest escalated or not (Fig .1), therefore we fitted an interaction term between these variables. Our overall model for non-escalated contests is thus given by

$$\begin{aligned} & \text{logit}[\text{pr}(i \text{ beats } j \text{ in contest } k)] \\ &= \beta(m_i - m_j) + \delta(z_{ik} - z_{jk}) + \gamma(g_{ik} - g_{jk}) + v(g_{ick} - g_{jck}) + e_i - e_j \end{aligned}$$

where m represents the body mass of lizard i or j , z_{ik} represents whether lizard i won the contest prior to contest k (same for lizard j – i.e z_{jk}), g_{ik} indicates whether lizard i initiated contest k (same for lizard j – i.e g_{jk}). When $g_{ik} = 1$, lizard i has a contest initiation advantage over lizard j (Agresti, 2002; Turner & Firth, 2012). ck indicates whether the contest was escalated or not and is the same value for both lizards. e_i is the random effect for lizard i . 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 cancelled out. Nonetheless, the estimates and standard errors for the other parameters are still valid (personal communication, Heather Turner) and can be used to test the prediction that the effects of contest initiation on contest outcome depend on assessment stage (i.e. escalated or not).

To explore whether biting influenced contest outcome, given 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 GLMMs (see supplementary materials, Table S1 – S2). We included fight and male ID as random effects to account for non-independence given that males were repeated in multiple contests and similarities may have arisen from males being in the same contest. All GLMM analyses were in accordance with our BT model, thus we present results from the BT models only.

Since we predicted that contest history could affect the probability of winning a contest indirectly through modification of male behaviours (Fig. 1). We used a GLMM to assess whether contest history, while controlling for standardized body mass, predicted the probability of initiating a contest (1 = initiated, 0 = not initiate) and the total number of bites in escalated contests.

Lastly, we tested whether differences in mass predicted contest duration of escalated contests only using generalized linear models. We also tested whether contest duration was longer between contestants that won both their previous contest compared to contests that did not win their previous contests using GLMMs. To assess the repeatability of winning and losing a contest for a given lizard, we calculated a GLMM-based repeatability from a binomial multiplicative model fitted by penalized quasi-likelihood on the original data scale following Nakagawa and Schielzeth (2010).

Ethical note

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 for behavioural trials. Lizards were

kept individually in opaque plastic tubs measuring 350 (W) x 487 (L) x 280 (H) mm in a temperature controlled room set at 28°C. 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 every second day. We observed no injuries or signs of stress from staged contests. All protocols in this study were approved by the Macquarie University Animal Ethics Committee (ARA 2014/036) and collection of lizards was approved by the New South Wales National Parks and Wildlife Service, Office of Environment and Heritage (SL100328).

RESULTS

There were two distinct contest stages in male *E. quoyii*. 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 (Fig. S1). For a detailed description of the contests, see supplementary materials. Eighty-five of 123 (69%) contests were resolved without escalation and the mean contest duration for non-escalated contests was 10.71 s (range = 0.40 – 473.20, SE = 5.84). Thirty-eight of 123 (31%) contests escalated to physical biting and the mean contest duration for escalated contests was 86.79 s (range = 1.60 – 818.20, SE = 23.77). As predicted, contest duration of escalated contests increased as the difference in body mass between contestants decreased (Fig. 2). Only 28% of contests occurred in the winning lizard's area ($n = 35/123$ contests), suggesting that the time the lizards were in their experimental arenas was insufficient for any significant residency effect.

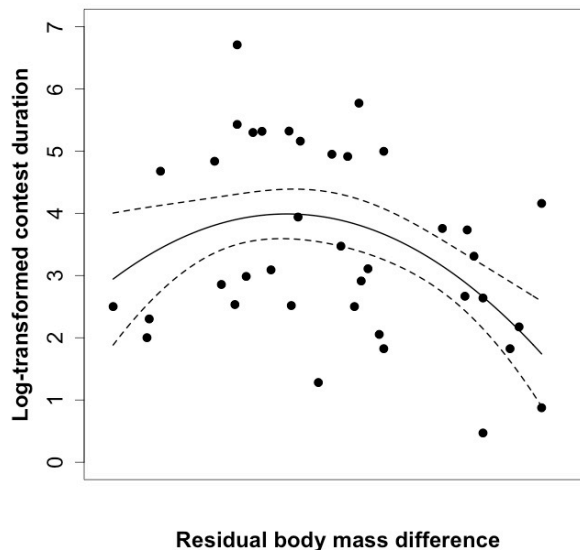


Figure 2

Behavioural 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 ($X+SE = 0.83+0.02$, $N = 123$).

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 3, Fig. 3). In non-escalated contests, a lizard that initiated a contest had an 88% probability of winning (Fig. 4). In contrast, in escalated contests, contest initiation only marginally increased the probability of winning compared to non-escalated contests and had little effect on contest outcome (ca. 41-59% of winning; Fig 4).

Figure 3

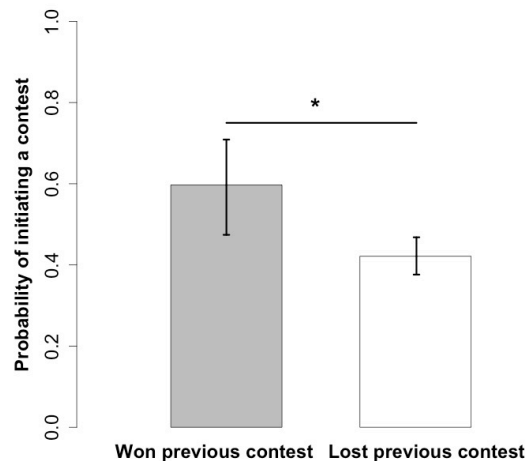
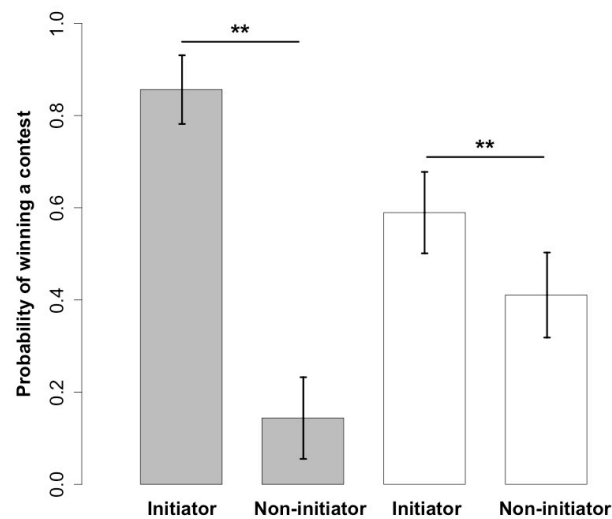


Figure 4

Body mass appeared to be an important predictor of contest outcome (Table 3–4). Our BT model predicted that a 1 unit increase in standardized mass, all else being equal, will

increase the estimated probability of winning by $\exp(1.0224)/(1 + \exp(1.0224)) = 0.74$. Body mass, however, was not a significant predictor in the GLMM analyses (Table S1–2).

We predicted that the most important predictor of contest outcome in escalated contests would be the total number of times a male bit his rival. The BT model using only escalated contests, suggested that the total number of bites was a significant predictor of contest outcome. However, this effect was marginally significant in GLMM analyses (Table S2). Given the highly skewed nature of this variable, we re-ran our GLMM using normalized quantiles of ranked total number of bites, which then became a marginally significant predictor of contest outcome in escalated contests (GLMM: estimate = 1.5137, SE = 0.8938, $Z = 1.694$, $P = 0.0904$, $N = 38$).

Prior contest experience on behaviours 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 3–4). However, we found a moderate between-individual repeatability of 0.28 (SE = 0.07, $P = 0.001$), which suggests that certain lizards tend to keep winning contests. If prior wins indirectly affects contest outcome through behavioural 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 contest initiation (Table 5 & 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 $\exp(0.7097)/(1 + (\exp(0.7097))) = 0.67$. Neither previous contest history or standardized body mass had an effect on the 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, $t = -0.4758$, $P = 0.6367$).

Sixteen of 38 (42%) escalated contests were between contestants that had both won their previous contest. Eight of 38 (21%) contests involved a male that had won his previous contest, however the previous winner did not always win ($n = 4/8$ contests). 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, $Z = 0.367$, $P = 0.714$). Contest duration not differ between contestants that had both won/lost their previous contests (estimate 0.1070, SE = 0.5960, $t = 0.2158$, $P = 0.8345$).

Table 3 – 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 $[x - \bar{\mu}(x)/\bar{\sigma}(x)]$ on the log-odds of winning a contest. The main effect for ‘escalate’ cannot be estimated in the BT model because lizard i and lizard j has the same value for escalate. The model includes both escalated and non-escalated contests (n = 123). Bolded estimates are significant.

Variable	Estimate	SE	Z	P(> Z)
Contest initiation	1.7842	0.3561	5.011	5.42e-07
Escalate	NA	NA	NA	NA
Previous win	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

Table 4 - Bradley-Terry model examining the effects of contest initiation, total number of bites, prior contest history (i.e. whether a male won his last contest) and standardized body mass $[x - \bar{\mu}(x)/\bar{\sigma}(x)]$ on the log-odds of winning a contest. The model includes only escalated contests (n = 38). Bolded estimates are significant.

Variable	Estimate	SE	Z	P(> Z)
Contest initiation	0.1572	0.5220	0.301	0.7633
Total bites	2.1490	0.9869	2.177	0.0294
Previous win	-1.4822	1.1343	-1.307	0.1913
Standardized body mass	2.0584	0.8558	2.405	0.0162

Table 5 - 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 [$x - \bar{\mu}(x)/\bar{\sigma}(x)$] on the log-odds of initiating a contest. The model includes both escalated and non-escalated contests (n = 123). Bolded estimates are significant.

Variable	Estimate	SE	Z	P(> Z)
Previous win	0.7097	0.3075	2.308	0.0210
Standardized body mass	0.1226	0.1484	0.826	0.4088

DISCUSSION

Contest initiation in non-escalated contests strongly predicted contest outcome in *E. quoyii*, whereas the total number of bites was a moderate predictor in escalated contests. As we predicted, previous winning experience was not important in prediction contest outcome. Instead, contest experience acted indirectly on contest outcome by affecting the probability that a male initiated a contest. In accordance with predictions from contest assessment models (Enquist & Leimar, 1983; Enquist et al., 1990), we also show that differences in body mass was negatively correlated with contest duration in escalated contests. Contests involving males that were similar in mass tended to be longer compared to contests involving males that were more asymmetric in mass.

In escalated contests, body mass difference between contestants was associated with contest duration. Body mass appears to play an important role even after we had size-matched contestants within 1.56% 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 & Miles, 2000). In aggressive contests, lizards often circle and shove each other while biting each other's tails. Males that are heavier may be able to endure such energetically demanding behaviours longer than lighter males. Body size is known to predict contest outcome in many reptile systems (Schuett, 1997; Tokarz, 1985). For example, in tree lizards, body mass and prior contest experience were the best predictors of contest outcome (Zucker & Murray, 1996). This study found that a prior loser must weigh at least 1g 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 1.04 g. The total number of times a male bit his rival during a contest appears to be moderately important in predicting contest outcome in escalated contests, however this was not influenced by prior winning experience. This suggests 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. However, our preliminary analyses show that head size, which is correlated with bite force, was not

important in predicting contest outcome. Despite the importance of body mass and total number of bites, contest initiation appears to be a better predictor of contest outcome overall.

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 experiences influences fighting behaviours to indirectly affect contest outcome. Jackson (1991) proposed that individuals should only initiate when they are likely to win a contest. Previous 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. 2006a 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, 2006b). Another study found that focal individuals (with no prior fighting experience) that initiated primary contests were more likely to win compared to non-initiators in green anoles (*Anolis carolinensis*, Garcia et al., 2014; Garcia et al., 2012). However, this study used random-selection methods where focal individuals were pitted against lighter or heavier opponents in order to assign experience effects for subsequent secondary contests and may reflect a mass effect on initiation. Moreover, we did not find body mass important in predicting contest initiation. 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).

Interestingly, the effect of prior contest experience on behavioural traits is context-dependent. We found that the effect of winning experience on initiation was only 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 are able to retrieve more accurate estimates of their RHP, therefore the outcome of escalated contests should be largely governed by the intrinsic fighting abilities of contestants (Hsu et al., 2006). Similar results were reported in male mangrove killifish where individuals with recent contest

success won significantly more non-escalated contests, but the outcome of escalated contests was unaffected (Hsu & Wolf, 2001). In contrast, prior losing experience in green anoles decreased the probability of winning in non-escalated contests, while prior winning experience had no effect (Garcia et al., 2014; Garcia et al., 2012). Contrary to previous studies, we did not find that previous contest experience influenced the probability of escalation, however 42% of escalated contests were between lizards that were both prior winners. Winning experience increased the probability of responding with an attack (bite or swimming rapidly towards the opponent) to a challenge display from an opponent in mangrove killifish (Hsu & Wolf, 2001). Similarly, Garcia et al. (2014) found that prior winners were more likely to escalate in their next contest in green anoles. These results suggest that winning experience is likely to cause behavioural changes in aggressiveness, however discrepancies across studies may be due to differences in methods used to assign experience. In green swordtail fish (*Xiphophorus helleri*) prior winners and losers obtained by random-selection methods (where contest experience is imposed by manipulating the relative sizes of contestants) compared to self-selection methods (where size-matched contestants are pitted in a fight to determine outcome) were more aggressive in terms of attacking more frequently and for longer periods of time (Beaugrand & Goulet, 2000).

Conclusions

In summary, we show that previous contest experience directly influences contest initiation, which ultimately influences contest outcome between male *E. quoyii*, while accounting for body size and residency effects. We show that an effect of previous contest experience is context-dependent with contest initiation being more important only in non-escalated contests. This study extends our current knowledge of winner-loser effects and contest competition in male lizards. Our results highlight an overlooked need to explicitly consider contest assessment stage when making predictions regarding the importance of particular traits in predicting contest outcome.

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SUPPLEMENTARY MATERIALS

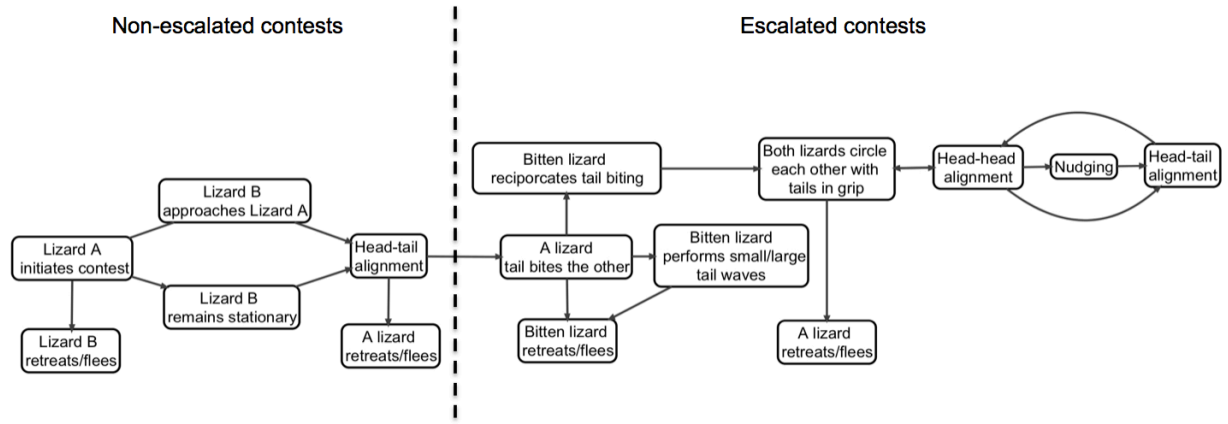


Figure S1 Flow diagram depicting the sequence of behaviours that occur in contests between size-matched male *E.quoyii*. Contest stages are separated by dashed line. For more detailed description of the contests, see supplementary material.

Description of male contests

Contests were initiated when one lizard either slowly approached ($n = 91/123$ contest) or chased ($n = 28/123$ contests) the second lizard. Initiators sometimes ($n = 12/123$ contests) performed small tail waves (rapid side to side undulation of tail tip at approximately 20° angles) prior to approaching the second lizard. Lizards that were approached often fled from the initiator ($n = 55/91$ contests).

In most instances, the lizard being approached remained stationary and was unaffected by the contest initiator, however in rare cases, both lizards would approach each other. Upon approach, lizards would shuffle beside each other and then align themselves so that each lizard lined up with his opponent's tail base or flank (head-tail alignment). This alignment lasted for on average 4.02 seconds ($SE = 0.72$, $n = 30$ contests) until one of the lizards (usually the initiator; $n = 17/30$ contests) bit and held down his opponent's tail. Bites were always directed at tail bases ($n = 33/38$ contests), in rare instances bites were directed at the flank, neck or head contests. The bitten lizard sometimes performed small and/or large tail waves (moderately slow, side to side undulation of tail approximately at $45^\circ - 60^\circ$ angles) when being held down ($n = 12/38$ contests). Frequently, the bitten lizard would nudge his opponent to terminate tail biting and would flee or retreat from the interaction.

If the bitten lizard does not retreat, the bitten lizard would reciprocate tail biting and the pair would circle each other, while grasping each other's tails in their mouth. Each male switched between biting and tail holding while in the contest. In more aggressive contests, each lizard would release each other's tail and align themselves head-to-head, in a parallel fashion (head alignment), approximately 2 cm apart. In the head alignment, the lizards would inch forward to line up their bodies and would sometimes nudge each other (n = 10/ 15 contests). Often the lizards would re-establish the head-tail alignment and continue circling and biting each other (n = 8/15 contests). Head-tail alignment usually preceded head alignment (n = 6/8 contests). In some escalated contests where opponents were in head-tail alignment, one lizard rolled his opponent, while still gripping on his opponent's tail. This often caused the opponent to rapidly tumble, after which the opponent often fled (n = 11/38 contests). Losers tended to perform small and/or large tail waves after escalated interactions (n = 18/38 contests). Overall, losers tail waved in 64/123 contests, while winners only tail waved in 23/123 contests, a proportion that was statistically significantly ($\chi^2 = 28.58$, $df = 1$, $P < 0.001$).

Table S1 - Generalized linear mixed effects model (GLMM) examining the effects of contest initiation, quantile-normalized total number of bite, prior contest history (i.e whether a male won his last contest) and standardized body mass [$x - \bar{\mu}(x)/\bar{\sigma}(x)$] on the probability of winning a contest. The model includes only escalated contests (n = 38).

Variable	Estimate	SE	Z	P(> Z)
Contest initiation	1.1754	0.8612	1.365	0.1723
Total bites	1.5137	0.8938	1.694	0.0904
Previous win	-1.0489	1.0786	-0.972	0.3308
Standardized body mass	0.6784	0.5287	1.283	0.1995

CHAPTER 2: Dominance relationships and social information use in a lizard

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ABSTRACT

Traditionally, the ability to learn from conspecifics (social learning) is considered to be limited to group-living species, however there is increasing evidence that less social species are capable of using social information too. This is not surprising given the potentially adaptive benefits of learning from others. Social learning has been reported in several reptile species, however the factors driving individual differences in social information use are generally unknown. We investigated the effects of an observer's dominance status on social information use in Eastern Water Skinks (*Eulamprus quoyii*) in an association and a reversal-learning task. We used pairs of male lizards that had previously encountered one another during staged contests of known dominance. We were thereby able to control the dominant-subordinate relationship of the demonstrator and observer relative to one another and in control groups. We show that lizards that viewed a demonstrator perform the task did not learn faster than the control group and moreover, dominance status did not affect social information use in both an association and reversal task. In light of previous work, our results suggest age might be a more important driver of social information use because demonstrators and observers were closely size-matched and are likely to be of similar age.

HIGHLIGHTS

- No evidence of social information use
- No differences in learning the tasks between dominant and subordinate lizards
- Lizards may rely on trial and error learning when it is not costly to do so
- Our results suggests lizards may ignore social information from conspecifics that are similar in size or age

KEYWORDS

Social learning, private information, social dominance, rank, lizard

INTRODUCTION

The social environment is a rich source of information that can be used in individual decision-making. Learning by interacting or observing the behaviour of others (social learning) can allow naïve individuals to acquire new foraging skills (Aplin, Sheldon, & Morand-Ferron, 2013), learn predator evasion tactics (Kavaliers, Colwell, & Choleris, 2005) and what mates to choose (Dugatkin & Godin, 1993). The use of social information allows observers to shortcut trial and error learning, thereby bypassing the costs associated with individual learning (Boyd & Richerson, 1995; Shettleworth, 2009). Costs, such as the time and energy expended learning a new problem and the increased predation risk while sampling the environment, should favour the use of social information (Kendal, Coolen, van Bergen, & Laland, 2005; Rieucou & Giraldeau, 2011). However, social information use is not inherently adaptive and theoretical analyses suggest that individuals should use social information selectively (Giraldeau, Valone, & Templeton, 2002; Rieucou & Giraldeau, 2011). The ‘costly information hypothesis’ postulates that individuals trade-off using accurate information that is costly to obtain against cheap information that is possibly less accurate (Boyd & Richerson, 1995). Socially acquired information may be unreliable or out-dated in a changing environment, thus selection may often favour plastic strategies (Kendal et al., 2005; Laland, 2004).

For social information use to be advantageous, individuals should be selective with regards to whom they learn from (Laland, 2004). Coussi-Korbel and Frigaszy (1995) proposed the idea of ‘directed social learning’, where social learning is dependent on the identity of a demonstrator. Observers may preferentially learn from certain individuals as the quality and relevance of information may vary between individuals (Galef Jr & Laland, 2005; Laland, 2004). As a consequence, social information transmission in the population can spread at different rates (Coussi-Korbel & Frigaszy, 1995). Animals can ‘copy-the-most-successful’ individuals to ensure they are maximising their social learning opportunities and avoid acquiring unproductive behaviours (Laland, 2004). Social cues such as dominance status, age or size may be indicators of success to an observer (Galef Jr & Laland, 2005). However, dominance, age and size are often confounded, where larger individuals tend to be older and more dominant than smaller individuals. Hence, it becomes quite difficult to disassociate these effects (Aplin et al., 2013; Duffy, Pike, & Laland, 2009). Body size may also be indicative of body condition and foraging

success, thus observers may prefer to watch larger individuals when making foraging decisions (Duffy et al., 2009). Since age comes with experience, observers could learn from older individuals who exhibit behaviours that have been effective in ensuring their survival (Duffy et al., 2009). Dominant individuals are likely to be highly skilled in monopolising resources and observers may choose to exploit their behaviours through scrounging (Laland, 2004). The role of dominance relationships on social information use may play an even more important role than age or size in species that show dominance hierarchies (Coussi-Korbel & Frigaszy, 1995).

The effect of social dominance on social information use has been extensively tested in birds and mammals (Aplin et al., 2013; Benson-Amram, Heinen, Gessner, Weldele, & Holekamp, 2014; Kavaliers et al., 2005; Kendal et al., 2014; Nicol & Pope, 1999; Pongracz, Vida, Banhegyi, & Miklosi, 2008; Stahl, Tolsma, Loonen, & Drent, 2001). Studies that investigate whether naïve individuals prefer to learn from dominant or subordinate demonstrators tend to support the idea that dominant individuals are more influential models (Kendal et al., 2014; Krueger & Heinze, 2008; Nicol & Pope, 1999 but see Awazu and Fujita, 2000). Individuals may also need to monitor dominant individuals more closely to avoid aggressive interactions therefore dominant individuals tend to be more salient than lower ranked animals (Nicol & Pope, 1999; Shepherd, Deaner, & Platt, 2006). Interestingly, studies that assess whether an individual's dominance status influences their propensity to use social information have been inconsistent (Aplin et al., 2013; Benson-Amram et al., 2014; Kavaliers et al., 2005; Kendal et al., 2014; Pongracz et al., 2008; Stahl et al., 2001). For example, dominant barnacle geese (*Branta leucopsis*) follow subordinates to new feeding sites to capitalise on foraging opportunities (Stahl et al., 2001). In contrast, Benson-Amram et al. (2014) found that subordinate spotted hyenas (*Crocuta crocuta*), were more attentive to a demonstrator, however this did not improve their ability to solve a foraging task. Other studies have found that subordinates are more likely to use social information to solve novel tasks (Aplin et al., 2013; Kavaliers et al., 2005; Kendal et al., 2014; Pongracz et al., 2008); however, the effects of an observer's dominance status on social information use remain poorly understood.

Social information use is most often associated with group-living species (Lefebvre, 2010) and reptiles are often considered to be less socially complex than other vertebrates; however, this does not preclude their ability to use social information (Davis & Burghardt, 2011;

Kis, Huber, & Wilkinson, 2014; Noble, Byrne, & Whiting, 2014; Pérez-Cembranos & Pérez-Mellado, 2015; Wilkinson, Kuenstner, Mueller, & Huber, 2010). Recent studies have found that Balearic lizards (*Podarcis lilfordi*) and Little Scrub Island ground lizards (*Ameivia corax*) cue on conspecifics to locate food patches (Eifler & Eifler, 2014; Pérez-Cembranos & Pérez-Mellado, 2015). There is also increasing evidence that reptiles are capable of social learning in a diverse set of species (Davis & Burghardt, 2011; Kis et al., 2014; Noble et al., 2014; Wilkinson et al., 2010). For example, red-footed tortoises (*Geochelone carbonaria*) were able to navigate through a detour task after watching a demonstrator do so, whereas a control group did not (Wilkinson et al., 2010). Red-bellied cooters (*Pseudemys nelsoni*) have also been shown to learn through stimulus enhancement, by associating a coloured bottle with food, after observing a demonstrator feed from it (Davis & Burghardt, 2011). Kis et al. (2014) demonstrated that bearded dragons (*Pogona vitticeps*) are able to socially learn from a demonstrator by imitation, a mechanism thought to only be used by mammals and birds (Heye, 1993). These studies collectively demonstrate that social information use is indeed not restricted to group-living species, however the drivers of variation in the use of social information remains largely unexplored in reptiles (except see Noble et al. 2014). Closing this gap could be fundamental to understanding social learning strategies and any links to social behaviour (Doody, Burghardt, & Dinets, 2013).

We investigated the effects of social dominance on social information use in Eastern Water Skinks (*Eulamprus quoyii*). Since lizards exhibit indeterminate growth, age and body size are linked (Halliday & Verrell, 1988). Thus, we attempted to account for the age of the lizards by randomizing the body size distribution across treatments and size-matching demonstrators and experimental lizards. Males of this species form dominance hierarchies, hence social dominance may be an important driver in social information use (Done & Heatwole, 1977). *Eulamprus quoyii* also perform well on a multitude of cognitive tasks (Noble, Carazo, & Whiting, 2012) and young lizards are capable of using social information to learn a novel association task (Noble et al., 2014). Nonetheless, dominance and age are likely tightly linked in *E. quoyii* and we were specifically interested in understanding the role of dominance relationships in social learning. Dominant lizards may use social information to take advantage of scrounging opportunities presented by other individuals (Giraldeau & Caraco, 2000; Stahl et al., 2001). Under this hypothesis, we would predict dominant observer lizards to use social information more readily to

learn faster than subordinate observer lizards. This may enable dominant lizards to reduce the costs of defending a territory and maintain their social status (Sinervo, Miles, Frankino, Klukowski, & DeNardo, 2000). On the other hand, subordinate lizards may be more at risk of predation and may incur high energetic costs when dispersing to avoid aggressive interactions with other males (Sinervo et al., 2000). Under this hypothesis we would predict that subordinate observer lizards that have access to social information may use it to learn tasks faster than dominant observer lizards. Subordinate lizards may therefore exploit social information to maximise foraging opportunities from dominant individuals.

METHODS

Lizard collection and Husbandry

We collected 56 adult male *E. quoyii* from nine sites in the Sydney region during 14 - 30 September 2014 and brought them back to Macquarie University for behavioral trials. We recorded the following body dimensions to the nearest 1mm: snout-to-vent length (SVL; from tip of snout to the beginning of the cloacal opening, total body length (from tip of snout to the distal tip of the tail in mm and body mass to the nearest 0.1g. Lizards were kept individually in opaque plastic tubs measuring 350 (W) x 487 (L) x 280 (H) mm in a temperature controlled room. Each tub had its own ultraviolet light and males had access to a refuge, a water bowl, and were fed crickets or dog food three days a week.

Determining male dominance status

Male contests were carried out between 22 September and 12 October 2014 in a temperature-controlled room set at 28°C. Males were sized matched based on SVL (mean size difference = 1.34 mm, range = 0 – 5 mm). We used a tournament design where individuals participated in two to seven different contests with different opponents (Whiting et al., 2006). Contests took place in neutral, opaque plastic arenas measuring 470 (W) x 690 (L) x 455 (H) mm, partitioned in half using a wooden divider. Each male occupied half of the arena. Males were left to habituate in the arena for 1.5 days before contests took place. On the day of the contest, refuges, water bowls and dividers were removed to allow males to interact. Males were given a maximum of 1.5 hours to interact, but contests are usually resolved within 15 minutes of removing the divider. Contests were closely monitored so that once a clear outcome was apparent, 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 behaviour and the lizards were at least half a body length apart (except if the losing male was constrained by the corners of the arena). After each contest, males were immediately placed in a new arena with a new opponent and separated by an opaque divider. 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). For further description of the contests see Kar et al. (in preparation) [Chapter 1].

Treatment groups

To ensure a clear dominance relationship between a demonstrator and an experimental lizard, we used lizards from contests in which there was a clear outcome. We accounted for body size so that pairs of males were either the same size or the dominant individual was slightly larger. Males were paired if dominant individuals had won more contests and experienced fewer losses than their subordinate counterpart. This was to ensure that the relative dominance relationship between the pair remained stable. Using this criterion, we obtained 28 pairs. To assess the stability of the relative dominance relationship between pairs, we calculated the repeatability of winning and losing a contest for a given lizard (Nakagawa & Schielzeth, 2010). The probability for a lizard winning a contest was moderately repeatable ($R = 0.28$, $SE = 0.07$, $P = 0.001$). We also staged another round of contests 59 days later to further assess the stability of the dominance statuses among pairs ($n = 28$). Of the 28 contests, 18 resulted in a clear outcome. The dominance relationship remained stable in 13/18 (72%) interactions two months after the initial contest, suggesting that relative relationships were likely fairly stable for most pairs.

Once dominance relationships were established between two males we randomly allocated pairs into one of two treatment groups: 1) a social treatment group where an experimental lizard was allowed to view the demonstrator execute the foraging task and 2) a control treatment, where the experimental lizard was allowed to view a demonstrator that was not performing the task (i.e. doing nothing). In each of these treatment groups experimental lizards were randomly allocated to: 1) a subordinate individual of the pair ($n = 9$) or 2) a dominant individual of the pair ($n = 8$). The control treatment had a mix of both subordinate ($n = 5$) and dominant ($n = 6$) experimental lizards. The mean SVL of the experimental lizards was not significantly different across our treatment groups (GLM: estimate = -0.04032, $SE = 0.02463$, $t = -1.637$, $P = 0.1138$).

Training and social demonstration

Cognition trials were carried out in the same room where the lizards were housed. Pairs of individuals were placed in opaque plastic tubs measuring 470 (W) x 690 (L) x 455 (H) mm, separated by a fixed piece of plexi-glass and a removable opaque divider. Each lizard occupied one half of the tub.

All lizards were trained to displace a lid from a dish to access a mealworm (*Tenebrio molitor*) and followed a similar protocol to that used by Noble et al. (2014) and Clark et al. 2014. We modified this protocol slightly to expedite learning and facilitate the training of lizards that had difficulty learning the task. Briefly, lizards were first trained to eat from an open dish containing a mealworm. Lizards had to eat from the open dish a minimum of 5/6 times before graduating to the next task (phase 1). Once lizards achieved this criterion, a yellow lid was placed over the food dish so that it covered 75% of the dish (phase 2). Again, lizards had to eat from the 75% covered dish a minimum of 5/6 times before graduating to a yellow lid that fully covered the dish and that required lizards to use their snout to open it (phase 3). Some lizards had difficulty learning this task ($n = 29/56$) and to expedite learning we provided all 56 lizards with two dishes (phase 4). One of these dishes contained a lid that was 75% covered while the second dish completely covered the food well. The dish that had a fully or 75% closed lid varied between trials (either the right or left). Lizards had to eat from both dishes a minimum of 5/6 times before graduating to the next phase where both lids completely covered the food well (phase 5). Lizards that did poorly on this task (i.e. ones that did not eat from both dishes in at least 2/3 of their last trials; $n = 16$) were then given two dishes that were 98% covered (phase 6). The purpose of this was to train the lizards to associate each dish with food when visual cues were absent, but to not make access to this food particularly difficult (i.e. lizards could simply slide the lid off). In contrast, lizards that ate from both dishes in 2/3 of their last trials (6 trials total) were allowed to continue with one lid fully closed and the second 75% (phase 4) closed until they achieved criterion. In 13 instances, lizards that achieved the 5/6 criterion for phase 4 (two dishes - 75% and fully covered) but then were unsuccessful in the first two trials of phase 5 (two dishes fully covered) were returned to phase 4. This variable training approach quickly trained many of the lizards that were having difficulty learning how to flip a fully covered lid and was particularly suitable for our needs given that we were not interested in instrumental learning abilities and it

allowed us to alleviate time constraints during the training period. For a schematic overview of the training phases see Fig. S1.

Once all lizards had learnt to flip and open a lid to access the mealworm, demonstrators of social treatment were given a new task consisting of two dishes, one was covered by a white lid, another by a blue lid. The dish covered by the white lid was fixed closed and contained no mealworm, so that the demonstrator lizard could only open the blue lid. This allowed demonstrators to unambiguously open the correct lid during social demonstration. Demonstrators were required to eat from the blue dish 5/6 times before social demonstration commenced. During demonstrator training, the training for experimental lizards that learnt to flip two fully closed lids was terminated to prevent satiation. Only experimental males who did not learn the task continued training during the demonstrator training phase ($n = 4$). In all cases, when experimental lizards commenced the task, they all continued to flip the lids immediately.

Association task

The apparatus given to the experimental lizards was the same design as that used by (Noble et al., 2014) and it consisted of two dishes attached to a wooden block. One dish was covered by a blue lid (food reward), while a white lid covered the control. We placed a mealworm in each dish to control for scent and auditory cues between the two dishes. In the association task, the reward could be accessed from the blue dish, while the mealworm in the white dish was obstructed by a piece of cardboard and was therefore inaccessible. This task required the experimental lizards to displace the correct lid (blue) to access the food reward. The position (right or left) of the blue dish was randomised and counter-balanced across treatment groups to account for differences in lateralisation between lizards. The position of the correct dish remained consistent within each task after this initial randomization. We therefore cannot disambiguate whether spatial or colour cues were used to learn the task.

At the beginning of each trial, the refuge, water bowl and wooden divider were removed to provide a clear view of the demonstrator. The social treatment lizards were given six trials to view the demonstrator complete the task. Following from this, they also received the task to

complete after viewing the demonstrator on each trial. Similarly, control lizards viewed their respective demonstrators for the same amount of time as social treatment lizards. We conducted two trials per day, in the morning (0830-1000) and the afternoon (1200-1400) with a minimum interval of 2 hours between trials. A lizard was considered to have learnt the task if it displaced the blue lid 5/6 consecutive times. We continued to give the task to lizards that learnt until every lizard had completed a maximum of 18 trials. All trials were filmed using CCTV cameras and a blind reviewer measured: 1) whether or not the lizard chose the correct dish; 2) the latency to displace the correct lid from the moment the task was placed inside the lizard's enclosure; and 3) whether the lizard displaced the lid from only the correct dish or from both dishes. All lizards learnt the association task before moving on to the reversal task.

Reversal task

The second task required the experimental lizards to unlearn the blue-reward association. The experimental setup was the same as that described for the association task except that the white dish now contained the accessible food reward. The position (right or left) of the white dish was again randomised and counter-balanced across the treatment groups and remained consistent within each task. Again, the social treatment lizards viewed their respective demonstrators perform the task prior to attempting the task, while control lizards viewed their demonstrators for the same amount of time. All lizards were given a maximum of 26 trials to learn the task. The same learning criterion from the association task was used in the reversal task.

Statistical analyses

We recognized that demonstrator lizards of different dominance status might differ in their motivation to execute the tasks in response to the experimental lizards. To assess these potential differences, we tested whether the number of trials that did not result in a successful demonstration differed between subordinate and dominant demonstrators using a GLM with negative binomial errors. We also considered potential differences in motivation across our treatments by only including experimental lizards that attempted at least 85% of trials in our analyses, however, only one lizard did not meet this criterion in the association task. All lizards were retained for the analysis of the reversal task.

To assess the robustness of our learning criterion, we tallied the number of correct choices after a lizard reached the learning criterion for a subset of lizards that had five or more trials beyond the trial they learnt. We tested whether the number of correct choices was significant according to an exact binomial choice test (association task: $n = 23$, reversal task: $n = 22$). In the association task, 18/23 (78%) lizards that had five or more trials beyond the trial they learnt chose the correct dish significantly more than expected by chance. While in the reversal task, 20/22 (91%) lizards that had five or more trials beyond the trial they learnt chose the correct dish significantly more than expected by chance. These results suggest that our learning criterion was sufficient in categorising lizards that learnt from those that did not.

Generalized linear models (GLM) and generalised linear mixed effects model (GLMM), using a Bayesian Markov chain Monte Carlo (MCMC) sampling approach, were used to analyse our data. We used the MCMCglmm package in R (Hadfield, 2010; R Development Core Team, 2010). Treatment (social and control) and status (dominant = DOM and subordinate = SUB) were coded as two level factors. We included an interaction term because we hypothesized that dominant and subordinate lizards may use social information differently. We mean centred and scaled SVL to have a unit standard deviation. Scaled SVL was then included in all models as a covariate. The mean number of trials it took to learn each task was modelled using a GLM with a negative binomial error distribution. We also calculated Hedge's g standardised effect sizes using an unbiased estimator following Nakagawa and Cuthill (2007) for the mean number of trials taken to learn the tasks. Individual ID was included as a random intercept and trial number as a random slope in all GLMM models. The variance-covariance matrix for the residuals is fixed at 1 as this is what the 'logit' family assumes. We used 2,000,000 iterations, a thinning interval of 5000 (i.e. one in every 5000 iterations of the Markov chain is used to estimate the posterior distribution of the model parameters) and a burn-in of 10,000 (i.e. we did not take the first 10,000 iterations from the Markov chain to avoid auto-correlation issues). We performed auto-correlation diagnostics to ensure our samples were not strongly correlated. We also visually inspected the plots of our samples to ensure chains were mixing well. We treated correct and incorrect choices as a binary variable and the probability of making a correct choice was analysed using a GLMM with binomial errors (logit link). We recorded whether a lizard displaced the lid from only the correct dish or not ('1' or '0') and modelled the probability of choosing only the

correct dish using a GLMM with binomial errors. We also estimated a fixed effect for trial number in our GLMMs as we expected the probability to make a correct choice and the probability to displace the lid from the correct dish only should increase across trials as lizards learn the task. The latency to displace the lid from the correct dish was log transformed to ensure normality. Latency to displace the correct lid was analysed with a linear mixed model with trial number (random slope) and individual ID (random intercept) as random effects. Trial number was also included as a fixed effect, as we expected latencies to decrease as lizards learnt the task.

Lastly, to test whether the exclusion of lizards that did not meet the learning criterion influenced our results, we assigned them with the maximum trial number (association task = 18 trials; reversal task = 26 trials) as the number of trials it took to learn the task and re-ran our analyses. We did not find any differences in our results when including the data of the excluded lizards. This suggests that excluding lizards that did not meet the learning criterion did not affect our results.

Ethical Note

All protocols in this study were approved by the Macquarie University Animal Ethics Committee (ARA 2014/036) and collection of lizards was approved by the New South Wales National Parks and Wildlife Service, Office of Environment and Heritage (SL100328).

RESULTS

Association task

The number of failed demonstrations was not significantly different between dominant or subordinate demonstrators (GLM: estimate = -0.3830, SE = 0.3672, $z = -1.043$, $P = 0.297$). Twenty-five of 27 (93%) of experimental lizards learnt the task. All 13 (100%) subordinate lizards learnt the task (9 social, 4 controls), whereas 12/14 (86%) of dominant lizards learnt the task (6 social, 6 control). The mean number of incorrect choices was 3.62 (SE = 0.64) for subordinate lizards and 3.07 (SE = 0.70) for dominant lizards. The mean number of incorrect choices was 3.94 (SE = 0.64) for social demonstration lizards and 2.30 (SE = 0.54) for control lizards. The mean number of trials it took for lizards to learn did not depend on treatment group or a lizard's dominance status (Fig 1a & Table 1a). The standardised mean difference (Hedge's g) between dominant social lizards and subordinate social lizards was -0.05 (95% CI = -1.00 to 0.90). There was a trend for both dominant and subordinate control lizards to take fewer trials to learn than their social treatment counterparts (Fig. 1a), although this was not significant. The standardised mean difference (Hedge's g) between subordinate social lizards and subordinate control lizards was 0.19 (95% CI = -0.99 to 1.37). Similarly, the standardised mean difference between dominant social lizards and dominant control lizards was 0.17 (95% CI = -0.89 to 1.23). The probability of choosing the correct dish did not depend on treatment group or a lizard's dominance status (Table 2a). The probability of choosing the blue dish only also did not differ between treatment group or a lizard's dominance status, but depended on the SVL of the lizard (Table 2a). If SVL is an adequate proxy of the age of the lizard, a marginally significant effect of SVL on the probability to displace the correct dish only, may actually reflect an age-dependent effect (Noble et al., 2014). Thus we tested whether SVL and treatment group influenced the probability of displacing the lid from the correct dish and fitted an interaction term between SVL and treatment group. We predicted smaller (potentially younger) lizards in the social group to have a higher probability to displace the lid from the correct dish compared to the control lizards. The probability of choosing the correct dish only did not depend on the SVL of a lizard or treatment group (SVL \times treatment SOCIAL: estimate = -1.05, 95% credible interval = -2.97 to 1.34). This suggests that slopes do not differ across treatment groups. We removed the interaction term and re-ran the model and found that treatment and SVL predicted the probability of

choosing the correct dish only, however these effects were marginally significant (see supplementary materials). The latency to displace the blue lid did not differ between treatment group or a lizard's dominance status (Table 3a).

Reversal task

The number of failed demonstrations between dominant or subordinate demonstrators was not significantly (estimate = -1, SE = 0.6872, $z = -1.455$, $P = 0.166$) different. All lizards attempted over 85% of trials, suggesting motivation did not affect their learning. Twenty-five of 28 (89%) experimental lizards learnt the task. All 14 (100%) subordinate lizards learnt the task (9 social, 5 controls), whereas 11/14 (79%) of dominant lizards learnt the task (7 of which were social and 4 were controls). The mean number of incorrect choices was 5.29 (SE = 1.11) for subordinate lizards and 7.50 (SE = 1.60) for dominant lizards. The mean number of incorrect choices was 7.35 (SE = 1.29) for social demonstration lizards and 4.91 (SE = 1.44) for control lizards. The mean number of trials it took for lizards to learn differed between treatment groups and dominance status (Fig. 1b, Table 1b), however this difference was marginally significant (Table 1b). The standardized mean difference (Hedge's g) between subordinate social lizards and subordinate control lizard was 0.17 (95% CI = -0.92 to 0.27), whereas the effect size negligible for the other groups subordinate social vs subordinate control = 0.00, 95% CI = -1.10 to 1.09; dominant social vs. subordinate social = 0.00, 95% CI = -1.09 to 1.10). The probability of choosing the correct dish did not differ between treatment groups or a lizard's dominance status (Table 2b). The probability of choosing the white dish only also did not differ between treatment groups or a lizard's dominance status (Table 2b). The latency to displace the white lid also did not differ between treatment groups or a lizard's dominance status (Table 3b).

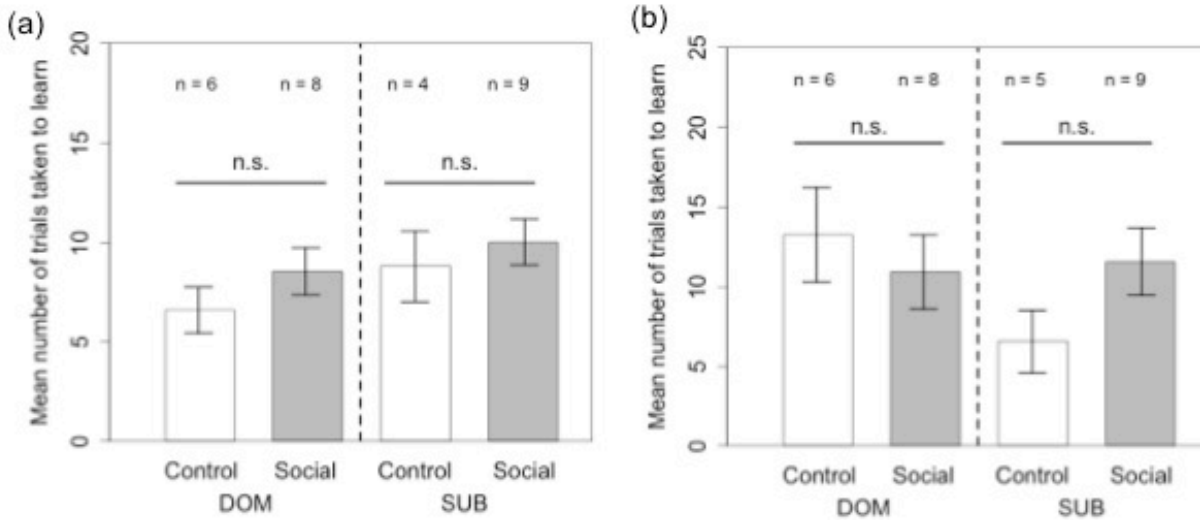


Figure 1. Predicted mean number of trials to learn (a) the association task and (b) the reversal task for dominant (DOM) and subordinate (SUB) lizards in the social demonstration treatment (social) and control treatment (control). SVL was set at the mean. Error bars represent standard error. One subordinate control lizard was excluded in the association task, as it did not meet the motivation criterion.

Table 1. Estimates and standard errors (SE) from a generalised linear model (GLM) examining the effects of a lizard's dominance status (dominant or subordinate), treatment group (social or control) and standardised SVL [$x - \bar{\mu}(x)/\bar{\sigma}(x)$] on the mean number of trials it took for a lizard to learn the a) association task (N = 27) and b) the reversal task (N = 28). Italicised estimates are marginally significant ($p < 0.10$)

	a) Association Task		b) Reversal Task	
	Estimate	SE	Estimate	SE
Intercept	2.18	0.20	1.88	0.30
Status DOM	-0.29	0.26	<i>0.70</i>	<i>0.36</i>
Treatment SOCIAL	0.13	0.24	0.57	0.36
Scaled SVL	0.11	0.08	0.09	0.13
Status DOM × Treatment SOCIAL	0.13	0.31	<i>-0.76</i>	<i>0.44</i>

Table 2. Posterior modes and highest posterior density intervals from a Bayesian Markov chain Monte Carlo generalised linear mixed effects model (MCMC-GLMM) examining the effects of a lizard's dominance status (DOM or SUB), treatment group (social or control), standardised SVL [$x - \bar{\mu}(x)/\bar{\sigma}(x)$] and trial number on the log odds of making a correct choice and the log odds of choosing the correct dish only in the a) association task (observations = 484, N = 27) and b) the reversal task (observations = 701, N = 28). Bolded estimates are significant. Italicised estimates are marginally significant ($p < 0.10$)

a) Association Task						
	Log odds of making correct choice			Log odds of choosing correct dish only		
	Estimate	Lower	Upper	Estimate	Lower	Upper
Intercept	-0.38	-1.94	1.81	-2.01	-5.11	-0.30
Status DOM	2.21	-0.73	4.00	1.04	-1.45	4.23
Treatment SOCIAL	0.03	-2.60	1.75	-1.38	-5.24	0.93
Scaled SVL	-0.36	-1.11	0.39	<i>-1.19</i>	-2.35	<i>0.08</i>
Trial number	0.23	0.12	0.47	0.08	-0.07	0.28
Status DOM × Treatment SOCIAL	-1.04	-3.97	1.48	-0.72	-3.49	4.06
b) Reversal Task						
	Estimate	Lower	Upper	Estimate	Lower	Upper
Intercept	1.57	-0.29	3.66	-0.86	-3.79	2.02
Status DOM	-0.72	-3.08	1.81	-0.58	-5.52	1.95
Treatment SOCIAL	-1.92	-4.38	0.53	-1.03	-5.80	1.67
Scaled SVL	0.12	-0.87	0.96	0.10	-1.30	1.35
Trial number	0.08	-0.00	0.27	0.03	-0.07	0.20
Status DOM × Treatment SOCIAL	1.80	-1.61	4.26	1.90	-2.84	6.62

Table 3. Estimates and standard errors (SE) from a linear mixed effects model examining the effects of a lizard's dominance status (dominant or subordinate), treatment group (social or control), standardised SVL [$x - \bar{\mu}(x)/\bar{\sigma}(x)$] and trial number on the log latency to displace a lid from the correct dish in the a) association task (observations = 484, N = 27) and b) the reversal task (observations = 701, N = 28).

	a) Association Task		b) Reversal Task	
	Estimate	SE	Estimate	SE
Intercept	5.96	0.36	5.39	0.35
Status DOM	-0.02	0.43	0.00	0.42
Treatment SOCIAL	-0.01	0.43	-0.09	0.42
Scaled SVL	-0.14	0.15	-0.09	0.16
Trial number	-0.05	0.01	-0.01	0.00
Status DOM × Treatment SOCIAL	-0.10	0.53	0.20	0.52

DISCUSSION

We show that viewing a demonstrator perform a foraging task did not accelerate learning in the social demonstration treatment compared to the control group. Therefore, the effects of a lizard's dominance status did not influence social information use in a foraging context. Subordinate control lizards appear to have learnt the task faster compared to subordinate social lizards in the reversal task, although this effect was only marginally significant. There was also a trend for lizards in the social demonstration treatment to make more incorrect choices than control individuals in the reversal task, however the probability of making a correct choice did not depend on treatment group or a lizard's dominance status. We discuss these results in light of previous work on social information use in *E. quoyii* and the 'costly information hypothesis', which posits that the costs of acquiring cheap, social information is traded-off against accuracy (Boyd & Richerson, 1995).

There was a marginal difference between subordinate control lizards and subordinate social lizards in the mean number of trials taken to learn. On average, subordinate control lizards learnt the task 5 trials faster than subordinate social lizards. However, this difference may be an artefact of the 'sliding window' nature of our learning criterion. Lizards were considered to have learnt the task if they chose the correct dish 5/6 consecutive times. If by chance, a lizard made an incorrect choice twice out of 6 consecutive trials, the lizard would need to choose correctly enough times to shift at least one of the incorrect choices out of the 'criterion window'. The effect size comparing the social vs. control group suggests that the difference in the mean number of trials taken to learn, irrespective of dominance status, was very small. The interpretation of this marginally significant result should thus be taken with caution despite it suggesting that watching a demonstrator decreased the propensity to learn this task. It is possible that social inhibition may affect the behaviour of lizards in the social demonstration group. Drea and Wallen (1999) reported that subordinate rhesus monkeys (*Macaca mulatta*) that learned a colour discrimination task in isolation were unable to express this knowledge in the presence of a dominant individual. The presence of a dominant demonstrator may be quite stressful for subordinate experimental lizards and may have suppressed their use of social information. Furthermore, social inhibition may have had a negative impact on learning ability as lizards in the social demonstration

treatment seem to have made more incorrect choices than the control group. However, given the effect sizes between these two groups are small, it is difficult to draw any substantial conclusions.

Contrary to our predictions, the presence of social information did not allow lizards to learn the tasks more quickly than our control group. We may not have detected social information use because trial and error learning may not be particularly costly in our experiment. Experimental lizards have little to lose from displacing lids from both dishes, as they would still be rewarded even if they had chosen the incorrect dish first. If trial and error learning is relatively inexpensive compared to social information, individuals should rely on private information, as it may be more accurate (Boyd & Richerson, 1995; Kendal et al., 2005; Rieucau & Giraldeau, 2011). Naïve European starlings (*Sturnus vulgaris*) ignored social information (sampling behaviour of a demonstrator) and relied on private information about the quality of a food patch when it was easy to acquire (Templeton & Giraldeau, 1996). As the difficulty of trial and error learning increased in a complex foraging environment, naïve starlings exploited social information to infer food patch depletion. Also, nine-spined sticklebacks initially rely on private information to make decisions about where to forage, however as private information becomes less reliable over time, sticklebacks switch to using social information (van Bergen, Coolen, & Laland, 2004). This suggests that the reliability and difficulty to acquire private information can affect the likelihood of social information use and may explain why we found no evidence of social information use in our experiment.

Interestingly, we found no evidence that suggests that a lizards' dominance status influenced social information use. A possible reason why we found this result may be due to how we size-matched the demonstrators and observers. Age and SVL are closely linked in lizards because they exhibit indeterminate growth (Halliday & Verrell, 1988). Noble et al. (2014) reported that, on average, young *E. quoyii*, in the presence of an old demonstrator, learnt an association task significantly faster than older lizards suggesting that individuals may not use social information when demonstrators are of a similar age or size. We may have effectively controlled for age effects when pairs of lizards were closely size-matched and randomised across our treatments. Exploiting social information from an individual of similar age may not be beneficial as they are likely to be ill-informed and the costs associated with doing so may be

substantial (Rieucau & Giraldeau, 2011). Thus, it may be more adaptive to learn from individuals that are older and therefore more experienced.

Naivety itself can be a strong driver of social information use in many systems (Duffy et al., 2009; Dugatkin & Godin, 1993; Noble et al., 2014). This is not surprising, as juveniles are able to shortcut trial and error learning during a vulnerable stage of their lives. In *E. quoyii*, young male lizards that are unable defend a territory may incur high energetic costs and be more at risk to predators. Hence, exploiting foraging skills from older males is likely to be advantageous as they may be more familiar with the environment. Studies have demonstrated that young, naïve individuals are able to copy mate preferences and foraging decisions by using the behaviour of older individuals (Duffy et al., 2009; Dugatkin & Godin, 1993; Galef Jr, Marczinski, Murray, & Whiskin, 2001). For example, young female guppies (*Poecilia reticulata*) were more likely to exhibit the same mate choice as older female demonstrators, while old females showed no preference (Dugatkin & Godin, 1993). In nine-spined sticklebacks, small observers that are presumably young used social information from larger (potentially older) demonstrators to make decisions about where to forage (Duffy et al., 2009). This age-dependent pattern was also shown in Norway rats (Galef Jr et al., 2001) suggesting that there maybe strong selection on young individuals to learn from older conspecifics in order to alleviate some of the costs associated with inexperience and trial and error learning. However, if a ‘copy-if-older’ strategy exists, this may put juveniles at risk to learn maladaptive behaviours from unsuccessful elders. Whether juveniles are able to distinguish adults of the same age but that differ in skill-level warrants further investigation.

Conclusions

This is the first study to explore the effect of social dominance on social information use in a lizard. We demonstrated that dominance status does not affect the use of social information in *E. quoyii* in a foraging context. In light of these results and those found previously (Noble et al., 2014) age differences among individuals and being young may be bigger drivers of social information use in this species. Due to the close association between dominance, size and age, it makes untangling these effects very difficult (Duffy et al., 2009). Future studies should try to

control for potential age effects that are likely to be confounded with social dominance when investigating its role in directed social learning

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SUPPLEMENTARY MATERIALS

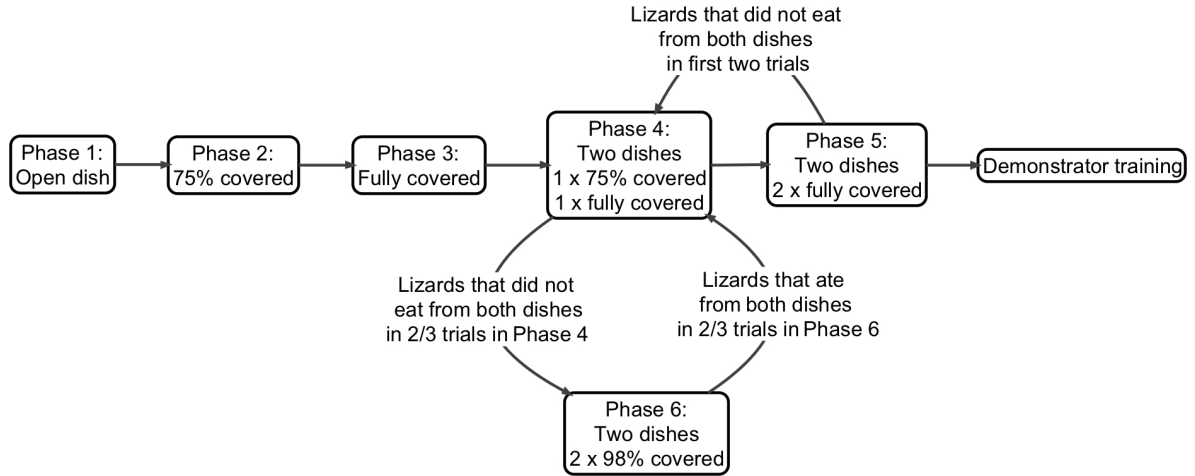


Figure S1. Schematic overview of phases used to train lizards to displace a lid to access a food reward. Lizards must eat from the dishes 5 out of 6 consecutive times to advance to the next phase. Lizards that did not eat from both dishes in 2/3 consecutive trials in Phase 4 were given the an easier task (Phase 6). As lizards improved in Phase 6 and ate from both dishes in 2/3 consecutive trials, they were returned to Phase 4 task. Lizards that struggled to eat from both fully covered dishes in the first two trials of Phase 5 were returned to Phase 4. Lizards that were assigned to be the demonstrator continued training after Phase 5.

Table S1. Posterior modes and highest posterior density intervals from a Bayesian Markov chain Monte Carlo generalised linear mixed effects model (MCMC-GLMM) examining the effects of a standardised SVL [$x - \bar{\mu}(x)/\bar{\sigma}(x)$], treatment group (social or control), a lizard's dominance status (DOM or SUB) and trial number on the log odds of choosing the correct dish only in the reversal task ($n = 710$). Italicised estimates are marginally significant ($p < 0.10$)

	Estimate	Lower	Upper
Intercept	-2.25	-4.69	-0.52
Scaled SVL	-0.85	-2.07	0.24
Treatment SOCIAL	-1.35	-3.90	0.15
Status DOM	0.09	-0.06	0.27
Trial	1.23	-0.54	3.36

CONCLUSION AND FUTURE DIRECTIONS

In summary, my thesis addressed two questions regarding the social dynamics in *E. quoyii*. How does prior contest experience affect behavior and the outcome of male contests and what consequences does the dominance status of an individual have on social information use. In chapter one, I showed that prior contest experience strongly influenced the likelihood for an individual to initiate a contest, and by doing so, initiators had a much higher probability of winning in non-escalated contests. In chapter two, I found that a lizard's dominance status did not influence the use of social information in a foraging paradigm. However, my results in combination with previous work seems to suggest that the age of an observer relative to the demonstrator may play a more important role in social information use (Noble et al. 2014). I hope my work will broaden our understanding of winner-loser effects in reptiles and highlight the importance of considering the level of escalation in a contest in understanding predictors of contest outcome. Furthermore, irrespective of the exact social learning strategy employed by *E. quoyii*, my work shows that the use of social information is not indiscriminate and individuals adaptively choose when to learn from others and whom to learn from. Nonetheless, there are certainly many more questions to ask regarding contest competition, winner-loser effects and the strategies individuals employ to maximize social learning opportunities.

1. What determines the outcome of escalated contests?

Only thirty percent of my contests escalated to physical fighting. Due to a relatively small sample size, it is still unclear what the predictors of contest outcome are for these escalated contests. My results suggested that the total times a lizard bit his rival somewhat predicted the outcome of escalated contests. There are other potential factors that I did not consider that could be important in escalated fights. For example, the endurance capacities of the lizards could possibly influence the outcome of escalated fights because rivals often wrestle each other while grasping each other's tails in their mouth. One would predict that lizards with greater endurance capacities are more likely to win because they are able to outlast a rival in prolonged fights. The duration or the number of bite holds (bite and lift of the tail), might also be a key predictor because extended bite holds may inflict more damage to a rival compared to multiple short-lasting bites. One prediction would be that, the longer a lizard grasps his opponent's tail the more likely he would win. Moreover, endurance capacity of a lizard maybe associated with the duration of bite holds. In the

future, closely matching males in mass, SVL and prior contest experience will possibly increase the chance of contest escalation. Increasing the statistical power could thus increase the likelihood of detecting the factors that are important for escalated contests in *E. quoyii*.

2. *Rival assessment strategies*

Animals adopt assessment strategies to decide whether to escalate or to retreat from a fight. An individual's decisions can either be based on an opponent's fighting abilities (mutual assessment, Enquist, Leimar, Ljungberg, Mallner, & Segerdahl, 1990) or it can be based on the individual's own energetic thresholds (self assessment, Mesterton-Gibbons, Marden, & Dugatkin, 1996; Payne, 1998). It is often implicitly assumed that animals adopt one global strategy for all types of contests, however recent studies have shown that animals are capable of employing different strategies at various stages of a contest (Garcia et al., 2012; Hsu, Lee, Chen, Yang, & Cheng, 2008). For example, mangrove killifish uses mutual assessment during the early display stages of a contest (Hsu et al., 2008). Once the contest escalates to physical attacks, losers appear to use self-assessment to make decisions about when to retreat (Hsu et al., 2008). Both mutual and self assessment models make specific predictions about how contestants' resource holding potential (RHP) can influence various aspects of contest dynamics such as duration and intensity. For example, in the cumulative assessment model (Payne, 1998), decisions to retreat from a fight is based on how long an individual can bear the costs inflicted by an opponent. Thus, contest duration is predicted to be strongly associated with the eventual loser's RHP because weaker individuals will reach their cost thresholds first (Payne, 1998). Body size is often used as a proxy for RHP to test predictions of assessments models, however when RHP is strongly influenced by contest experience, as in *E. quoyii*, body size may not be a suitable proxy (Stuart-Fox, 2006). Moreover, according to my results, the effects of contest experience on RHP and contest outcome can vary depending on the level of escalation and this is likely to influence rival assessment. Stuart-Fox (2006) proposed the use of a composite measure of RHP that incorporates the effects of multiple morphological traits, as well as contest experience effects to test assessment model predictions. A useful study to conduct would involve testing the predictions of both self and mutual assessment models using a composite RHP proxy for both non-escalated and escalated contests in *E. quoyii*. Understanding the nature of assessment strategies will be important for the advancement of contest theoretical models.

3. *Formation of dominance hierarchies*

Done and Heatwole (1977) reported that small groups of *E. quoyii* are capable of forming feeding hierarchies. Theoretical analyses have suggested that winner-loser effects play an important role in the hierarchy formation (Dugatkin, 1997; Dugatkin & Druen, 2004), however empirical support for this conclusion is lacking and winner-loser effects is always examined in pairwise interactions. Dugatkin (1997) developed a model that showed that winner effects alone were able to form unambiguous linear hierarchies. In contrast, when only loser effects were operating, the ranks of individuals were difficult to discern because losers were unmotivated to fight.

Eulamprus quoyii may be a suitable candidate to empirically test these theoretical predictions because my results show that male contests are strongly influenced by prior contest experience. An interesting study would be to allow a sample of size-matched lizards to compete and ‘self-select’ their own contest experiences. One would then allocate individuals into three treatments, i) a group of three prior losers, ii) a group of three prior winners, iii) a mixed group of both a prior winner and loser and a neutral competitor with no contest experience. One would predict that the ‘all prior winners’ treatment would be successful in forming a linear hierarchy, but the ‘all prior losers’ treatment would not be. While in the mixed group, one can assess whether the prior winner emerged as top-ranking individual and prior loser occupied the lower rank. Testing these theoretical predictions will allow further understanding of the adaptive function of winner-loser effects.

4. *Can young males distinguish between knowledgeable individuals?*

Previous results suggest that young male *E. quoyii* were able to learn an association task from a demonstrator (Noble, Byrne, & Whiting, 2014), and I have shown that this is not due to the confounding effects of dominance status between different age groups. Given that age seems to be a more important driver of information use, are all juveniles good learners? Moreover, are all adults good teachers? Sex biased social learning has been documented in a range of species (Aplin, Sheldon, & Morand-Ferron, 2013; Laland & Reader, 1999; van de Waal, Renevey, Favre, & Bshary, 2010) and may reflect differences in foraging and reproductive behaviours (Choleris & Kavaliers, 1999). For example in blue tits (*Cyanistes caeruleus*), young females are more likely to disperse and are twice as likely to acquire social information compared to young males (Aplin et al., 2013). This could be an adaptation to maximize foraging opportunities at a vulnerable stage. Another study found that in wild vervet monkeys (*Chlorocebus pygerythrus*), female

demonstrators promoted more social learning compared to male demonstrators (van de Waal et al., 2010). Female models may be more salient because they show a high degree of philopatry in this species (van de Waal et al., 2010). An interesting experiment in *E.quoyii* would involve pairing young females and males with either an adult female and male demonstrator and assess whether there are differences in the rate of social learning between each pair. Understanding how social learning is transmitted in reptile populations will bridge the knowledge gap between ectotherms and endotherms.

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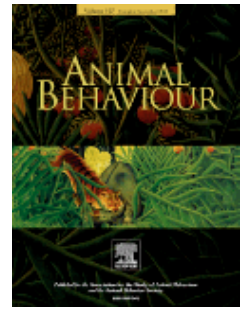
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APPENDIX

This appendix contains the author instructions for Animal Behaviour.

ANIMAL BEHAVIOUR

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INTRODUCTION

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