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ORIGINAL PAPER

# Dominance and social information use in a lizard

**Fonti Kar**[1,2] · **Martin J. Whiting**[1] · **Daniel W. A. Noble**[1,2]

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**Abstract** There is mounting evidence that social learning is not just restricted to group-living animals, but also occurs in species with a wide range of social systems. However, we still have a poor understanding of the factors driving individual differences in social information use. We investigated the effects of relative dominance on social information use in the eastern water skink (*Eulamprus quoyii*), a species with age-dependent social learning. We used staged contests to establish dominant–subordinate relationships in pairs of lizards and tested whether observers use social information to more quickly solve both an association and reversal learning task in situations where the demonstrator was either dominant or subordinate. Surprisingly, we found no evidence of social information use, irrespective of relative dominance between observer and demonstrator. However, dominant lizards learnt at a faster rate than subordinate lizards in the associative learning task, although there were no significant differences in the reversal task. In light of previous work in this species, we suggest that age may be a more important driver of social information use because demonstrators and observers in our study were closely size-matched and were likely to be of similar age.

**Keywords** Social learning · Private information · Social status · Social rank · Reptile

## Introduction

The social environment is a rich source of information that can be used in individual decision-making and learning. Social information allows observers to shortcut trial-and-error learning, thereby bypassing the costs associated with individual learning (Boyd and Richerson 1995; Shettleworth 2010 pp. 468). Costs, such as the time and energy expended acquiring new information and the increased risk of predation while sampling the environment, should favor the use of social information (Rieucau and Giraldeau 2011). However, social information use is not inherently adaptive, and theoretical analyses suggest that individuals should use social information selectively (Rieucau and Giraldeau 2011). Socially acquired information also may be costly to obtain, unreliable or outdated in changing environments, thus selection may be expected to favor plastic learning strategies (Laland 2004).

For social information use to be advantageous, individuals should be selective about whom they learn from (Laland 2004). Observers may preferentially learn from certain individuals as the quality and relevance of information is predicted to vary between individuals (Coussi-Korbel and Fragaszy 1995). As a consequence, transmission of social information in the population can spread at different rates because information use may be restricted to a subset of individuals with particular traits. Social cues such as dominance status, age or size may be indicators of success, and an observer may use these cues to assess whether to 'copy' an individual's behavior or not (Galef and Laland 2005). Dominance status may be indicative of

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✉ Fonti Kar
fonti.kar@gmail.com

[1] Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

[2] Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2052, Australia

resource monopolization and observers may employ a 'copy-if-dominant' strategy to maximize resource gathering opportunities (Laland 2004). However, dominance, age and size are often confounded, whereby larger individuals tend to be older and more dominant than smaller individuals. Hence, it becomes difficult to disassociate these effects (Aplin et al. 2013; Duffy et al. 2009). In order to understand individual variation in social learning particularly in species that show dominance hierarchies, one must account for confounding factors such as age and size.

Social information use is most often associated with group-living species (Lefebvre 2010). Indeed, the role of dominance in social information use has been extensively tested in birds and mammals. While reptiles are often considered to be less socially complex than other vertebrates; this does not preclude their ability to use social information (Davis and Burghardt 2011; Kis et al. 2014; Noble et al. 2014; Pérez-Cembranos and Pérez-Mellado 2015; Whiting and Greeff 1999; Wilkinson et al. 2010). Moreover, the drivers of variation in social information use, particularly that of dominance, remain unexplored. Dominant individuals are predicted to be more salient than lower ranking animals because subordinates may need to monitor dominant individuals more closely to avoid aggressive interactions (Nicol and Pope 1999; Shepherd et al. 2006). Many studies have found that dominant individuals are more influential models (Kendal et al. 2014; Krueger and Heinze 2008; Nicol and Pope 1999 but see Awazu and Fujita 2000). Other studies show that subordinates are more likely to use social information to solve novel tasks compared to their dominant counterparts (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). Using reptilian models to test questions of how dominance influences social information use will close this taxonomic gap, which could be fundamental to understand the evolution of social learning strategies and any links to social behavior (Doody et al. 2013).

We investigated whether relative dominance impacts social learning in eastern water skinks (*Eulamprus quoyii*). *Eulamprus quoyii* perform well on a multitude of cognitive tasks, and previous work has shown that age is an important factor in social information use in this species (Noble et al. 2014). Males of this species experience contest competition over territories and exhibit alternative reproductive tactics (Kar et al. 2016; Noble et al. 2013). They are also known to form feeding hierarchies (Done and Heatwole 1977), suggesting that social dominance may be an important driver in social information use. We therefore only used male lizards to test whether dominant–subordinate relationships between demonstrating and observing lizards affect their use of social information. We staged dyadic contests between lizards to establish dominance relationships between pairs and then conducted social learning experiments in which the demonstrator and observer differed in their relative dominance. Given that lizards continue to grow after sexual maturity (indeterminate growth), age and body size are closely correlated (Halliday and Verrell 1988). Thus, we attempted to control for age and body size of the lizards by closely size-matching demonstrator and observer lizards and randomizing the body size distribution across our treatments.

## Methods

### Lizard collection and husbandry

We collected 56 adult male *E. quoyii* from nine sites in the Sydney region during September 14–30, 2014 and brought them back to Macquarie University. We recorded 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) and body mass of all lizards to the nearest mm.

### Apparatus

All trials were conducted in white opaque plastic arenas measuring 470 (W) × 690 (L) × 455 (H) mm. In the dominance assays, each lizard occupied half of the arena separated by a removable wooden divider. During contests, the divider was removed to allow lizards to interact. Similarly, in the cognition trials, the arena was partitioned by a permanently fixed piece of plexiglass as well as, a removable wooden divider. At the start of each trial, this divider was removed to allow pairs of lizards to observe each other. Volatile chemical cues could be exchanged through the gaps and cracks of the dividers, but animals were not able to physically interact during trials.

For our cognition trials, all lizards were trained to displace lids from two black dishes mounted on a wooden block to access a mealworm (*Tenebrio molitor*). For more details of training procedures, see supplementary materials. Once all lizards had been trained, observer lizards were given an association and a reversal task. The association task consisted of one dish that was covered by a blue lid, while the other was covered with a white lid (incorrect dish) and required the observer lizard to displace the blue lid (correct dish) to access a mealworm (Fig. S3). The reversal task was essentially the same as the association task, except that the dish containing the accessible mealworm was covered by a white lid (correct dish, Fig. S3). We placed mealworms in both dishes to control for scent and auditory cues that may differ between the two dishes, but a piece of cardboard was placed inside the 'incorrect'

dish to obstruct the food reward (association task—white, reversal task—blue). The position (right or left) of the correct dish was randomized and counter-balanced across treatment groups to account for differences in lateralization between lizards. The position of the correct dish remained consistent within each task after this initial randomization. We therefore cannot disambiguate whether spatial or color cues were used to learn the tasks, as our goal was to determine whether lizards used social information to learn the task and not specifically test what cue was being used to learn.

### Determining male dominance status

Male contests were carried out between September 22 and October 12, 2014 in a temperature-controlled room set at 28 °C. Males were size-matched based on SVL (mean size difference = 1 mm, range = 0–5 mm). We used a tournament design where individuals participated in up to seven contests with different opponents (Whiting et al. 2006). On the day of the contest, refuges, water bowls and dividers were removed to allow opponents to interact. Contests were closely monitored so that once a clear outcome was apparent the opponents were immediately separated. A clear contest outcome occurred when one lizard fled from his opponent following an aggressive behavior such as a chase and the lizards were at least half a body length apart. For more details of the contest setup, see Kar et al. (2016).

### Treatment groups

We obtained 28 demonstrator–observer pairs from contests that only resulted in a clear outcome. The winner of the contest was assigned as the dominant lizard, while the loser became the subordinate lizard. We assessed the stability of the dominance relationship within pairs by staging another round of contests, on average, 61 days (range 53–72 days) after the pair's initial interaction ($n = 26$, two pairs did not re-fight). In short, we found that 91% of pairs that interacted in the second round of contests, the dominance relationship was consistent within each pair. For details on how we assessed the stability of dominance relationships, see supplementary materials. We also performed sensitivity analyses, which showed that the status of demonstrator–observer pairs that changed in dominance relationships did not impact our overall results (see supplementary materials).

The demonstrator–observer pairs were randomly allocated to one of the two treatment groups: (1) a social treatment group where the observer lizard was allowed to view the demonstrator performs the task; and (2) a control group, where the observer lizard was allowed to view a demonstrator that was not performing the task. In these treatment groups, the observer of the pair was randomly chosen to be: (1) the subordinate individual ($n = 12$); or (2) the dominant individual ($n = 16$). The other individual of the pair was assigned as the demonstrator such that a subordinate observer was paired with a dominant demonstrator and vice versa. While it would have been ideal to include additional dominant–dominant and subordinate–subordinate pairs, this was not possible given sample size and logistical constraints. Overall, we had four treatments consisting of: (1) subordinate control observers ($n = 3$); (2) subordinate social observers ($n = 9$); (3) dominant control observers ($n = 8$); and (4) dominant social observers ($n = 8$).

### Association and reversal task

Social learning trials were carried out in the same room where contests assays were held. We conducted two trials per day, in the morning (08:30–10:00 h) and in the afternoon (12:00–14:00 h) with a minimum interval of 2 h between trials. 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 observer lizards were first given six trials to view the demonstrator complete the task, while control lizards viewed their demonstrators for the same amount of time (Fig. S3). During the six trials, the observer lizards did not receive the apparatus, and therefore, these six trials did not count toward the total number of trials taken to learn. Following from this, the observers viewed the demonstrator on each trial prior to receiving the apparatus. A lizard was considered to have learnt the task if it displaced the correct lid 5/6 consecutive times (a robust learning criterion—see supplementary materials). Lizards were allowed to continue with the task even if an incorrect choice was initially made; however, these trials did not count toward the learning criterion. We continued to give the task to lizards that had reached criterion in order to evaluate the robustness of our learning criterion. Lizards were given 18 trials in total to complete the task. Lizards that did not learn the association task were excluded from the reversal task ($n = 1$).

In the reversal task, lizards had to reverse previously learnt contingencies regarding the correct dish (i.e., blue reward in association task). All demonstrators were first trained to displace only the white lid using the same learning criterion as the association task prior to the commencement of social demonstration. We continued to give the task to lizards that had reached criterion. Lizards received more trials in total in the reversal task because lizards took slightly longer to reach criterion. In total, lizards received 26 trials to interact with the task. However, the total number of trials varied slightly in both tasks as

some lizards did not interact with the task on every trial or were given an extra trial as they were close to reaching criterion (association task range 14–19, reversal task range 21–27). All trials of both tasks were filmed using CCTV cameras and a blind reviewer measured: (1) whether or not the lizard chose the correct dish first; (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. A lizard was considered to have made a choice if it actively displaced the dish with its snout or forelimbs.

### Statistical analyses

We explored the robustness of our learning criterion and also motivation differences due to body condition and dominance status. These analyses are presented in the supplementary materials.

We analyzed our data in three different ways that tested different aspects of learning. First, given that social learning and trial-and-error learning were occurring concurrently throughout the trials, we used a Fisher's exact test to test whether dominance status influenced the number of individuals making a correct choice on the first trial in each treatment group, for both tasks.

Second, we assessed how quickly lizards learnt the task, based on our learning criterion, by modeling the mean number of trials it took to learn using a generalized linear model (GLM) with a negative binomial error distribution. Lizards that did not reach the learning criterion were not included in the final GLM analysis (association task: $n = 1$, reversal task: $n = 2$); however, exclusion of these lizards did not impact our results. We tested the significance of a lizard's dominance status, treatment group and their interaction using likelihood ratio tests (LRT).

Given the logistical constraints in obtaining large samples sizes, which can impact $P$ values, we also calculated a log response ratio (lnRR) to estimate an effect size (Hedges et al. 1999). We compared the effect sizes for the mean number of trials taken to learn the tasks between: (a) control and social lizards, (b) dominant control and dominant social lizards, (c) subordinate control and subordinate social lizards and (d) subordinate social and dominant social lizards.

We also ran additional analyses to investigate how lizard cognitive performance changed across trials using generalized linear mixed effect models. We modeled the 'probability of choosing the correct dish first,' the probability of 'choosing *only* the correct dish,' as well as 'latency to displace the correct lid.' The results of these analyses were largely congruent with our GLM results and are presented in the supplementary materials.

In all models, treatment (social and control) and status of the observer (dominant = DOM and subordinate = SUB) were coded as two-level factors. We tested whether differences in cognitive performance depended on a lizard's treatment group and/or dominance status by including an interaction term between treatment and status because we hypothesized that dominant and subordinate lizards may use social information differently. We z-transformed SVL and included it in all models as a covariate to account for any differences between treatments in body size that may influence learning. Data for this study is available from doi:10.6084/m9.figshare.4981958.

## Results

### Association task

Dominance status did not influence the number of individuals making a correct choice on the first trial in either treatment group ($P = 0.20$). Overall, 27 of 28 (96%) observer lizards learnt the task. All 12 (100%) subordinate lizards learnt the task (nine social, three controls), whereas 15/16 (94%) of dominant lizards learnt the task (seven social, eight control).

There were no differences in the mean number of trials taken to learn between control and social lizards in a model pooling lizards of both dominance statuses (GLM: estimate = −0.15, SE = 0.16, $P = 0.35$; LRT: $\chi^2 = 0.89$, $P = 0.35$). The mean number of trials it took for lizards to learn depended on a lizard's dominance status (Table 1a, LRT: $\chi^2 = 7.92$, $P = 0.01$), but not its treatment group (Table 1a, LRT: $\chi^2 = 0.21$, $P = 0.65$), or their interaction (Table 1a, LRT: $\chi^2 = 0.05$, $P = 0.82$). Dominant social lizards learnt the association task in significantly fewer trials compared to subordinate social lizards (Fig. 1a, Table 1a). The mean number of trials taken to learn was 20% smaller in control lizards compared to social lizards (lnRR = 0.18, $\sigma^2 = 0.13$). The mean number of trials taken to learn for dominant control lizards was 8% smaller than dominant social lizards (lnRR = 0.08, $\sigma^2 = 0.14$), whereas it was 10% smaller in subordinate control lizards compared to subordinate social lizards (lnRR = 0.09, $\sigma^2 = 0.37$). The mean number of trials taken to learn was 29% smaller in dominant social lizards compared to subordinate social lizards (lnRR = 0.34,$\sigma^2 = 0.24$).

### Reversal task

The number of individuals making a correct choice on the first trial was not associated with dominance status, in either treatment group ($P = 0.20$). Twenty-six of 28 (93%)

**Table 1** Estimates and standard errors (SE) from a generalized linear model (GLM) examining the effects of a lizard's dominance status (dominant or subordinate), treatment group (social or control) and standardized SVL $[x - \mu/\sigma]$ on the mean number of trials it took for a lizard to learn the **a** association task ($n = 27$) and **b** the reversal task ($n = 25$)

| | (a) Association task | | (b) Reversal task | |
|---|---|---|---|---|
| | Estimate | SE | Estimate | SE |
| Intercept | **2.31** | **0.10** | **2.40** | **0.14** |
| Status DOM | **−0.43** | **0.15** | −0.06 | 0.21 |
| Treatment control | 0.08 | 0.18 | −0.42 | 0.25 |
| Scaled SVL | 0.12 | 0.08 | 0 | 0.12 |
| Status × treatment | −0.07 | 0.30 | 0.38 | 0.44 |

Bolded estimates are significant. Main effects are presented from a model without the interaction

observer lizards learnt the task. All 12 (100%) subordinate lizards learnt the task (nine social, three controls), whereas 13/15 (86%) of dominant lizards learnt the task (seven social and six were controls).

There was a weak significant difference in the mean number of trials taken to learn between control and social lizards in a model pooling lizards of both dominance statuses (GLM: estimate = −0.46, SE = 0.23, $P = 0.05$; LRT: $\chi^2 = 4.37$, $P = 0.038$). The mean number of trials it took for lizards to learn did not depend on treatment group (Table 1b, LRT: $\chi^2 = 2.86$, $P = 0.09$), dominance status (Table 1b, LRT: $\chi^2 = 0.08$, $P = 0.78$) or their interaction (Table 1b, LRT: $\chi^2 = 0.76$, $P = 0.38$). There was a trend for both dominant and subordinate control lizards to take fewer trials to learn than their social treatment counterparts; however, this was not significant (Fig. 1b). The mean number of trials taken to learn for control lizards was 57% smaller compared to social lizards (lnRR = 0.45, $\sigma^2 = 0.30$). The mean number of trials taken to learn for dominant control lizards was 33% smaller than dominant control lizards (lnRR = 0.28, $\sigma^2 = 0.83$), whereas it was 93% smaller in subordinate control lizards compared to subordinate social lizards (lnRR = 0.66, $\sigma^2 = 0.43$). The mean number of trials taken to learn was 20% smaller in dominant social lizards compared to subordinate social lizards (lnRR = 0.18, $\sigma^2 = 1.21$).

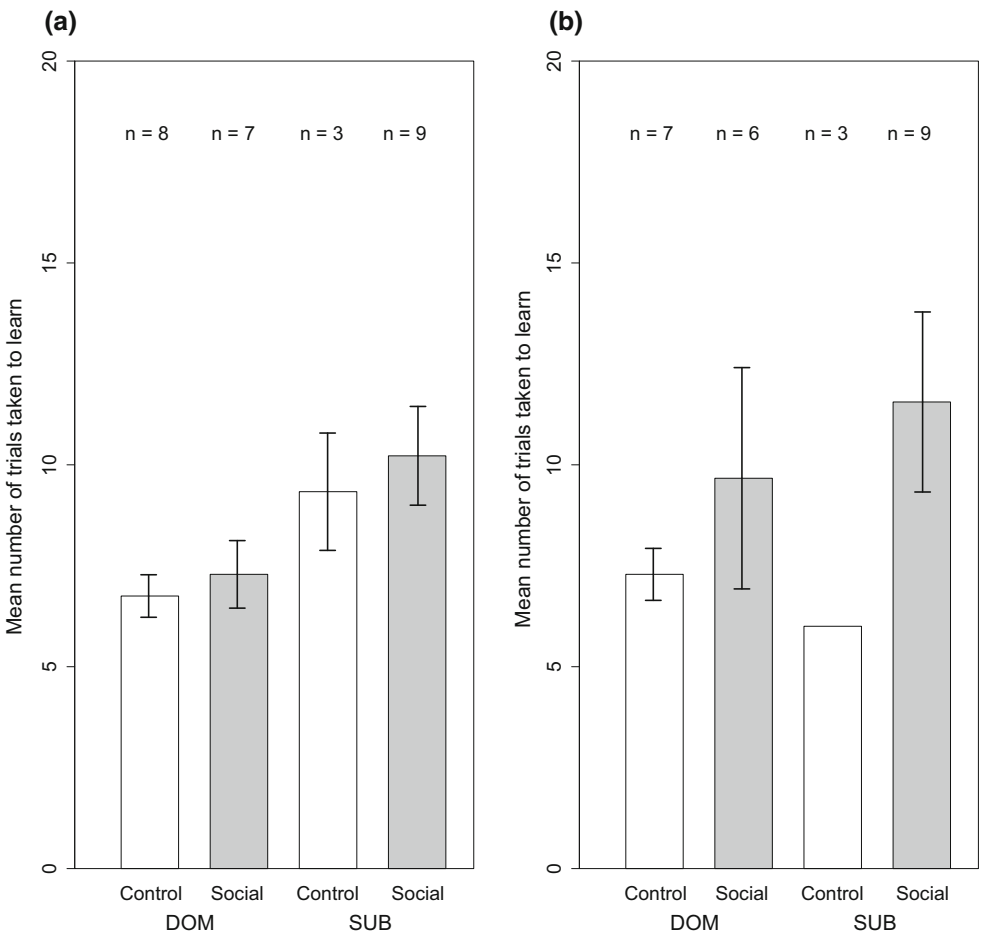


**Fig. 1** Raw mean number of trials and sample sizes to learn for **a** the association task and **b** the reversal task for dominant (DOM) and subordinate (SUB) lizards in the social demonstration (*gray bars*) and control (*white bars*) treatments. *Error bars* represent standard error. Note that subordinate control lizards all achieved the learning criterion at the same time and therefore do not have an error estimate

## Discussion

We show that lizards from the social demonstration treatment were no more likely to make a correct choice on the first trial compared to the control group. To our surprise, the social demonstration treatment did not learn more quickly than the control group, providing weak evidence that observers were using social information to learn the association or reversal task. Our results also suggest that dominant social lizards learnt the association task in significantly fewer trials, compared to subordinate social lizards. However, there were no differences in the number of trials required to reach criterion in the reversal task. Given that we did not find evidence of social information use, this result may reflect underlying differences in trial-and-error learning between dominant and subordinate lizards during associative learning.

### Lack of social learning in a novel foraging task

Contrary to our predictions, watching a demonstrator execute the task did not expedite learning in the association and reversal tasks compared to the control group. This may be because trial-and-error learning was not particularly costly in our experiment. Observer lizards have little to lose from displacing lids from both dishes, as they would still eventually be rewarded if they chose the incorrect dish first. Individuals are predicted to rely on private information if trial-and-error learning is relatively inexpensive compared to social information, as it may be more accurate (Boyd and Richerson 1995; Kendal et al. 2005; Rieucau and Giraldeau 2011). Indeed, naïve European starlings (*Sturnus vulgaris*) have been shown to ignore the sampling behavior of a demonstrator and rely on private information about the quality of a food patch when private information was easy to acquire (Templeton and Giraldeau 1996). However, as the difficulty of trial-and-error learning increased, naïve starlings were more likely to exploit social information to infer food patch depletion. Nine-spined sticklebacks (*Pungitius pungitius*) initially relied on private information to make decisions about where to forage, but as private information becomes less reliable over time, they switched to using social information (van Bergen et al. 2004). This suggests that the reliability and difficulty of acquiring private information can affect the use of social information to acquire new information and may explain why we found no evidence of social information use in our experiment.

Alternatively, we may not have detected social information use because we size-matched demonstrators and observers and by doing so, we may have age-matched them as well. In *E. quoyii,* young lizards in the presence of larger, older demonstrators learnt an association task significantly faster than older lizards watching same-aged demonstrators, suggesting that older *E. quoyii* may not use social information when demonstrators are of a similar age or size (Noble et al. 2014). Given that our experiment attempted to disassociate age and dominance, we may have effectively removed age effects and thus did not detect social information use. Taken together, these results seem to suggest that age may be the major driver of social information use (at least on association tasks) in *E. quoyii*. The results of these two studies together represent a unique situation where the confounding effects of age and dominance have been successfully disassociated in a single study system. Indeed, naivety can be a strong driver of social information use in many systems (Duffy et al. 2009; Galef et al. 2001; Noble et al. 2014). This is not surprising, as juveniles have much to gain by using social learning during a vulnerable stage of their lives by exploiting social information from older, more experienced individuals (Rieucau and Giraldeau 2011). However, we do need to consider that these effects may be the result of the low statistical power in our study and future work replicating these experiments would be needed to verify these conclusions.

### Dominance and trial-and-error learning

Dominant social lizards learnt the association task in significantly fewer trials compared to subordinate social lizards based on our learning criterion. Given that we did not detect the use of social information in either task, this result seems to suggest differences in the rate of trial-and-error learning between dominant and subordinate lizards and may reflect differences in motivation or foraging behavior between dominant and subordinate lizards. Dominant individuals have been reported to be superior at trial-and-error learning in a range of species including meadow voles and European starlings (Boogert et al. 2006; Spritzer et al. 2004). While dominant individuals may be intrinsically better than subordinates at cognitive tasks, learning ability may also be affected by social context. For example, dominant individuals tend to excel in both group contexts as well as in isolation, whereas subordinate individuals tend to thrive only in isolated contexts (Drea and Wallen 1999). Stress associated with learning in the presence of a dominant demonstrator may have also reduced learning ability of subordinate individuals. Future studies should consider testing subordinate and dominant individuals in isolation in order to test for differences in trial-and-error learning.

## Conclusions

We found no support for the hypothesis that relative dominance affects social information use in *E. quoyii*. Lizards that viewed a demonstrator perform a task,

regardless of whether they were subordinate or dominant, did not learn faster than the control group. Interestingly, social dominance predicted associative learning ability: dominant individuals reached criterion faster than subordinate individuals. Many of the lizards in dominant–subordinate pairs were matched in size, and therefore, they may also be similar in age. Using this design, we had more power to detect an effect for dominance at the expense of an age effect. It is possible that there may be an effect with greater disparity in dominance or age. Future studies that are able to use individuals of known age would be very valuable in studying the interaction between age and dominance and its potential role in social learning.

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**Compliance with ethical standards**

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

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

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