Received: 27 June 2020 | Revised: 29 November 2020 | Accepted: 1 December 2020

DOI: 10.1111/jeb.13752

RESEARCH PAPER

JOURNAL OF Evolutionary Biology eseb WILEY

Sexual selection on performance traits in an Australian lizard with alternative reproductive tactics

Daniel W. A. Noble[1,2,3] | Fonti Kar[2] | Shinichi Nakagawa[2] | J. Scott Keogh[3] | Martin J. Whiting[1]

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

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

[3]Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, ACT, Australia

Correspondence
Daniel W. A. Noble, Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, ACT 2602, Australia.
Email: daniel.noble@anu.edu.au

Funding information
Natural Sciences and Engineering Research Council of Canada; Australian Research Council, Grant/Award Number: DE150101774

Abstract

Sexual selection shapes the adaptive landscape in complex ways that lead to trait integration. Much of our understanding of selection comes from studies of morphological traits. However, few studies attempt to quantify the form and direction of selection on performance even though it is predicted to be a more direct target of selection in nature. We measured sexual selection on performance traits (bite force, sprint speed and endurance) in an Australian lizard, the Eastern water skink (*Eulamprus quoyii*). We first staged 123 contests between size-matched males to investigate whether performance traits were important in determining contest outcome. In a second experiment, we established six breeding populations in large replicate semi-natural enclosures to estimate whether performance traits predicted reproductive success. Our results show that none of the performance measures were important in predicting contest outcome and were not generally strong predictors of reproductive success. However, our analyses suggest a complex fitness landscape driven by males adopting different alternative reproductive tactics (ARTs). We provide a rare test of the role performance plays in sexual selection and highlight the need to test common assumptions regarding the link between maximal performance and fitness. Our results suggest that performance traits may not necessarily be direct targets of sexual selection, but rather indirect targets through their integration with morphological and/or behavioural traits, highlighting a need for more explicit tests of the predicted links between performance and fitness.

KEYWORDS

bite force, correlational selection, endurance, *Eulamprus quoyii*, fitness, post-copulatory sexual selection, precopulatory sexual selection, sexual selection, sprint speed, water skink

1 | INTRODUCTION

Natural and sexual selection act on phenotypic variability in complex ways to shape the adaptive landscape. Sexual selection in particular has played a prominent role in the evolution of sexual size dimorphism (Andersson, 1994), performance (Lailvaux & Husak, 2014), elaborate male ornamentation (Andersson, 1994) and alternative male reproductive tactics (Miles et al., 2007; Sinervo et al., 2000). Directional selection is now recognized as a pervasive evolutionary force (Hoekstra et al., 2001; Kingsolver et al., 2001), which can lead to rapid evolutionary responses over ecological timescales (Grant & Grant, 1995; Reznick et al., 1997).

However, traits are often not selected upon in isolation and correlational selection can favour the integration of traits (Brodie III, 1992; McGlothlin et al., 2005; Miles, Sinervo, et al., 2007). Although there are thousands of selection estimates from natural populations (Kingsolver et al., 2001, 2012), much of our understanding about the strength and form of selection comes from studies on morphological traits. Only a few studies have estimated selection gradients on what are thought to be more direct targets of selection, such as behaviour and performance (Arnold, 1983; Irschick et al., 2008; Kaplan & Phillips, 2006).

Selection on behavioural and performance traits can lead to the evolution of alternative reproductive tactics (ARTs), where behavioural, physiological and/or morphological traits are integrated in ways that allow different strategies to compete for mating opportunities (Miles, Sinervo, et al., 2007; Sinervo & Lively, 1996; Sinervo & Svensson, 2002). Intrasexual competition often leads to dominant and subordinate males adopting different behavioural strategies that may be closely integrated with functional performance, such as sustained running endurance for winning male contests or defending territories (Miles, Sinervo, et al., 2007). For example, male side-blotched lizards (*Uta stansburiana*) are known to exhibit one of three throat colour morphs (orange, blue and yellow) (Sinervo & Lively, 1996). Hyper-aggressive orange males guard large territories and have high endurance capacities, presumably to aid in their defence (Sinervo & Lively, 1996; Sinervo et al., 2000). In contrast, blue morphs have small territories and are less aggressive while yellow morphs sneak matings. Importantly, yellow and blue morphs have lower endurance capacities compared to orange males (Sinervo et al., 2000). In dung beetles (*Onthophagus taurus*), horned males are large and vigorously defend dung patches, whereas small hornless males adopt "sneaker-like" behavioural tactics, digging intersecting tunnels which allow them to sneak copulations with females (Emlen, 1997). Horn size is a strong predictor of endurance capacity and pulling force suggesting that the connection between large horns and behavioural tactic is mediated by performance traits (Lailvaux et al., 2005).

Lizards are excellent study systems to explore hypotheses about selection on performance traits in the context of ARTs because of well-established links between functional performance and key behaviours, such as dominance and territoriality (Lailvaux et al., 2004; Losos et al., 2002; Miles, Sinervo, et al., 2007). For example, dominance and resource holding potential (RHP) can often be predicted by large body size and biting force in lizards because larger, stronger biting lizards are capable of winning contests over subordinate males allowing them to gain access to more resources and mates (Husak et al., 2006; Lailvaux et al., 2004). Dominance has also been linked to locomotor performance in lizards such that more dominant individuals have better performance (Perry et al., 2004; Sinervo et al., 2000). Both sprint speed and endurance have been shown to be correlated with winning dyadic contests in *Urosaurus ornatus* (Robson & Miles, 2000). Similarly, in collard lizards (*Crotophytus collaris*), faster lizards sire more offspring because they are able to more effectively defend their territories preventing other males from usurping them (Husak et al., 2006, 2008). However, these patterns are not always consistent. For example, sprint speed is not important for male dominance in the territorial lizard *Anolis cristatellus* (Perry et al., 2004) and can be important for sneaking copulations in systems with ARTs (Husak et al., 2008). The role of performance traits in dominance and reproductive success likely depends on the behavioural tactics adopted by males and the mating system of the given species. Nonetheless, performance is often assumed to be an important trait governing fitness in many lizard systems with this assumption rarely being rigorously tested in the context of precopulatory and post-copulatory sexual selection (Irschick et al., 2008).

Using a widely distributed Australian lizard, the Eastern Water Skink (*Eulamprus quoyii*), we conducted dyadic contests and a large-scale breeding experiment under semi-natural conditions to understand whether performance traits (sprint speed, endurance and bite force) are important for reproductive success (Husak & Fox, 2008; Irschick et al., 2008; Lailvaux & Irschick, 2006). *Eulamprus* spp. are ideal model systems for such studies because they are abundant, habituate quickly to new environments, breed readily under semi-natural conditions and have been the topic of considerable study (Keogh et al., 2012; Noble et al., 2012, 2013, 2014). Body size is one of the most important predictors of reproductive success in *E. quoyii*, but among large males, individuals can adopt behaviourally driven ARTs with, as of yet, no known morphological correlates. Noble et al. (2013) proposed a conceptual framework to understand ARTs in *E. quoyii* that relate to subtle, but important, behavioural differences among the tactics. Territorial/resident males are predicted to be active over a longer period but have small home ranges that they explore less. In contrast, floater males are predicted to have large home ranges, be observed less often and move frequently while active (Keogh et al., 2012, 2013; Noble, Wechmann, et al., 2013; Stapley & Keogh, 2004, 2005). Territorial and floater males obtain similar reproductive success with evidence of correlational disruptive selection on behavioural traits among large males adopting the two tactics (Keogh et al., 2013; Noble, Wechmann, et al., 2013; Stapley & Keogh, 2005). Behavioural differences among ARTs may also be linked with performance traits in *E. quoyii*, some of which have shown to be heritable (Noble et al., 2014), particularly given their association with ARTs in other systems (Miles et al., 2007; Miles, Sinervo, et al., 2007; Sinervo et al., 2000).

We tested two alternative hypotheses about how locomotor performance and bite force influence reproductive success (Husak & Fox, 2008). First, we tested the hypothesis that performance traits play an important role in male contest outcome leading to higher reproductive success for better performing males (hypothesis 1). If this were true, then we would predict directional selection on performance traits such that better performers would win dyadic contests and obtain the highest reproductive success. Alternatively, given the existence of behaviourally driven ARTs in *E. quoyii*, correlational/nonlinear selection might result in a more complex fitness landscape that relates to the different mechanisms by which ARTs obtain paternity (hypothesis 2). In this scenario, we predict that performance traits would not show simple linear relationships with reproductive success. Additionally, they may impact on the number of clutches

sired because territorial males obtain high reproductive success by ensuring greater paternity within a clutch, whereas floater males are expected to sire a small proportion of offspring across many clutches. If performance traits are targets of sexual selection, these hypotheses also predict that the relationship between performance and reproductive success would be sex-dependent with stronger selection for better male performers (Husak & Fox, 2008; Lailvaux & Husak, 2014). Evidence for sexual selection on performance traits would support previous work that has shown sex differences in performance and morphology in this species (Noble, Fanson, et al., 2014).

2 | MATERIALS AND METHODS

2.1 | Lizard collection and natural history

We collected 272 (164 males and 108 females) adult *E. quoyii* from five sites in the Sydney region for our experiments. *Eulamprus quoyii* is a medium-sized skink (~90–130 mm, snout–vent length) that likely lives between 8 and 15 years (based on other species) and exhibits little sexual dimorphism (Dubey et al., 2013; Noble, Fanson, et al., 2014; Schwarzkopf, 2005). It inhabits rocky open creeks and forests along the east coast of Australia (Law & Bradley, 1990). It is a viviparous species giving birth to between 1 and 9 offspring in a single litter each year with a high level of multiple paternity (65% clutches have more than 1 sire) (Noble, Keogh, et al., 2013; Noble, Wechmann, et al., 2013). Lizards were captured along creeks by noose and brought back to the laboratory at Macquarie University campus where they were sexed and measured (head width, length, depth and snout–vent length [SVL] to the nearest 1 mm and mass to the nearest 0.1 g). From each lizard, we excised a small (~3 mm) tail tip for later genetic analysis. Lizards were then transferred to plastic bins [487 (L) × 350 (W) × 260 mm (H)] in a temperature-controlled room for three days to measure performance traits. Each bin had a hide box and a water bowl with newspaper as a substrate. Lizards were maintained at ambient temperatures of ~22–26°C with an elevated basking site of ~28–30°C. Ultraviolet lighting and water were provided at all times and lizards were fed once during the three days with crickets or mealworms.

2.2 | Quantifying maximal performance traits

We measured lizard bite force, sprint speed and endurance daily over three consecutive days. Prior to all measurements, lizards were heated to their preferred body temperature, 28°C (Law & Bradley, 1990), by placing lizards in plastic zip-lock bags and floating them in warm water until they reached near optimal body temperature. For each lizard, we recorded the time lizards began performance trials and the body temperature of lizards before the start (i.e. prior to bite force) and at the end (i.e. after endurance measurements) of performance measurements using a Miller-Weber cloacal thermometer. We took the maximal measurement for all our performance variables because lizards frequently have poor runs (Losos et al., 2002).

2.2.1 | Bite force

Bite force (N) was measured a total of six times on all lizards using a Kistler force transducer (Kistler Inc., Winterthur Switzerland) that was connected to a Kistler charge amplifier (Model 5995, Kistler Inc.). For additional details of the setup, including a diagram, see, Herrel et al. (2001). We measured each lizard twice a day, once before our measurement of sprint speed and once after, over three consecutive days. We took a second measurement of bite force after running down the racetrack because lizards appeared to be more motivated to bite after they had run. We induced lizards to bite the two plastic bite plates (20 × 6 mm) by gently pinching the sides of their mouth. The gap between the plates was typically a few mm and adjusted according to the size of the lizard in order to maintain the minimum distance between plates necessary to prevent the transducer exceeding its threshold. We ensured consistency in our measurements by making sure the tip of the snout touched a plastic contact point perpendicular to the plates.

2.2.2 | Sprint speed

Using a racetrack, we measured sprint speed over a 2 m length immediately after the first bite force measurement. The running surface of the racetrack was lined with rubber matting, and a bucket was placed at the end of the racetrack, which the lizard fell into once the run was complete. Lizards were placed at the starting line and stimulated to run by taping them gently on their tail-base. In most cases, lizards ran extremely well to the end of the finish line, with few incidences of stops and reversals. We recorded sprinting lizards using a Panasonic HD video camera (30 fps) and quantified the speed of each of the three runs using MotionPro Motion Analysis Software (http://www.motionprosoftware.com/).

2.2.3 | Endurance

We measured endurance immediately following the lizard's sprint. Lizards were run on a modified human treadmill to measure their maximal endurance. A transparent plexiglass box with adjustable compartments was placed on top of the treadmill. The middle compartment was adjusted so that the lizards could run unobstructed, while also ensuring that they could not easily turn around. All trials were run at a speed of 1.0 km/h, which was an optimal speed for keeping lizards running at a consistent pace. This speed is also commonly used in lizard performance studies (e.g. Garland, 1999). Lizards were placed on the treadmill and were stimulated to run by gently tapping the base of their tail. After each tap, we gave the

lizard a few seconds to continue running. If the lizard was not stimulated to run, we allowed the lizard to move closer towards the end of the treadmill and tapped the lizard again. We continued this until the lizard could no longer run at which point we allowed the lizard to fall into a container at the base of the treadmill. We then placed the lizard back on the treadmill and continued the same procedure until the lizard had fallen into the container three times, at which point we considered the lizard exhausted. The time when the lizard started running on the treadmill to when it fell in the container the third time was recorded as its time to exhaustion.

2.3 | Do performance traits predict contest success?

Fifty-six size-matched male lizards were used for staged contests. We matched males based on their SVL following similar protocols to other lizard contest studies (McLean & Stuart-Fox, 2014; Stuart-Fox et al., 2006). Overall, the mean size difference between lizards was 1.34 mm (ranging from 0 to 5 mm) (See Kar et al., 2016 for more details). We used a tournament design where each lizard faced multiple opponents (e.g. Kar et al., 2016; Whiting et al., 2006). Contests took place in the same room performance measures were taken. We used plastic neutral arenas measuring 470 (W) × 690 (L) × 455 (H) mm, where each lizard occupied half of the arena separated by an opaque divider. Lizards had access to a hide box and a water bowl and were habituated to the arena for 1.5 days. On the day of the contest, the refuge, water bowl and divider were removed to allow opponents to interact without obstruction. A clear contest outcome was reached when a lizard fled from his opponent following an aggressive behaviour, such as a chase, and the two lizards were at least half a body length apart. Winners were defined as any individual that consistently (on at least 2–3 occasions) displayed aggressive behaviour such as chasing, to his opponent, while losers were defined as any individual that exhibited submissive behaviour, such as fleeing. Contests were very short lived, and none resulted in any injuries to lizards.

2.4 | Do performance traits predict reproductive success?

2.4.1 | Semi-natural mating experiments

In a separate experiment, 216 (108 males, 108 females) lizards were allocated to one of six semi-natural, experimental enclosures, measuring 16 × 10 m (length × width) located on Macquarie University campus (Noble, Fanson, et al., 2014; Noble, Keogh, et al., 2013; Noble, Wechmann, et al., 2013). The enclosures were not netted because we wanted lizards to behave as naturally as possible in the presence of potential predators (e.g. laughing kookaburras, *Dacelo novaeguineae*). Each enclosure had natural vegetation, two large rock piles in opposite corners of the enclosure and a pile of large logs that connected each rock pile. We used 2–3 clay roofing tiles stacked on each other that were spread out across the entire enclosure in a grid at approximately 2-m intervals with two large water buckets dug into the ground for water. These conditions mimic the rocky water side riparian habitat that these skinks occupy in the wild (Law & Bradley, 1990). We allocated 18 male and 18 female water skinks per enclosure. We ensured that lizards from each collection site were represented within each enclosure and that there was natural variation in body size among males and females. The densities of lizards in our enclosures fall within the range of natural variation in the wild, including on Macquarie University campus (DWAN, 2016 unpublished data; Gerry Swan 2010, personal communication).

Lizards were allowed to mate freely under these semi-natural conditions, and all lizards were collected at the end of the breeding season (20 October 2010). The enclosures prevented immigration and emigration, and we searched enclosures exhaustively for any surviving lizards. Surviving females were brought back into the laboratory and placed in individual bins until parturition. At parturition, offspring were measured and weighed and a small amount of tail tissue (~3 mm) was excised for paternity analysis.

2.4.2 | Paternity assignment

Whole genomic DNA was extracted from tail tissue using a Blood and Tissue Extraction Kit (Qiagen) according to the manufacturers protocol. We assigned paternity to offspring using 6 microsatellite DNA loci (Noble, Keogh, et al., 2013; Noble, Wechmann, et al., 2013). PCR reactions were carried out in 20 μl reaction volumes containing 1.0 μl of genomic DNA, 10 μl of GoTaq® (Promega), 0.5 μl (10 pmol/μl) of forward and reverse primers and 8.0μl of nuclease-free water. PCR conditions for each locus are described in Scott et al. (2001) and Sumner et al. (2001). Forward primers were labelled with different fluorescent dyes (TET, NAD, VIC, FAM), and product from the final PCR reactions was pooled into a single plate, ran on an ABI 3730 DNA analyzer (Applied Biosystems) and scored by the Australian Genomic Research Facility (AGRF) using GENEMAPPER software (Applied Biosystems).

Parentage was assigned using the likelihood-based method in the program CERVUS 3.0 (Kalinowski et al., 2007). We simulated 100,000 offspring with 95% loci typed and 1% mistyped loci, using a strict confidence level of 95% and a relaxed confidence level of 80%. The loci used in our study were highly variable, ranging from 3 to 34 alleles at a single locus with mean polymorphic information content (PIC) of 0.7014. The combined nonexclusion probability for a parent pair was 4.46×10^{-6}. Paternity was assigned conservatively, and we excluded males as being putative sires if they had one or more mismatches with an offspring. In some cases, males could only be compared at four loci with offspring because of differences in the loci missing between the male and offspring. In these situations, we assigned paternity to the male only if he had no mismatches and the trio (male, female and offspring combination) LOD scores were significant.

2.5 | Data analysis

2.5.1 | Does performance predict contest success?

We were able to obtain a total of 165 contests; however, 42 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 predicted the probability of winning a contest. The BT model is a logistic model for paired comparisons where the probability of opponent *i* beating *j* is modelled as a function of the differences in 'abilities' between the opponents. Abilities are calculated from opponent-specific traits such as performance measures and body dimensions. All continuous traits were *z*-transformed prior to analysis (e.g. performance traits, body mass). We used the package "BradleyTerry2" (Turner & Firth, 2012) in the R environment (R Development Core Team, 2010) for our analyses.

In our initial analyses, we included body mass and SVL in all our models to check whether we had effectively size-matched lizards. These initial analyses revealed that body mass appeared to be important in predicting contest outcome, suggesting that we did not fully account for mass differences between our contestants. As a consequence, body mass was included in all our models as a covariate.

Given that predictors of contest outcome can vary depending on the level of escalation reached during the fight (Kar et al., 2016), we modelled nonescalated and escalated contests separately. Nonescalated contests were defined as contests that were resolved without physical biting, whereas escalated contests were fights where at least one contestant bit his rival. In nonescalated contests, we assessed how sprint speed, endurance and their interactions with body mass, predicted the probability of winning a contest because sprint speed could be associated with how quickly a lizard engages with his rival and endurance could be important for ritualized displays or prolonged contests which might occur over a high value resource. Due to the small sample size for escalated contests, we assessed the effects of bite force and endurance in separate models to avoid over-parametrization. We fitted one model with bite force and its interaction with body mass and another model with endurance and its interaction with body mass. We predicted that only bite force and endurance would be important in escalated contests because inflicting damage and outlasting a rival should increase the probability of winning the contest.

2.5.2 | Does performance predict reproductive success?

We excluded three lizards from analyses (two females, 1 male) because we did not obtain any performance measurements for one female, while one male and female were extreme outliers, being extremely heavy for their body size [greater than 3 standard deviations (σ_x) from the mean ($\overline{x}$)]. We did not obtain bite force measurements for 13 lizards (10 males; 3 females) because they were not motivated to bite the plates. In addition, we were unable to obtain measurements on maximal sprint speed for six lizards (all females) and endurance for one lizard (female).

We estimated selection gradients using generalized linear models (GLMs) with a Tweedie error distribution (log link) for reproductive success and the number of clutches sired. Tweedie probability distributions contain an index parameter, *p*, which permits modelling of a compound Poisson-gamma distribution, allowing us to model zeros and positive, noninteger continuous data (characteristics of relative reproductive success) under a single statistical framework while also controlling for over-dispersion (Noble, Wechmann, et al., 2013). To estimate what value of *p* was best for our data, we fitted our full models and varied *p* between 1.1 and 1.6 in intervals of 0.1 and compared AIC_C between respective models. Models containing the value of *p* with the lowest AIC_C were deemed the best fit, and this value of *p* was used for all candidate models in the same analysis.

While we predicted that behavioural ARTs may be related to performance, it was unclear exactly how such traits would be integrated, if at all, given that we could not categorize these tactics *a priori*. As such, we fitted a global model that included all main effects along with quadratics for SVL, bite force, sprint speed and endurance. Additionally, we included interactions we predicted may result if ARTs were present including those between bite force and endurance, bite force and sprint speed and sprint speed and endurance. Linear selection gradients (β_i) indicate selection that changes the population mean, while nonlinear selection gradients (γ_{ii}; quadratic selection gradients or γ_{ij}; correlational selection gradients) describe how the phenotypic variance of a trait is changed (Brodie III, 1992; Brodie III et al., 1995; Lande & Arnold, 1983). We converted the number of offspring sired to relative reproductive success (i.e. the number of offspring sired divided by the male and female population mean within each of the six enclosures) and standardized each of the traits by subtracting each value from the trait mean of each enclosure, $\overline{x}$, and dividing by its standard deviation, σ_x (Brodie III et al., 1995; Lande & Arnold, 1983). We calculated relative reproductive success for the sexes separately in each of the enclosures because of the differences in the mean number of offspring between the sexes. Linear selection gradients (β_i) are normally presented from models without quadratics or cross-products and quadratic coefficients are normally doubled (Brodie III et al., 1995; Lande & Arnold, 1983; Mitchell-Olds & Shaw, 1987; Stinchcombe et al., 2008). However, given we utilized a multimodel inference framework, we present our model-averaged estimates across the candidate set.

We assumed the same model structure for females, although we predicted that females would not exhibit similar selection surfaces to males because there is no *a priori* reason to suggest that performance traits would be important to female reproductive success or that these would be integrated to ARTs. Nonetheless, females act as a useful control to compare with results from male fitness surfaces. To understand the possible behavioural mechanisms that males adopt to obtain paternity, we ran similar models

using the number of clutches sired. If ARTs obtain paternity through different mechanisms, we would expect the model predictions for relative reproductive success and the number of clutches sired to differ for males.

We used multi-model inference to understand the relationship between performance traits, relative reproductive success and clutches sired for males and females separately. Model averaging is particularly useful when there is substantial uncertainty in model structure and has clear advantages over stepwise model selection procedures (Burnham & Anderson, 2002; Grueber et al., 2011; Symonds & Moussalli, 2011) as it allows inferences to be made over all possible models. However, it is important to evaluate the degree of collinearity among predictors and to ensure that coefficients are comparable across models (Cade, 2015). We assessed these points by exploring model coefficients in our top models and levels of multi-collinearity (i.e. variance inflation factors) in our global model prior to model-averaging estimates. From our global model, we generated a candidate set of models and averaged over top models within 3 ΔAIC_C units of each other (Symonds & Moussalli, 2011) using the *MuMIn* package (Bartoń, 2013). Two different model-averaging techniques exist, conditional (i.e. 'natural') model averaging, where coefficients are averaged over the models in which they occur, and full model averaging, where coefficients are averaged across all models in the model set with models not containing the coefficients assumed to have a zero estimate. Although it is recommended to use conditional averaging when there is strong support for a single model (i.e. Akaike weight >0.90), Symonds and Moussalli (2011) suggest the use of conditional averaging when the goal is to understand how predictor variables relate to the response. Since our estimates seemed weak, but potentially biologically important in relation to our predictions, we adopted the conditional averaging method. While this may result in upward bias of parameter estimates compared with full model averaging (Lukacs et al., 2010), as of yet it is unclear which of these two methods is most appropriate (Grueber et al., 2011)

In addition to model averaging, we used principle components analysis (PCA) to help understand the link between performance and fitness. Given that traits may be highly integrated, we reduced the dimensionality of our traits using PCA and ran a generalized linear model with relative reproductive success and clutches sired as a response variables and each PC axis as independent variables. We again modelled response variables assuming a Tweedie error distribution to better understand what trait combinations had highest fitness.

3 | RESULTS

3.1 | Performance as predictors of contest outcome

None of the performance measures or their interactions with body mass were important predictors of contest outcome (Table 1). Body mass only was important in predicting contest outcome for escalated contests (Table 1b–c). For males that differed by 1 standard deviation in mass, the probability that the heavier male would beat his rival was 82%. Locomotor performance and bite force are therefore relatively weak predictors of contest outcome overall.

TABLE 1 Parameter estimates, standard errors (se), upper (U) and lower (L) 95% confidence interval and *p* values (*p*) from a Bradley-Terry model, examining the effects of maximal sprint speed, endurance, bite force and body mass on the log odds of winning a nonescalated contest ($n = 85$) and an escalated contest ($n = 38$). Bolded estimates are significant at $\alpha = 0.05$

Parameter	Est.	*SE*	U	L	*p*
(a) Nonescalated contests					
Endurance	0.34	0.3	0.93	−0.25	.27
Sprint speed	−0.28	0.24	0.19	−0.75	.23
Body mass	0.56	0.48	1.5	−0.38	.24
Endurance*Body mass	−0.04	0.32	0.59	−0.67	.90
Sprint speed*Body mass	0.02	0.32	0.65	−0.61	.96
(b) Escalated contests—Bite force					
Bite force	0.09	0.46	0.99	−0.81	.84
Body mass	**1.52**	**0.75**	**2.99**	**0.05**	**.04**
Bite force*Body mass	0.27	0.36	0.98	−0.44	.44
(c) Escalated contests—Endurance					
Endurance	0.55	0.45	1.43	−0.33	.22
Body mass	1.66	0.85	3.33	−0.01	.05
Endurance*Body mass	−0.16	0.41	0.64	−0.96	.70

3.2 | Performance and reproductive success in males

Fifty-six males did not sire any offspring (56/97 = 58%), while 41 males sired at least one offspring (42%). The number of offspring sired by males ranged from 1 to 17, and offspring were sired across 1–6 clutches. Relative reproductive success ranged from 0 to 7.65 across individuals. Male body size was strongly correlated with bite force ($r = 0.62$, $p < .001$, $n = 97$; Figure 1b) and endurance ($r = 0.33$, $p < .001$, $n = 97$; Figure 1c). Bite force was also significantly correlated with endurance ($r = 0.40$, $p < .001$, $n = 97$; Figure 1f). However, there were weak, nonsignificant correlations between all other variables (Table S1; Figure 1). These patterns were the same for females (Table S2).

Inspection of the distribution of males with above average reproductive success (Figure 1) showed that large males with high bite force had high reproductive success (Figure 1b). In contrast, large (>1 σ_x above the $\bar{x}$) and medium (~1 σ_x above the $\bar{x}$) males with high and low sprint speeds had the highest reproductive

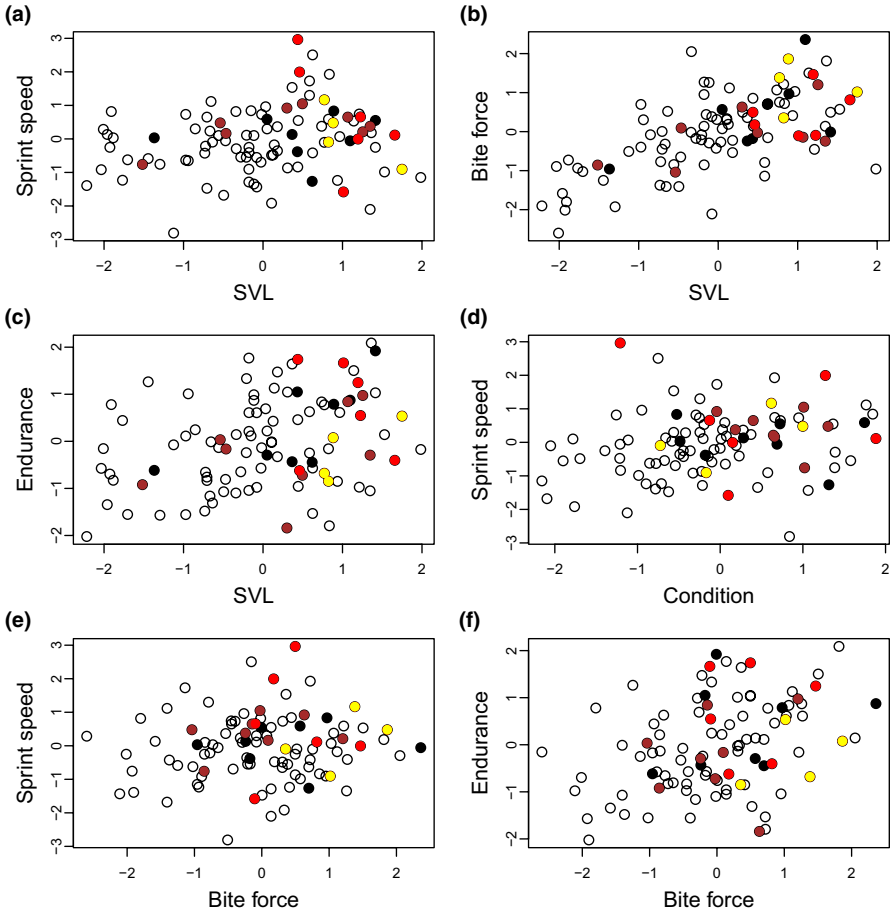

FIGURE 1 Relationship between morphological traits [body size (SVL), body condition] and performance traits (sprint speed, bite force and endurance) for males. Relative reproductive success (RRS) of each male is overlaid on these plots. Open circles: RRS ≤ 1, solid black circles: RRS = 1–2, Solid brown circles: RRS 2 – 4, Solid red circles: RRS 4 – 6 and Solid yellow circles: RRS ≥ 6

success (Figure 1a). This pattern was also reflected in the bite force–sprint speed plots where males with high and medium bite force that had low and high sprint speed, respectively, sired the majority of offspring (Figure 1e). There was no clear pattern between traits and relative reproductive success in the other plots (Figure 1c, d, f, g).

Overall, there was substantial model uncertainty in predictors of male reproductive success with a total of 22 models within 3 ΔAICc units of each other, with model weights ranging from 2.6% to 11.4% (Table S3). Models explained a small to moderate amount of total variability in reproductive success (R^2 ~20.3%–28.4% - Table S3). The top models for male relative reproductive success contained the main effects of SVL and all performance traits, along with their quadratic selection gradients. A correlational selection gradient between bite force and sprint speed was also present in eight of the top models (Table S3). No major differences in relative reproductive success were observed between enclosures, and as a result, it never featured in the top models. While selection for body size (SVL) was strong, model-averaged predictions (Figure 2a–c), along with their estimates (Table 2), also suggest directional selection for sprint speed and bite force (although estimates were not significant). In contrast, directional selection was weak for endurance (Table 2). Models also contained correlational selection gradients between bite force and sprint speed, suggesting both slow and fast sprinters of moderate body size were predicted to obtain above average reproductive success (Figure 2a).

Models predicting the number of clutches males sired offspring across also showed high uncertainty, although less so than for relative reproductive success (Table S3). Seven models were within 3 ΔAICc units of each other and model weights ranged from 8.1% to 31.7% (Table S3). The top models contained all main effects for each performance trait and body size along with quadratics for performance traits. One model also contained an interaction between bite force and sprint speed (Table S3). Overall, models explained a small proportion of variation in clutch size (R^2 ~15.6%–16.2% - Table 1), but there was strong and significant directional selection on body size and sprint speed (Table S3).

Decomposing variation in body size and performance traits using PCA identified four major axes (Table 3 & Figure S1). Principle component (PC) 1 and 3 were positively correlated with relative reproductive success (Figure 3), while PC2 showed a weaker negative trend (Table 4a). Unsurprisingly, males with large body size, bite force and to a lesser extent high endurance were predicted to obtain highest reproductive success (Figure 3a); however, males that had low endurance were also predicted to obtain high reproductive success, but to a lesser degree (Figure 3b & Table 4 – PC3).

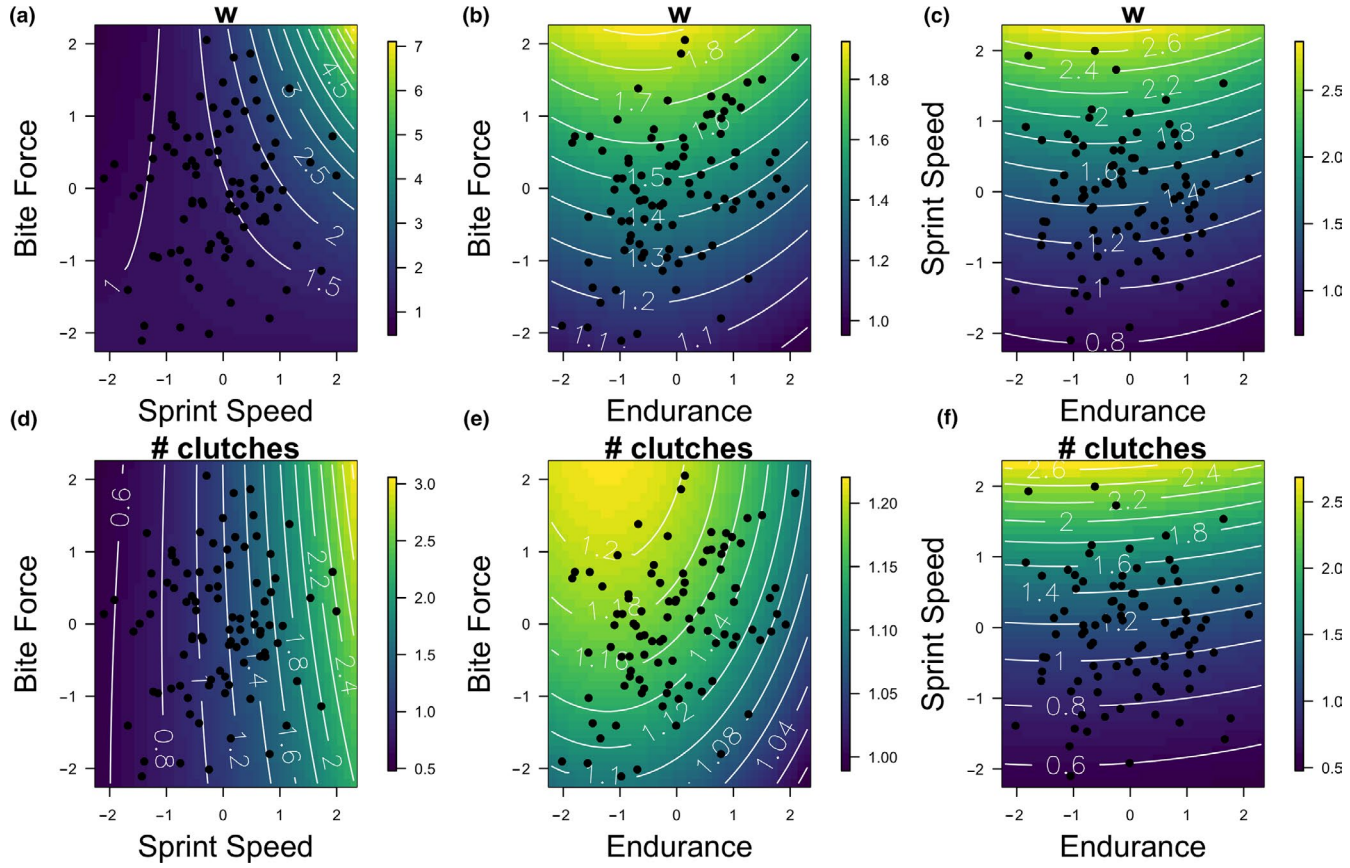

FIGURE 2 Model-averaged predictions for males ($n = 97$) as a function of performance traits. (a–c) Relative reproductive success (w) of males in replicate semi-natural enclosures. (d–f) number of clutches sired by males (# clutches). Predictions are made assuming male SVL was 1SD above the mean given that we predict large males to exhibit different ARTs. Raw data are also plotted ('black' points). Model predictions were done using full model-averaged estimates

TABLE 2 Model-averaged parameter estimates for relative reproductive success and clutches sired for males ($n = 97$) and females ($n = 96$). We used conditional model averaging (see text). Enclosure was included in the candidate set of models but was not present in the top model set. Estimates that are *italics* = $p < .10$ and bold = $p < .05$. Abbreviations of parameter estimates are provided in Tables 1 and 2

	Male relative reproductive success			Male clutches sired			Female relative reproductive success		
Parameter estimate	**Estimate**	***SE***	**Adj. *SE***	**Estimate**	***SE***	**Adj. *SE***	**Estimate**	***SE***	**Adj. *SE***
(Intercept)	−0.407	0.252	0.255	**−0.342**	**0.175**	**0.177**	−0.047	0.175	0.176
SS	*0.307*	*0.179*	*0.181*	**0.350**	**0.144**	**0.145**	**0.301**	**0.141**	**0.143**
SVL	**0.725**	**0.231**	**0.234**	**0.495**	**0.180**	**0.182**	**0.623**	**0.130**	**0.132**
BF	0.230	0.225	0.228	0.113	0.188	0.190	0.024	0.150	0.152
BF*SS	*0.384*	*0.232*	*0.235*	0.261	0.192	0.194	–	–	–
SVL^2	0.216	0.174	0.176	–	–	–	–	–	–
Endur	−0.116	0.180	0.182	−0.138	0.151	0.153	−0.044	0.106	0.107
$Endur^2$	−0.112	0.167	0.169	−0.071	0.138	0.139	−0.109	0.079	0.080
BF^2	−0.040	0.180	0.181	−0.038	0.127	0.129	*−0.176*	*0.094*	*0.095*
SS^2	−0.012	0.109	0.111	0.017	0.088	0.089	*−0.204*	*0.118*	*0.119*

Regressing PCs on the number of clutches sired identified significant negative effects of PC1 and PC2, with a marginally significant negative effect of PC3 (Table 4b). While males with large body size, bite force and endurance sired offspring across the most clutches, males that had high endurance and low sprint speed were also very likely to sire offspring across many clutches (Table 4b).

3.3 | Performance and reproductive success in females

Forty-four females (44/96 = 46%) did not produce offspring, while 52 females (54%) produced from 0 to 9 offspring. Relative reproductive success ranged from 0 to 3.86 for individual females. Female body size was also strongly correlated with bite force ($r = 0.63$, $p < .001$, $n = 96$) and endurance ($r = 0.42$, $p < .001$, $n = 96$). All other variables were not correlated in females (Table S2).

There was also substantial model uncertainty in how body size and performance were related to female reproductive success, with model weights ranging from 1.9% to 7.8% and R^2 for individual models ranging from 19% to 24% (Table S4). All models in the top model set contained female SVL and none contained any interactions between performance traits. However, most contained quadratic coefficients or main effects for performance traits. Model-averaged coefficients for sprint speed and body size were significant, whereas other coefficients were not or were marginally significant (Table 2). Model-averaged predictions for the different performance traits suggest stabilizing selection with a wide peak of high reproductive success for individuals of average performance (or slightly above average) (Figure 4a–c). However, there was very weak effects of performance traits on relative reproductive success overall with predictions suggesting a small effect on relative reproductive success.

Regressing PCs on relative reproductive success for females also suggested a link with certain performance traits (Table 4); however, coefficients for PC1 and PC3 were much smaller compared to male coefficients and instead body size related traits (PC1 and PC4) seemed to explain most variation in relative reproductive success for females.

TABLE 3 Loadings of variables and percentage of variance explained by each principle component axes (1–4) for z-transformed body size and performance traits (bite force, endurance and sprint speed) for males (a) and females (b)

Variable	PC1	PC2	PC3	PC4
(a) Males	49%	24%	18%	9%
SVL	0.623	–	0.366	0.692
Sprint speed	0.212	−0.959	−0.162	−0.100
Size corrected bite force	0.603	0.154	0.321	−0.714
Endurance	0.451	0.240	−0.858	–
(b) Females	51%	24%	16%	9%
SVL	0.636	–	0.291	0.713
Sprint speed	0.159	0.964	−0.158	−0.141
Size corrected bite force	0.580	−0.126	0.427	−0.682
Endurance	0.484	−0.228	−0.842	−0.073

4 | DISCUSSION

We did not find strong support for the hypothesis that better performing individuals (i.e. higher endurance, stronger bite force and faster sprint speed) win more contests and, as a result, have increased reproductive success (hypothesis 1). None of our analyses support a simple direct linear relationship between performance traits and contest outcome or reproductive success which is predicted from this hypothesis. While performance traits were not linked to contest outcome, they still featured in the top models and PCA analysis, suggesting that particular body size-performance combinations can yield similar fitness payoffs. Given that numerous studies have provided evidence of ARTs in *Eulamprus* spp. (Noble, Fanson, et al., 2014; Noble, Wechmann, et al., 2013; Stapley & Keogh, 2004, 2005), we suggest that behaviourally driven ARTs may explain this high degree of model uncertainty (hypothesis 2). However, it is still unclear whether performance traits are direct targets of selection or are simply correlated with other unmeasured behavioural, morphological or physiological traits. While performance traits appeared to be under stronger sexual selection in males, females also exhibited similar selection coefficients to males with respect to the links with performance and fitness. We discuss the implications of these findings to our understanding of sex-dependent differences in performance and the evolution of ARTs.

4.1 | Effect of performance traits on contest outcome and reproductive success

In general, the ability to win aggressive interactions is often predicted to have a major effect on reproductive fitness with this effect

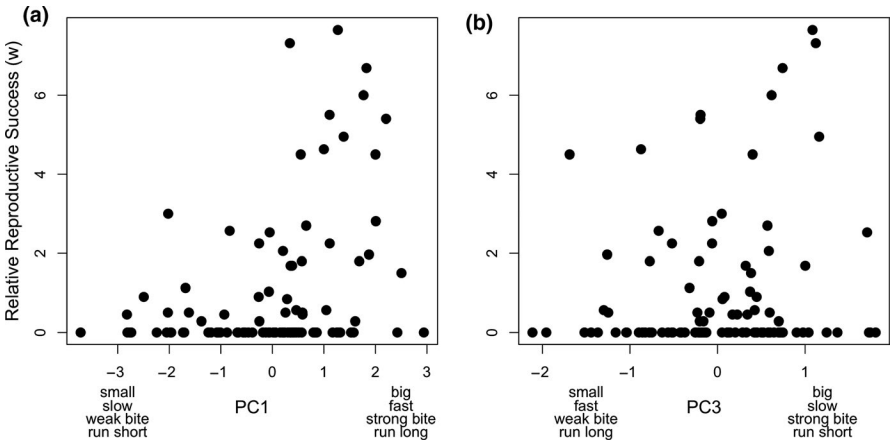

FIGURE 3 Relative reproductive success in relation to principle component axis 1 (PC1) and 3 (PC3). Loadings of performance and body size on each axis are provided in Table 3

being mediated by performance as a predictor of contest outcome (Husak & Fox, 2008; Husak, Lappin, et al., 2006; Irschick et al., 2008; Le Galliard & Ferrière, 2008; Sinervo et al., 2000). Aggressive, dominant males with high maximal performance capacity are expected to have high resource holding potential and are better able to defend territories and monopolize females. Despite this commonly held view, the role of performance traits in contest outcome, or its correlation with reproductive success, is seldom explicitly tested (Husak & Fox, 2008; Husak, Fox, et al., 2006; Husak et al., 2008; Le Galliard & Ferrière, 2008). Predicting simple linear relationships between performance and fitness is likely to be too simplistic (Husak & Fox, 2008), particularly given the presence of different reproductive strategies in many mating systems (Oliviera et al., 2008). In support of this notion, our results suggest that performance traits, even ones predicted to be important (i.e. bite force and endurance) (Husak & Fox, 2008; Miles, Calsbeek, et al., 2007), are weakly related to dominance and reproductive success in *E. quoyii*. Better performing individuals did not have a higher probability of winning contests or siring more offspring. The lack of strong relationships between performance and contest outcome we observed is likely because so few contests escalated to levels that would require sustained performance (i.e. strong biting and endurance) (Lailvaux & Irschick, 2007). These patterns may be different in species where territoriality is more strongly linked to reproductive success. Nonetheless, our results highlight the need to have more explicit tests of the relationship between performance, contest outcome and reproductive success and to carefully consider the mating system in question prior to making assumptions about their expected links (Husak & Fox, 2008). Predictions are likely to be complex, and we argue that combining experiments on both dyadic contests with some measure of field or semi-natural estimate of fitness will help elucidate if, and how, performance affects fitness.

TABLE 4 Effect of principle component axes on relative reproductive success (males and females) and the number of clutches sired (males). Loadings of variables are provided in Table 3

PC Axis	Estimate	*SE*	*t*-Value	*p*-Value
Male relative reproductive success				
(Intercept)	−0.357	0.205	−1.74	.085
PC1	**0.592**	**0.153**	**3.858**	**<.001**
PC2	−0.277	0.17	−1.632	.106
PC3	*0.409*	*0.209*	*1.953*	*.054*
PC4	0.293	0.276	1.061	.291
Clutches sired				
(Intercept)	**−0.365**	**0.164**	**−2.228**	**.028**
PC1	**0.380**	**0.124**	**3.058**	**.003**
PC2	**−0.341**	**0.147**	**−2.329**	**.022**
PC3	*0.307*	*0.179*	*1.717*	*.089*
PC4	0.178	0.245	0.726	.470
Female relative reproductive success				
(Intercept)	−0.196	0.117	−1.684	.096
PC1	**0.408**	**0.079**	**5.151**	**<.001**
PC2	**0.263**	**0.115**	**2.282**	**.025**
PC3	0.181	0.122	1.488	.140
PC4	**0.437**	**0.173**	**2.517**	**.014**

Estimates that are italics = $p < .10$ and bold = $p < .05$.

4.2 | Alternative reproductive tactics and the role of behaviour in understanding patterns of selection on performance

Sexual selection often leads to males adopting status-dependent alternative reproductive tactics (Andersson, 1994; Gross, 1996). The integration of behavioural, physiological and performance traits permit males to acquire paternity through subtly different mechanisms, and such behavioural variation has important consequences for understanding selection on performance in nature (Irschick, 2002). The mechanistic link between performance and

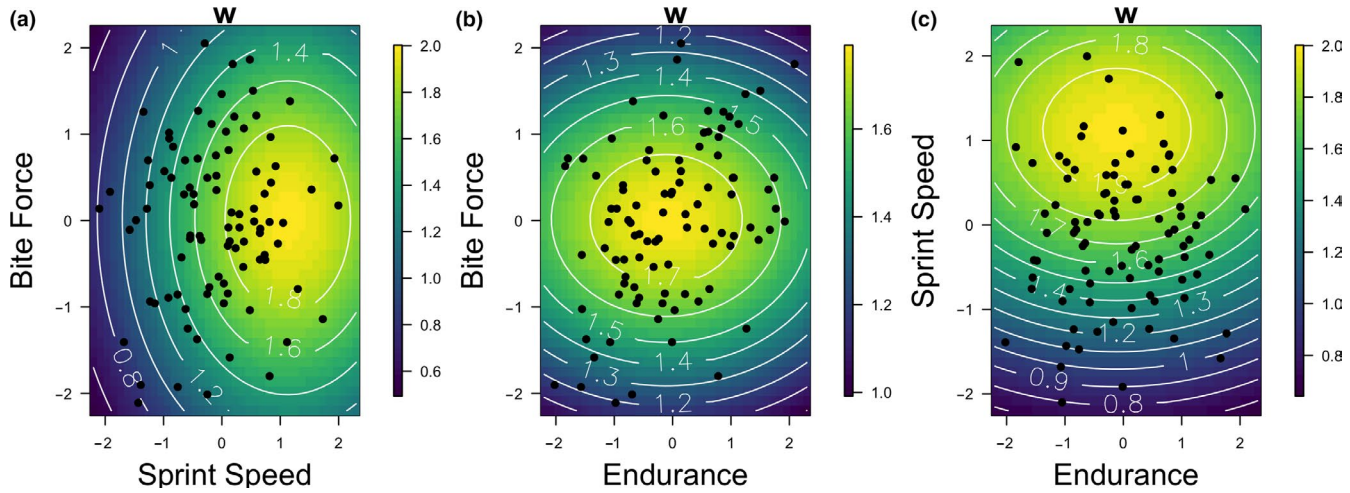

FIGURE 4 Model-averaged predictions of relative reproductive success (*w*) for females ($n = 96$) as a function of performance traits. Model predictions were done using full model-averaged estimates

fitness in *E. quoyii*, should one exist, likely depends on the specific reproductive strategies males and females adopt. The high degree of model uncertainty, the presence of an interaction between sprint speed and bite force in males and the fact that PCAs suggested multiple links between fitness and performance lend support to this notion. Model-averaged predictions and the raw data (Figure 1) also show subtle but potentially important differences among large males that suggest an integration between performance and behavioural tactic. Male *E. quoyii* have been shown to exhibit different, behaviourally driven ARTs (Noble, Wechmann, et al., 2013; Stapley & Keogh, 2004, 2005), with floater and territorial males exhibiting different activity levels and home ranges. Performance traits may be different for these tactics for two reasons. First, while we found weak evidence for direct selection on performance traits, they may still be targets of selection and integrated with behavioural tactics through correlational selection. In other words, performance traits may be necessary or facilitate the success of behavioural tactics; however, experiments would be necessary to explicitly test this hypothesis.

Alternatively, performance may simply be a consequence of the specific physical and behavioural demands imposed by the behavioural tactic individuals adopt with behavioural traits being the direct targets of selection. For example, large home ranges and higher activity levels of floater males may provide an environment that facilitates better locomotor capacity compared to territorial males. This is analogous to increased exercise training that often accompanies heightened performance (Van Damme et al., 2008). However, we acknowledge that we cannot provide robust evidence for either of these hypotheses because we do not have behavioural data that would elucidate the specific male tactic. Indeed, in the closely related *E. heatwolei* both males and females have been shown to adopt different alternative reproductive tactics that yield similar fitness outcomes (Keogh et al., 2013; Stapley & Keogh, 2004, 2005). The fact that female *E. heatwolei* adopt different ARTs may provide an explanation for the observed links between performance and fitness in female *E. quoyii*, when we predicted only selection on female body size. As of yet it is unclear whether female *E. quoyii* do adopt different reproductive strategies or whether the relationship between performance and fitness we observed is simply an indirect consequence of strong collinearity with other physiological/behavioural traits we were not able quantify.

4.3 | Sex-specific selection and the evolution of sex differences in morphology and performance

Sexes of many species differ in morphology and performance (Van Damme et al., 2008). In lizards, males most often have higher sprinting speed, endurance and bite force (Lappin et al., 2006; Van Damme et al., 2008). Sex differences have been attributed to sexual dimorphism in body size and head dimensions as a result of sexual and natural selection on morphology or performance (Van Damme et al., 2008). In *E. quoyii*, males and females do not differ in body size, but they do differ in head and limb dimensions (Noble, Fanson, et al., 2014; Schwarzkopf, 2005) and exhibit sex differences in bite force, endurance and sprinting speed (Noble, Fanson, et al., 2014).

We show that selection on body size is similar in magnitude in males and females possibly explaining the lack of sexual size dimorphism (SSD) we see in this species (Noble, Fanson, et al., 2014). In addition, there is weak evidence that performance affected survival across sexes in our mating experiment (See Table S5). Strong sexual selection on body size in males confers an advantage in intrasexual competition (Cox et al., 2003). Indeed, we show larger body size in male *E. quoyii* is advantageous in winning escalated staged contests. In contrast, selection on large females provides a fecundity advantage and these selective processes together can lead to a lack of SSD (Cox et al., 2003; Olsson et al., 2002). As such, the unexpected similarities in the relationship between performance and reproductive success between males and females may be an indirect consequence of strong selection on body size in both sexes, which is correlated with performance. Stronger directional selection on bite force, independent of body size, in males compared to females may also explain the differences in bite force between the sexes (Noble, Fanson, et al., 2014). Bite force is closely linked to head dimensions (Herrel et al., 2007), and while it was not important in predicting contest outcome, head dimensions could be a signal of male dominance explaining its stronger relationship to fitness in males compared to females. The proximate underpinnings of sexual shape dimorphism and bite force in this species are still unclear (Noble, Fanson, et al., 2014). Different organisational effects of anabolic steroids, leading to differences in head shape or muscle development, may result in differences in bite force, despite similar selection on adult body sizes between the sexes. Alternatively, differences in aggression or dietary preferences between the sexes might also help build jaw musculature and lead to increased bite force in males.

5 | CONCLUSIONS

Evolutionary biologists have expressed great interest in understanding how selection acts on performance traits given they are predicted to have a direct relationship with fitness. Yet, most work often assumes these links or establishes links using indirect fitness measures. While sex differences in performance exist across diverse taxa (Van Damme et al., 2008), it is not yet clear whether sexual selection is a major player generating these differences. Indeed, there have only been a few studies quantifying sexual selection (i.e. reproductive success) on performance traits. Our results suggest that performance traits are not likely direct targets of sexual selection in *E. quoyii*, but rather an indirect result of strong sexual selection on behaviour / body size or a developmental outcome of the different environmental niches individuals

adopting different ARTs occupy. While males and females exhibit clear differences in performance in *E. quoyii*, sexual selection is likely only a minor force in generating these differences. Our study highlights the importance of explicitly testing the link between fitness and performance in both pre- and post-copulatory contexts. We also stress the need to incoperate aspects of a species' mating system when making predictions on the links between performance and fitness in the future.

ACKNOWLEDGEMENTS

We would like to thank Yian Noble and Sebastian Schwarz for help with performance measurements on lizards and Kerrie Wechmann for helping collect lizards. DN was supported by a grant from the Natural Sciences and Engineering Research Council (NSERC) of Canada, an ARC Discovery Early Career Research Award (DECRA) (DE150101774) and UNSW Vice Chancellors Fellowship. This work was also partially funded by an internal grant from Macquarie University to MJW. All procedures were approved by the Animal Ethics Committee at Macquarie University (ARA 2014/036) and the National Parks and Wildlife service of NSW (licence # SL100328). We would like to thank staff at the Sydney Olympic Park (SOPA), Cromer Golf Course and the Elanora Country Club and Ryde, Kuring-Gai, Warringah and Pittwater councils for granting us permission to collect lizards.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

DWAN, MW and SK involved in funding. DWAN, FK and MW conceptualized and designed the study. DWAN, FK and SK collected the data. DWAN, SN and FK involved in analysis. DWAN wrote initial draft. DWAN, FK, SN, SK and MW edited and revised the study.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/jeb.13752.

OPEN RESEARCH BADGES

This article has earned an Open Data Badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://osf.io/hwpfa/.

DATA AVAILABILITY STATEMENT

All data and analysis code used in this paper can be found on the Open Science Framework (OSF) at https://osf.io/hwpfa/.

ORCID

Daniel W. A. Noble https://orcid.org/0000-0001-9460-8743
Fonti Kar https://orcid.org/0000-0002-2760-3974
Shinichi Nakagawa https://orcid.org/0000-0002-7765-5182
J. Scott Keogh https://orcid.org/0000-0002-1373-6186
Martin J. Whiting https://orcid.org/0000-0002-4662-0227

REFERENCES

Andersson, M. (1994). *Sexual selection*. Princeton University Press.
Arnold, S. J. (1983). Morphology, performance, fitness. *American Zoologist*, *23*, 347–361.
Bartoń, K. (2013). *MuMIn: Multi-model inference. R package version 1.9.0*. Retrieved from http://CRAN.R-project.org/package=MuMIn
Brodie, E. D. III (1992). Correlatonal selection for color pattern and antipredator behavior in the gartersnake *Thamnophis ordinoides*. *Evolution*, *46*, 1284–1298.
Brodie, E. D. III, Moore, A. J., & Janzen, F. J. (1995). Visualizing and quantifying natural selection. *Trends in Ecology and Evolution*, *10*, 313–318. https://doi.org/10.1016/S0169-5347(00)89117-X
Burnham, K. P., & Anderson, D. R. (2002). *Model selection and inference: A practical information theoretic appraoch*. Springer-Verlag.
Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology (Washington D C)*, *96*, 2370–2382. https://doi.org/10.1890/14-1639.1
Cox, R. M., Skelly, S. L., & John-Alder, H. B. (2003). A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution*, *57*, 1653–1669. https://doi.org/10.1111/j.0014-3820.2003.tb00371.x
Dubey, S., Sinsch, U., Dehling, M. J., Chevalley, M., & Shine, R. (2013). Population demography of an endangered lizard, the Blue Mountains Water Skink. *BMC Ecology*, *13*, 4–8.
Emlen, D. J. (1997). Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behavioral Ecology and Sociobiology*, *41*, 335–341. https://doi.org/10.1007/s002650050393
Garland, T. (1999). Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Animal Beahviour*, *58*, 77–83. https://doi.org/10.1006/anbe.1999.1132
Grant, P. R., & Grant, B. R. (1995). Predicting microevolutionary responses to directional selection on heritable variation. *Evolution*, *49*, 241–251. https://doi.org/10.1111/j.1558-5646.1995.tb02236.x
Gross, M. R. (1996). Alternative reproductve strategies and tactics: Diversity within the sexes. *Trends in Ecology & Evolution*, *11*, 92–98.
Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology*, *24*, 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x
Herrel, A., Grauw, E. D., & Lemos-Espinal, J. A. (2001). Head shape and bite performance in *Xenosaurid* lizards. *Journal of Experimental Zoology*, *290*, 101–107. https://doi.org/10.1002/jez.1039
Herrel, A., Mcbrayer, L. D., & Larson, P. M. (2007). Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. *Biological Journal of the Linnean Society*, *91*, 111–119. https://doi.org/10.1111/j.1095-8312.2007.00772.x
Hoekstra, H., Hoekstra, J., Berrigan, D., Vignieri, S., Hoang, A., Hill, C., Beerli, P., & Kingsolver, J. (2001). Strength and tempo of directional selection in the wild. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 9157–9160. https://doi.org/10.1073/pnas.161281098
Husak, J., & Fox, S. F. (2008). Sexual selection on locomotor performance. *Evolutionary Ecology Research*, *10*, 213–228.
Husak, J., Fox, S., Lovern, M., & Van Den Bussche, R. (2006). Faster lizards sire more offspring: Sexual selection on whole-animal performance. *Evolution*, *60*, 2122–2130. https://doi.org/10.1111/j.0014-3820.2006.tb01849.x
Husak, J. F., Fox, S. F., & Van Den Bussche, R. (2008). Faster male lizards are better defenders not sneakers. *Animal Behaviour*, *75*, 1725–1730. https://doi.org/10.1016/j.anbehav.2007.10.028
Husak, J. F., Lappin, A. K., Fox, S. F., & Lemos-Espinal, J. A. (2006). Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia*, *2006*, 301–306. https://doi.org/10.1643/0045-8511(2006)6[301:BPPDIM]2.0.CO;2

Irschick, D. J. (2002). Evolutionary approaches for studying functional morphology: Examples from studies of performance capacity. *Integrative and Comparative Biology*, *42*, 278–290. https://doi.org/10.1093/icb/42.2.278

Irschick, D. J., Meyers, J. J., Husak, J. F., & Le Galliard, J.-F. (2008). How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evolutionary Ecology Research*, *10*, 177–196.

Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, *16*, 1099–1106. https://doi.org/10.1111/j.1365-294X.2007.03089.x

Kaplan, R. H., & Phillips, P. C. (2006). Ecological and developmental context of natural selection: Maternal effects and thermally induced plasticity in the frog *Bombina orientalis*. *Evolution*, *60*, 142–156. https://doi.org/10.1111/j.0014-3820.2006.tb01089.x

Kar, F., Whiting, M. J., & Noble, D. W. A. (2016). Influence of prior contest experience and level of escalation on contest outcome. *Behavioral Ecology and Sociobiology*, *70*, 1679–1687. https://doi.org/10.1007/s00265-016-2173-4

Keogh, J. S., Noble, D. W. A., Wilson, E. E., & Whiting, M. J. (2012). Male activity predicts male reproductive success in a polygynous lizard. *PLoS One*, *7*, 1–5. https://doi.org/10.1371/journal.pone.0038856

Keogh, J. S., Umbers, K. D. L., Wilson, E. E., Stapely, J., & Whiting, M. J. (2013). Influence of alternate reproductive tactics and pre- and post-copulatory sexual selection on paternity and offspring performance in a lizard. *Behavioral Ecology and Sociobiology*, *67*, 629–638. https://doi.org/10.1007/s00265-013-1482-0

Kingsolver, J. G., Diamond, S. E., Siepielski, A. M., & Carlson, S. M. (2012). Synthetic analyses of phenotypic selection in natural populations: Lessions, limitations and future directions. *Evolutionary Ecology*, *26*, 1101–1118.

Kingsolver, J. G., Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hill, C. E., Hoang, A., Gibert, P., & Beerli, P. (2001). The strength of phenotypic selection in natural populations. *The American Naturalist*, *157*, 245–261. https://doi.org/10.1086/319193

Lailvaux, S. P., Hathway, J., Pomfret, J., & Knell, R. J. (2005). Horn size predicts physical performance in the beetle *Euoniticellus intermedius* (Coleoptera: Scarabaeidae). *Functional Ecology*, *19*, 632–639. https://doi.org/10.1111/j.1365-2435.2005.01024.x

Lailvaux, S. P., Herrel, A., Vanhooydonck, B., Meyers, J. J., & Irschick, D. J. (2004). Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society B: Biological Sciences*, *271*, 2501–2508.

Lailvaux, S. P., & Husak, J. (2014). The life history of whole-organism performance. *The Quarterly Review of Biology*, *89*, 285–318. https://doi.org/10.1086/678567

Lailvaux, S. P., & Irschick, D. J. (2006). A functional perspective on sexual selection: Insights and future prospects. *Animal Behaviour*, *72*, 263–273. https://doi.org/10.1016/j.anbehav.2006.02.003

Lailvaux, S. P., & Irschick, D. J. (2007). The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *The American Naturalist*, *170*, 573–586.

Lande, R., & Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution*, *37*, 1210–1226. https://doi.org/10.1111/j.1558-5646.1983.tb00236.x

Lappin, A. K., Hamilton, P. S., & Sullivan, B. K. (2006). Bite-force performance and head shape in a sexually dimorphic crevice-dwelling lizard, the common chuckwalla [*Sauromalus ater* (=*obesus*)]. *Biological Journal of the Linnean Society*, *88*, 215–222.

Law, B. S., & Bradley, R. A. (1990). Habitat use and basking site selection in the Water Skink, *Eulamprus quoyii*. *Journal of Herpetology*, *24*, 1–7.

Le Galliard, J.-F., & Ferrière, R. (2008). Evolution of maximal endurance capacity: Natural and sexual selection across age classes in a lizard. *Evolutionary Ecology Research*, *10*, 157–176.

Losos, J. B., Creer, D. A., & Schulte, J. A. II (2002). Cautionary comments on the measurment of maximum locomotor capabilities. *Journal of Zoology (London)*, *258*, 57–61.

Lukacs, P. M., Burnham, K. P., & Anderson, D. R. (2010). Model selection bias and Freedman's paradox. *Annals of the Institute of Statistical Mathematics*, *62*, 117–125. https://doi.org/10.1007/s10463-009-0234-4

McGlothlin, J. W., Parker, P. G., Nolan, V. Jr, & Ketterson, E. (2005). Correlational selection leads to genetic integration of body size and an attractive plumage trait in dark-eyed juncos. *Evolution*, *59*, 658–671. https://doi.org/10.1111/j.0014-3820.2005.tb01024.x

McLean, C. A., & Stuart-Fox, D. M. (2014). Rival assessment and comparison of morphological and performance-based predictors of fighting ability in Lake Eyre dragon lizards, *Ctenophorus maculosus*. *Behavioral Ecology and Sociobiology*, *69*, 523–531.

Miles, D., Calsbeek, R., & Sinervo, B. (2007). Corticosterone, locomotor performance, and metabolism in side-blotched lizards (*Uta stansburiana*). *Hormones and Behavior*, *51*, 548–554.

Miles, D. B., Sinervo, B., Hazard, L. C., Svensson, E. I., & Costa, D. (2007). Relating endocrinology, physiology and behaviour using species with alternative mating strategies. *Functional Ecology*, *21*, 653–665.

Mitchell-Olds, T., & Shaw, R. G. (1987). Regression analysis of natural selection: Statistical inference and biological interpretation. *Evolution*, *41*, 1149–1161. https://doi.org/10.1111/j.1558-5646.1987.tb02457.x

Noble, D. W. A., Carazo, P., & Whiting, M. J. (2012). Learning outdoors: Male lizards show flexible spatial learning under semi-natural conditions. *Biology Letters*, *8*, 946–948. https://doi.org/10.1098/rsbl.2012.0813

Noble, D. W. A., Fanson, K. V., & Whiting, M. J. (2014). Sex, androgens, and whole-organism performance in an Australian lizard. *Biological Journal of the Linnean Society*, *111*, 834–849.

Noble, D. W. A., Keogh, J. S., & Whiting, M. J. (2013). Multiple mating increases fecundity, but provides no evidence for genetic benefits. *Behavioral Ecology*, *24*, 1128–1137.

Noble, D. W. A., McFarlane, E. S., Keogh, J. S., & Whiting, M. J. (2014). Maternal and additive genetic effects contribute to variation in offspring traits in a lizard. *Behavioral Ecology*, *25*, 633–640. https://doi.org/10.1093/beheco/aru032

Noble, D. W. A., Wechmann, K., Keogh, J. S., & Whiting, M. J. (2013). Behavioral and morphological traits interact to promote the evolution of alternative reproductive tactics in a lizard. *The American Naturalist*, *182*, 726–742.

Oliviera, R. F., Taborsky, M., & Brockmann, H. J. (2008). *Alternative reproductive tactics: An integrative approach*. Cambridge University Press.

Olsson, M., Shine, R., Wapstra, E., Ujvari, B., & Madsen, T. (2002). Sexual dimorphism in lizard body shape: The roles of sexual selection and fecundity selection. *Evolution*, *56*, 1538–1542.

Perry, G., Levering, K., Girard, I., & Garland, T. (2004). Locomotor performance and social donimance in male *Anolis cristatellus*. *Animal Beahviour*, *67*, 37–47.

R Development Core Team (2010). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from http://www.R-project.org. ISBN 3-900051-07-0.

Reznick, D. N., Shaw, F. H., Rodd, F. H., & Shaw, R. G. (1997). Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science*, *275*, 1934–1937.

Robson, M. A., & Miles, D. B. (2000). Locomotor performance and dominance in male Tree Lizards, *Urosaurus ornatus*. *Functional Ecology*, *14*, 338–344.

Schwarzkopf, L. (2005). Sexual dimorphism in body shape without sexual dimorphism in body size in water skinks (*Eulamprus quoyii*). *Herpetologica*, *61*, 116–123.

Scott, I. A. W., Hayes, C. M., Keogh, J. S., & Morrison, S. F. (2001). Isolation and characterization of novel microsatellite markers from

the Australian water skink *Eulamprus kosciuskoi* and cross-species amplification in other members of the species-group. *Molecular Ecology Notes*, *1*, 28–30.

Sinervo, B., & Lively, C. M. (1996). The rock-paper-scissors game and the evolution of alternative male strategies. *Nature*, *380*, 240–243.

Sinervo, B., Miles, D. B., Frankino, W. A., Klukowski, M., & DeNardo, D. F. (2000). Testosterone, endurance, and Darwinian fitness: Natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior*, *38*, 222–233.

Sinervo, B., & Svensson, E. (2002). Correlational selection and the evolution of genomic architecture. *Heredity*, *89*, 329–338. https://doi.org/10.1038/sj.hdy.6800148

Stapley, J., & Keogh, J. S. (2004). Exploratory and antipredator behaviours differ between territorial and nonterritorial male lizards. *Animal Behaviour*, *68*, 841–846. https://doi.org/10.1016/j.anbehav.2004.02.008

Stapley, J., & Keogh, J. S. (2005). Behavioral syndromes influence mating systems: Floater pairs of a lizard have heavier offspring. *Behavioral Ecology*, *16*, 514–520. https://doi.org/10.1093/beheco/ari019

Stinchcombe, J. R., Agrawal, A. F., Hohenlohe, P. A., Arnold, S. J., & Blows, M. W. (2008). Estimating nonlinear selection gradients using quadratic regression coefficients: Double or nothing? *Evolution*, *62*, 2435–2440. https://doi.org/10.1111/j.1558-5646.2008.00449.x

Stuart-Fox, D. M., Firth, D., Moussalli, A., & Whiting, M. J. (2006). Multiple signals in chameleon contests: Designing and analysing animal contests as a tournament. *Animal Beahviour*, *71*, 1263–1271. https://doi.org/10.1016/j.anbehav.2005.07.028

Sumner, J., Rousset, F., Estoup, A., & Moritz, C. (2001). 'Neighbourhood' size, dispersal and density estimates in the prickly forest skink (*Gnypetoscincus queenslandiae*) using individual genetic and demographic methods. *Molecular Ecology*, *10*, 1917–1927.

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodal inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*, 13–21.

Turner, H., & Firth, D. (2012). Bradley-Terry models in R: The BradleyTerry2 package. *Journal of Statistical Software*, *48*, 1–21.

Van Damme, R., Entin, P., Vanhooydonck, B., & Herrel, A. (2008). Causes of sexual dimorphism in performance traits: A comparative approach. *Evolutionary Ecology Research*, *10*, 229–250.

Whiting, M. J., Stuart-Fox, D. M., O'Connor, D., Firth, D., Bennett, N. C., & Blomberg, S. P. (2006). Ultraviolet signals ultra-aggression in a lizard. *Animal Beahviour*, *72*, 353–363. https://doi.org/10.1016/j.anbehav.2005.10.018

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Noble DWA, Kar F, Nakagawa S, Keogh JS, Whiting MJ. Sexual selection on performance traits in an Australian lizard with alternative reproductive tactics. *J Evol Biol*. 2021;34:451–464. https://doi.org/10.1111/jeb.13752

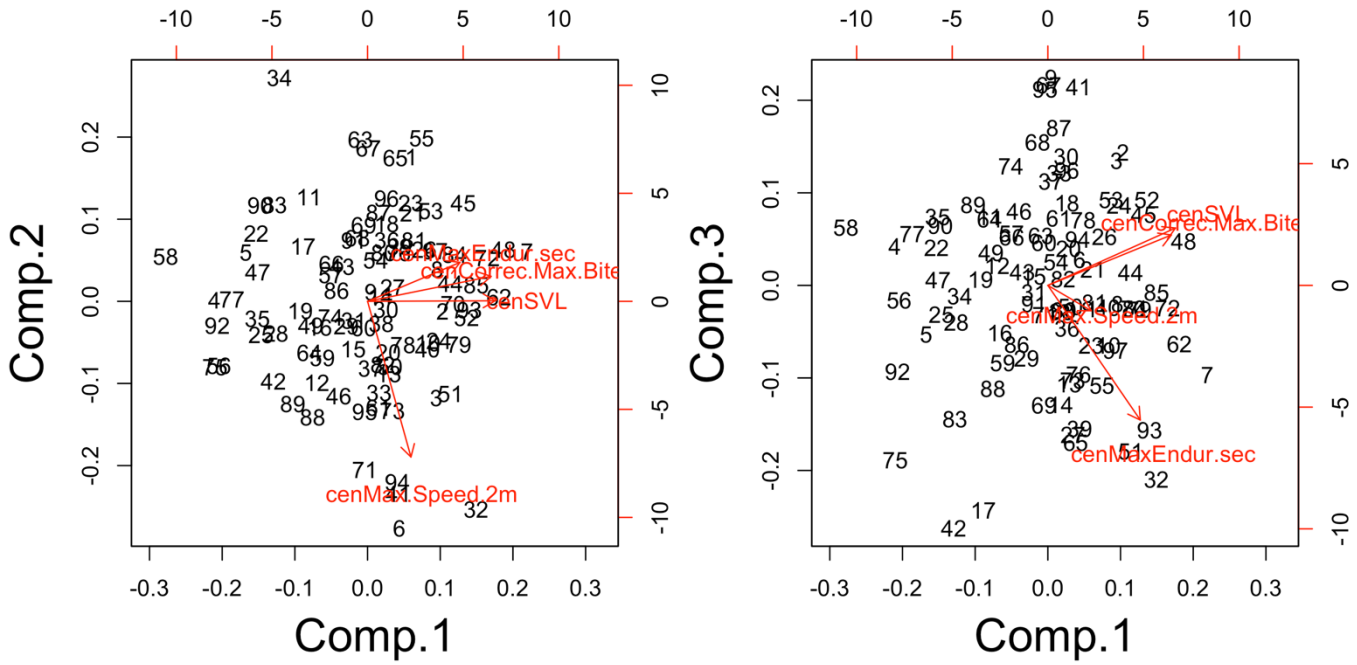

Figure S1 – Biplot of principle components 1 and 2 and 1 and 3 showing loadings of performance traits.

Table S1 – Pearson's correlation coefficients between body size, sprint speed, bite force and endurance in males. Below diagonal are coefficients and above diagonal is the significance of coefficients. Sample size for all correlations is n = 97. '***' $P < 0.001$; '**' $P < 0.01$; 'NS' not significant.

	SVL	Sprint speed	Bite force	Endurance
SVL	-	NS	***	***
Sprint speed	0.18	-	NS	NS
Bite force	0.62	0.10	-	***
Endurance	0.34	0.06	0.36	-

Table S2 – Pearson's correlation coefficients between body size, sprint speed, bite force and endurance in females. Below diagonal are coefficients and above diagonal is the significance of coefficients. Sample size for all correlations is n = 96. '***' $P < 0.001$; '**' $P < 0.01$; 'NS' not significant.

	SVL	Sprint speed	Bite force	Endurance
SVL	-	NS	***	***
Sprint speed	0.18	-	NS	NS
Bite force	0.63	0.06	-	***
Endurance	0.42	0.04	0.38	-

Table S3 – Top model set used for model averaging for male (n = 97) relative reproductive success and clutches sired (n = 97). Abbreviations are as follows* SVL = snout-vent length; SS = sprint speed; BF = size corrected bite force; Endur = Endurance; df = degrees of freedom; logLik = model log likelihood; Δ = ΔAICc; *w* = model weight. Enclosure was included in the global model but was not present in the top model candidate set (i.e. ΔAICc < 3) for any of the traits.

Models	**df**	**logLik**	**AICc**	**Δ**	***w***	**R^2**
Male Relative Reproductive Success						
1 + SS+ SVL	3	-133.273	272.805	0	0.114	0.235
1 + BF + SS+ SVL + BF*SS	5	-131.367	273.393	0.588	0.085	0.265
1 + SS+ SVL + SVL^2	4	-132.666	273.767	0.963	0.070	0.245
1 + BF + SS+ SVL	4	-132.735	273.905	1.101	0.066	0.244
1 + BF + SS+ SVL + SVL^2	5	-131.736	274.132	1.327	0.059	0.259
1 + BF + SS+ SVL + SVL^2 + BF*SS	6	-130.621	274.176	1.372	0.057	0.276
1 + SS+ Endur + SVL	4	-133.065	274.564	1.759	0.047	0.239
1 + BF + SS+ SVL + $Endur^2$ + BF*SS	6	-130.881	274.696	1.891	0.044	0.272
1 + SVL	2	-135.307	274.742	1.937	0.043	0.203
1 + SS+ SVL + $Endur^2$	4	-133.160	274.755	1.951	0.043	0.237
1 + SS+ SVL + BF^2	4	-133.180	274.794	1.990	0.042	0.237
1 + SS+ SVL + SS^2	4	-133.273	274.981	2.177	0.038	0.235
1 + BF + SS+ Endur + SVL + BF*SS	6	-131.158	275.250	2.445	0.034	0.268
1 + BF + SS+ SVL + $Endur^2$ + SVL^2 + BF*SS	7	-130.072	275.402	2.598	0.031	0.284
1 + BF + SS+ SVL + BF^2 + BF*SS	6	-131.254	275.441	2.637	0.031	0.266
1 + BF + SS+ Endur+ SVL	5	-132.409	275.477	2.672	0.030	0.249
1 + BF + SVL	3	-134.640	275.539	2.734	0.029	0.213
1 + BF + SS+ SVL + SS^2 + BF*SS	6	-131.330	275.593	2.789	0.028	0.265
1 + SS+ Endur + SVL + SVL^2	5	-132.490	275.639	2.835	0.028	0.248
1 + BF + SS+ SVL + BF^2 + SVL^2 + BF*SS	7	-130.206	275.670	2.865	0.027	0.282
1 + SS+ SVL + $Endur^2$ + SVL^2	5	-132.526	275.712	2.908	0.027	0.247
1 + BF + SS+ Endur + SVL + SVL^2	6	-131.416	275.765	2.960	0.026	0.264
Male Clutches Sired						
1 + SS + SVL	3	-117.246	240.751	0	0.311	0.156
1 + SS + Endur+ SVL	4	-116.911	242.256	1.505	0.147	0.162
1 + BF + SS + SVL	4	-117.071	242.576	1.825	0.125	0.160
1 + SS + $Endur^2$ + SVL	4	-117.132	242.699	1.948	0.118	0.158
1 + BF^2 + SS + SVL	4	-117.208	242.852	2.101	0.109	0.157
1 + SS + SS^2 + SVL	4	-117.230	242.894	2.143	0.107	0.157
1 + BF + SS + SVL + BF*SS	5	-116.361	243.382	2.631	0.084	0.172

Table S4 – Top model set used for model averaging female (n= 96) relative reproductive success. Abbreviations are the same as Table 1.

Models	df	logLik	AICc	Δ	*w*	R^2
Female Relative Reproductive Success						
1 + BF^2 + SS + SS^2 + SVL	5	-124.063	258.792	0	0.080	0.23
1 + BF^2 + SS + SVL	4	-125.270	258.979	0.187	0.072	0.21
1 + SS + SS^2 + SVL	4	-125.332	259.104	0.312	0.068	0.21
1 + SS + SVL	3	-126.464	259.189	0.398	0.065	0.19
1 + SVL	2	-127.572	259.272	0.480	0.063	0.17
1 + BF^2 + SVL	3	-126.674	259.608	0.816	0.053	0.19
1 + $Endur^2$ + SVL	5	-124.685	260.037	1.246	0.043	0.22
1 + SS + SS^2 + $Endur^2$ + SVL	3	-126.901	260.062	1.270	0.042	0.19
1 + SS + $Endur^2$ + SVL	4	-125.844	260.127	1.336	0.041	0.20
1 + BF^2 + SS + SS^2 + $Endur^2$ + SVL	6	-123.600	260.144	1.352	0.040	0.24
1 + SS^2 + SVL	5	-124.828	260.323	1.531	0.037	0.22
1 + BF^2 + SS + $Endur^2$ + SVL	3	-127.079	260.420	1.628	0.035	0.18
1 + BF^2 + $Endur^2$ + SVL	4	-126.155	260.750	1.958	0.030	0.20
1 + BF^2 + SS^2 + SVL	4	-126.156	260.752	1.960	0.030	0.20
1 + BF + BF^2 + SS + SS^2 + SVL	6	-123.992	260.928	2.136	0.027	0.23
1 + Endur + SVL	6	-124.047	261.037	2.245	0.026	0.23
1 + BF^2 + SS + SS^2 + Endur + SVL	5	-125.223	261.112	2.320	0.025	0.21
1 + BF + BF^2 + SS + SVL	3	-127.447	261.156	2.364	0.024	0.18
1 + SS^2 + $Endur^2$ + SVL	5	-125.257	261.180	2.388	0.024	0.21
1 + SS + SS^2 + Endur + SVL	5	-125.260	261.187	2.395	0.024	0.21
1 + BF^2 + SS + Endur + SVL	4	-126.388	261.215	2.423	0.024	0.19
1 + SS + Endur + SVL	4	-126.402	261.243	2.451	0.023	0.19
1 + BF + SVL	5	-125.328	261.322	2.530	0.022	0.21
1 + BF + SS + SVL	4	-126.453	261.345	2.554	0.022	0.19
1 + BF + SS + SS^2 + SVL	3	-127.566	261.393	2.601	0.022	0.17
1 + BF^2 + Endur + SVL	4	-126.616	261.672	2.881	0.019	0.19
1 + BF + BF^2 + SVL	4	-126.636	261.713	2.921	0.018	0.19

Survival Analysis

We tested the extent to which lizard survival across the season might be predicted by performance traits. To test this, we fit a logistic regression model with survival ('1' = survived; '0' = died) as our response variable and z-transformed performance, bite force, endurance and spring speed as fixed effects. We also included enclosure, sex, body size (SVL) and condition as a fixed effects to account for any possible differences between enclosures and control for body size and sex differences in performance traits. We fit a series of models that included main effects of these variables, subsequently dropping a single variable at a time and calculating AICc. We also fit a null model (intercept only model). We did not include any interactions because we did not have any *a priori* reason to expect non-linear and correlational selection on these traits.

Overall, we found that the top supported model was the null model (Table S5) with a 61% probability that it is the best approximating model and it was greater than 4 ΔAIC_C units away from the second best model. Unsurprisingly, effect sizes (as shown from the full model – Table S5) were very small,

suggesting little evidence that performance traits were important for survival in our semi-natural enclosures.

Table S5 – Log odds and standardized selection differentials (Janzen & Stern, 1998) for the effects of body size (SVL), body condition, sprint speed and endurance on survival probability during the breeding period. Each variable was dropped from the full model to assess impact of its removal on model explanatory power. All models were compared with a null model (intercept only). Estimates are presented from the full model, which contained enclosure. All phenotypic traits were standardized ($\bar{x} = 0$, $\sigma_x = 1$) prior to analysis. Final sample size for the analysis included 97 males and 96 females (n = 193) for which we had complete data.

	Logistic Regression		**Standardized Coefficients**	
Coefficient	**Estimate**	**SE**	**Estimate**	**SE**
Intercept	0.61	0.41	0.150	0.102
Sex (M)	-0.30	0.33	-0.080	0.084
Body condition	0.17	0.19	-0.040	0.046
SVL	-0.03	0.18	-0.010	0.046
Sprint Speed	0.01	0.18	0.002	0.046
Endurance	-0.15	0.19	-0.037	0.048

Single term deletion	**AIC_C**	**ΔAIC_C**	*w*
Null	222.84	0	0.617
Speed	226.90	4.06	0.081
SVL	226.91	4.07	0.081
Endurance	227.48	4.64	0.061
Sex	227.72	4.88	0.054
Condition	227.77	4.93	0.052
Full Model	229.05	6.21	0.028
Enclosure	229.15	6.31	0.026

References

Janzen, F. J. & Stern, H. S. 1998. Logistic regression for empirical studies of multivariate selection. *Evolution* **52**: 1564-1571.