Repeatability, locomotor performance and trade-offs between performance traits in two lizard species, *Oligosoma alani* and *O. smithi*

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Locomotor performance has often been used as a proxy for fitness and is likely to be highly repeatable. Trade-offs between locomotor performance traits can occur when selection acts in opposing directions on traits that rely on common morphological structures. We assessed the repeatability of sprint speed and dive duration in robust (*Oligosoma alani*) and shore skinks (*O. smithi*), compared locomotor performance among intraspecific groups and investigated whether a trade-off between sprint speed and diving behaviour exists. Sprint speed and dive duration were measured in the field and analysed for average maximum and absolute maximum performance using Bayesian hierarchical models. In robust skinks, sprint speed was repeatable, but sprint speed and dive duration in shore skinks had moderately low repeatability. Juvenile female robust skinks displayed faster average maximum speeds than adult males, while the absolute maximum speeds of adult males were slower than other groups. Sprint speed and dive duration in shore skinks were similar between sexes. Intraspecific differences in locomotor performance probably reflect variation in the proportion of maximum capacity used, or divergent foraging and behavioural ecologies. Research into the biology and ecology of the two species is required to reveal the proximal causes for the observed relationships.

ADDITIONAL KEYWORDS: dive duration – endurance – robust skink – shore skink – sprint speed.

INTRODUCTION

Knowledge of the functional relationship between phenotypic traits and biological fitness relies on an understanding of the heritability of these traits and how selection acts upon them (Arnold, 1983). Phenotypic traits that have high heritability may also have high repeatability (Boake, 1989). Repeatability quantifies the temporal stability of a given phenotypic trait within individuals relative to the variation attributed to inter-individual differences in that trait (Bulmer, 1980; Falconer, 1981; Lessells & Boag, 1987). Thus, a trait has high repeatability if multiple measures of that trait are more similar within individuals than they are among individuals (Van Berkum *et al.*, 1989). Accordingly, repeatability has been used as a proxy for the upper limit of heritability (e.g. Conradsen *et al.*, 2016).

Anti-predator behaviours that maximize survival are likely to be highly repeatable as predators exert a strong selective pressure upon their prey (Blumstein *et al.*, 2010). A key strategy used by many vertebrates to escape predators is to outrun them (Irschick & Losos, 1998; Irschick, 2003; Miles, 2004). A fast sprint speed also confers significant advantages on individuals due

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to its intrinsic links to prey capture (Irschick & Losos, 1998; Miles, 2004), social interactions (Garland Jr., Hankins & Huey, 1990), territory defence and reproduction (Husak *et al.*, 2006). For these reasons, locomotor performance is frequently used as a proxy for fitness, and research into phenotypic repeatability has often emphasized locomotor performance (e.g. Miller, Hare & Nelson, 2010; Conradsen *et al.*, 2016; Goulet, Thompson & Chapple, 2017). Much of this research has been based upon individuals maintained in laboratory conditions (e.g. Garland Jr., 1988; Austin & Shaffer, 1992; Peterson & Husak, 2006; Goulet *et al.*, 2017) where the natural pressures that act on individuals in the wild are not present. Certainly, performance in the laboratory may not accurately reflect the performance of animals *in situ* (Irschick, 2003; Hare *et al.*, 2012), and thus field-based studies into the repeatability of performance traits are required.

Individuals cannot rely upon speed in all contexts, and therefore alternative predator-escape behaviours may increase in importance in certain situations (Irschick, 2003). Such behaviours include jumping, clinging (Marchisin & Anderson, 1978; Irschick, 2003), climbing, digging (Marchisin & Anderson, 1978) and swimming or diving (Pianka & Vitt, 2003; Hare & Miller, 2009). However, the physiological tolerances and morphologies required to perform the gamut of predator-escape behaviours may be functionally specific. For example, if animals engage in multiple predator-escape behaviours that conflict with the demands of opposing predator-escape strategies, selection cannot concurrently act on both traits. Performance trade-offs may occur in such situations and have been shown in a variety of locomotor traits (e.g. Losos & Sinervo, 1989; Reidy, Kerr & Nelson, 2000; Vanhooydonck, Van Damme & Aerts, 2001; Tulli, Abdala & Cruz, 2012). For example, sprint speed in West Indian *Anolis* lizards comes at the expense of stability on narrow surfaces (Losos & Sinervo, 1989), while a negative relationship exists between endurance and burst swimming performance in Atlantic cod (*Gadus morhua*) (Reidy *et al.*, 2000). Likewise, Vanhooydonck *et al.* (2001) identified a trade-off between endurance and sprint speed in Lacertid lizards.

However, not all divergent predator-escape strategies result in performance trade-offs. Indeed, many studies have reported a lack of trade-offs in performance measures (e.g. Jayne & Bennett, 1990; Goodman, Krockenberger & Schwarzkopf, 2007; Tulli *et al.* 2012; Herrel *et al.*, 2013). For example, Prenter, Pérez-Staples & Taylor (2010) found a positive relationship between running and climbing speed in orb-web spiders (*Argiope keyserlingi* and *Nephila plumipes*), while Vanhooydonck & Van Damme (2001) reported positive correlations between sprinting, climbing and clambering ability in lacertid lizards. Such positive

relationships may reflect common, underlying links to morphological features (Garland Jr., 1988; Irschick & Losos, 1998; Goodman *et al.*, 2007; Herrel *et al.*, 2013). Thus, the presence of trade-offs may depend on whether underlying morphological structures and/ or behaviours are incompatible (Reidy *et al.*, 2000; Vanhooydonck & Van Damme 2001; Goodman *et al.*, 2007; Goodman, Miles & Schwarzkopf, 2008).

Here, we examined the repeatability of locomotor performance in two skink species – robust, *Oligosoma alani* (Robb, 1970) and shore skinks, *O. smithi* (Gray, 1845) – and compared locomotor performance among age and sex groups. We also investigated whether a trade-off between sprint speed and diving behaviour was evident in shore skinks. The robust skink is a nocturnal, primarily forest-dwelling species that occupies seabird burrows, rocky areas and deep forest litter (Towns, Daugherty & Newman, 1985). It is the largest skink in New Zealand [maximum snout–vent length (SVL) of 150 mm; Cree & Hare, 2016]. The smaller shore skink (maximum SVL of 71 mm; Cree & Hare, 2016), a diurnal, semi-aquatic species, dwells exclusively along the shoreline and surrounding sand dunes (Hare & Miller, 2009; Chapple, 2016). It escapes predators by dashing to nearby cover and/or diving underwater (Miller, 2007; Hare & Miller, 2009).

Our aims were threefold: (1) to identify whether sprint speed is repeatable within individuals of both species, and in shore skinks, whether dive duration is repeatable; (2) to establish whether sprint speed varies between demographic groups in both species (sex and age group for robust skinks; pregnant females, non-pregnant females and males for shore skinks) and (3) to determine whether there are any correlations between sprint speed and diving performance in shore skinks. We predict that both sprint speed and dive duration will be repeatable, since congenerics (*O. suteri*) have shown high repeatability in both of these performance measures (Miller *et al.*, 2010). Juveniles are often slower than adults (Irschick *et al.*, 2000; Miller *et al.*, 2010), so we expect that juvenile robust skinks will not achieve the same speeds of adults. In contrast, given the lack of intersexual differences in SVL of the two species (Cree & Hare, 2016), we suggest that sexes of each species are likely to achieve comparable sprint speeds, though pregnant female shore skinks will probably display reduced speeds due to the additional physical burden and physiological changes imposed by pregnancy (Shine, 2003). However, since pregnancy does not appear to detrimentally impact dive duration in this species (Hare & Miller, 2009), we expect that dive duration will be similar among groups. Finally, we predict that there will be no trade-off between sprint speed and dive duration in shore skinks, since the relationship between endurance, represented here by dive duration, and sprint

speed is often positive (e.g. Garland Jr., 1988; Jayne & Bennett, 1990; de Albuquerque, Bonine & Garland Jr., 2015), and because breath holding capacity and sprinting are unlikely to have a similar physiological or morphological basis.

MATERIAL AND METHODS

CAPTURE AND MAINTENANCE OF SKINKS

Details of animal capture and husbandry are provided elsewhere (Hare & Miller, 2009). Briefly, we captured robust skinks (*n* = 22) and shore skinks (*n* = 60) from Korapuki Island (18 ha) in the Mercury Island group (36°40′S, 175°52′E), New Zealand during November to December, 2006. The population of robust skinks on Korapuki Island is derived from 14 founders translocated from nearby Green Island in 1992 (Towns & Ferreira, 2001). Animals were captured using baited pitfall traps and were housed individually indoors for 2–3 days (depending on their size) before performance trials to ensure all were post-absorptive. Water was provided *ad libitum* using a small moistened sponge, and animals were kept in filtered light. For shore skinks, only adults were captured in order to determine the maximum duration of voluntary diving (Hare & Miller, 2009). SVL was used as a proxy for age.

LOCOMOTOR PERFORMANCE

Standard morphometric measurements, including mass (digital balance with a precision ± 0.01 g), SVL, tail length, hind-limb length (digital callipers with a precision ± 0.1 mm) and tail regeneration (if present), were taken prior to speed tests (Supporting Information, Table S1). Sex of adults was determined by eversion of the hemipenes in males. Pregnancy status (yes/no) of female shore skinks was determined by abdominal palpation (see Holmes & Cree, 2006 for accuracy of this procedure in a congeneric species, *O. maccanni*). Under the terms of our ethics permit, only non-gravid females of robust skinks were used in trials.

Sprint trials were conducted using a transportable 1.5-m plastic racetrack (a modified version of that described by Huey *et al.*, 1981) adjusted to a width appropriate for the size of the species (100 and 80 mm for robust and shore skinks, respectively). The racetrack comprised four segments separated by five paired infrared lights, which were placed at 0.25 m intervals at a height of 4 mm and connected to a digital time counter (±1 ms: modified from Huey *et al.*, 1981). Sprint speed was based on speed over any 0.25-m interval.

Animals were left undisturbed for 30 min prior to the first sprint speed trial to acclimate to experimental field temperatures, which varied between 16.5 and 18.1 °C and 15.5 and 19.4 °C, for robust and shore skinks, respectively, across all trials. We conducted three trials per individual. The order in which individuals were run was randomized, though each individual received at least 15-min rest between trials. Sprinting was encouraged by touching the tail with a paintbrush. During sprint trials, some individuals paused after being touched by the paintbrush and required another touch to continue running. The number of such pauses over 1 m was recorded. Due to time constraints imposed by other experiments simultaneously being conducted on other species (see Hare & Miller, 2009; Miller *et al.*, 2010), speed was measured at 0830–1500 h NZST for robust skinks and 1400–2030 h NZST for shore skinks, all during daylight hours.

Diving performance of shore skinks follows methods presented in Hare & Miller (2009). Briefly, diving was performed three times a day between 0945 and 1730 h NZST, with at least 60-min rest between each trial. Artificial rock pools were created using a plastic bin (base 340 mm diameter; 20 L to water line) with the bottom of the bin completely covered with rocks, and locally abundant brown seaweed of unknown species included as hiding recesses. A diving platform was constructed in the centre using a flat 150 × 130 mm rock surface above the water. The bin was filled with intertidal sea water (17.0 ± 0.1 °C) to a depth of 200 mm. Skinks were placed on diving platform facing away from the researcher and lightly tapped on the tail. Skinks either dove underwater or swam about on the surface of the water. If after 10 s of swimming an animal did not dive, we removed it from the water. If an animal dove beneath the water, we recorded the duration of diving using a manual stopwatch (accurate to 1 s). All trials were conducted in the field under natural climatic conditions.

STATISTICAL ANALYSES

All statistical analyses were completed using R (version 3.3.1), with Markov chain Monte Carlo (MCMC) simulations run within the JAGS software (version 4.2.0) via the R2jags package (version 0.5-7). MCMC simulations were run on three separate chains for a total of 1 000 000 iterations, each using a thinning of 100 after a burn-in of 10 000 iterations. To ensure proper mixing, model convergence was assessed by visualizing MCMC chains and using the R-hat statistic (Gelman *et al.*, 2014), while autocorrelation within each parameter was assessed by visualizing the autocorrelation function (ACF) across iterations. All models utilized uninformative prior distributions for both beta (diffuse normal) and sigma estimates (half-Cauchy). Parameter estimates were accepted as influential when the 95% confidence intervals from their posterior distributions did not cross zero.

Variation in sprint speed (robust and shore skinks) and diving performance (shore skinks) among demographic groups were assessed using linear models with Gaussian error distributions. Potentially confounding variables (body size, SVL and ambient temperature) were included as covariates to correct for their possible effects on sprint speed and dive duration. Intra-class correlations (ICCs) were calculated following Nakagawa & Schielzeth (2010) on mixed-effects models that contained an individual-level random effect. Preliminary analyses showed a low ICC between sprint speed trails of shore skinks, suggesting that individuals were not performing at their maximum capacities within trials. Consequently, we assessed both the average maximum speed (i.e. the fastest 0.25-m segment in each trial, averaged over three trials) and the absolute maximum speed (i.e. the fastest 0.25-m segment across the three trials) and dive durations between individuals. Likewise, for diving performance, both the average and maximum durations of the three trials were assessed.

The average maximum performance of lizards was compared among demographic groups by modelling the mean, within trial, maximum sprint speed and mean dive duration of all trials conducted (hereafter full models). These data contained repeated measures within individuals, and as such, an individual-level random effect was included in models. Comparisons of absolute maximum performance among demographic groups were made by modelling the maximum sprint speed/dive duration recorded for an individual across all trials, hereafter maximum models. As there was only a single value for each individual, these models were fitted without the random effect of individual.

For shore skinks, we also assessed the relationship between sprint speed and dive duration. To account for the influence of different temperatures on the response (sprint speed) and predictor (dive duration) variables, we modelled the residual variation from linear models of sprint speed or dive duration and temperature (positive residuals would mean individuals dove longer/ran faster than was expected for the temperature at which they were performing, negative residuals the opposite) with residual sprint speed compared with residual dive duration.

Preliminary analyses suggested the possibility of a non-linear relationship between the two performance measures. As such, all models were fitted using generalized additive models (GAMs) with O'Sullivan smoothing splines (Wand & Ormerod, 2008). There were multiple trials per individual of each performance measure but the performance measures were not linked to one another (i.e. Sprint Trial 1 was not related to Dive Trial 1 any more than it was related to Dive Trials 2 or 3), making a single comparison between the performance measures inappropriate. We instead fitted multiple models consisting of all possible combinations of sprint speed and dive duration with each individual and interpreted the combined posterior distributions from all model iterations.

RESULTS

REPEATABILITY OF LOCOMOTOR PERFORMANCE

Overall, 66 and 180 sprint trials of 22 robust and 60 shore skinks, respectively, were included in repeatability estimates. Sprint speed in robust skinks was relatively consistent within individuals, with an ICC of 0.62. This indicates moderate repeatability. In contrast, repeatability for both performance measures in shore skinks was moderately low, with ICC values of 0.04 and 0.39 for sprint speed and dive duration, respectively.

INTRASPECIFIC VARIATION IN LOCOMOTOR PERFORMANCE

The sprint trials of 22 robust and 60 shore skinks were included in analyses. The full model for sprint speed in robust skinks showed strong support for juvenile females attaining faster sprint speeds, on average, than adult males (Fig. 1A; Table 1). However, despite the presence of a general trend towards juveniles sprinting at faster speeds than adults, at the 95% confidence threshold, there was no evidence of differences among all other groups (adult females and males of both age classes; and juvenile females, and adult and juvenile males, Fig. 1A; Table 1). The trend towards faster speed in juvenile robust skinks remained in maximum models, but here, adult males were slower than all other classes (Fig. 1B; Table 1). No differences among the other age/sex classes were supported.

For shore skinks, full models indicated no difference in average maximum sprint speeds between pregnant females, non-pregnant females and males (Fig 2A; Table 1). Likewise, maximum models did not show strong support for any differences among sex/age classes, though a general trend towards greater speed in non-pregnant females relative to other groups was evident (Fig. 2B; Table 1). A total of 142 dive duration trials were incorporated into analyses. Within the full model, at the 95% confidence level, there were no clear differences in average maximum and absolute maximum dive duration between non-pregnant females, pregnant females and males (Fig. 2C, D; Table 1).

SPRINT SPEED VS. DIVE DURATION IN SHORE SKINKS

There was no relationship, either positive or negative, between sprint speed and dive duration in shore skinks at the 95% confidence level (Supporting Information, Fig. S1 and Table S2).
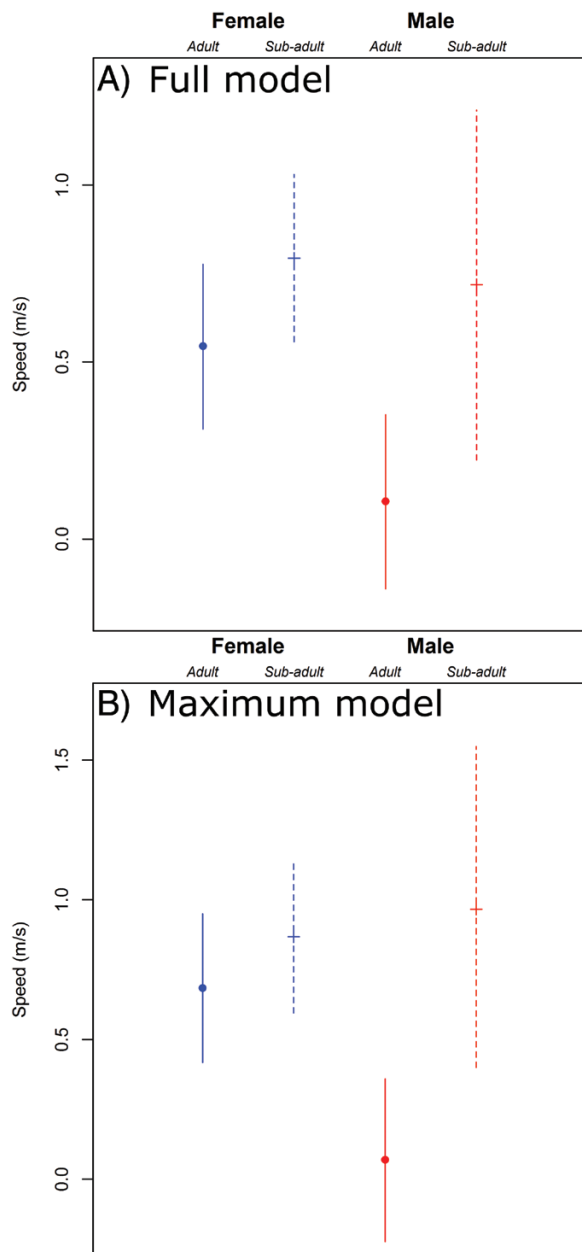
Figure 1. Comparison of the maximum recorded sprint speeds in robust skinks (*Oligosoma alani*) averaged across all trials (A) and including only the fastest speed recorded among trials (B). Means ± 95% CI are shown.

DISCUSSION

REPEATABILITY OF LOCOMOTOR PERFORMANCE

Sprint speed in robust skinks was moderately repeatable. The ICC value of 0.62 is within the range typically reported for other squamates (Austin & Shaffer, 1992; Bonine & Garland Jr., 1999; Goulet *et al.*, 2017) and suggests that sprint performance plays a key role in the biology of many species. Robust skinks feed mainly on mobile invertebrates (Southey, 1985), and fast speed may have a role in prey capture, and escaping predators (e.g. Husak, 2006). Robust skinks are relatively large (Cree & Hare, 2016) and cryptic, but lack other common anti-predator strategies, such as body armour (Pianka & Vitt, 2003). Fleeing predators may therefore be their primary predator-escape mechanism, and thus sprint speed constitutes a performance trait that is likely to be under selection.

In shore skinks, repeatabilities for sprint speed, and to a lesser extent, dive duration, were low relative to other squamates (Austin & Shaffer, 1992; Bonine & Garland Jr., 1999; Goulet *et al.*, 2017). This could imply that other anti-predator strategies are more important in this species. For example, Baling *et al.* (2016) reported a rapid inter-generational shift in the prevalence of shore skink colour patterns towards patterns that enable skinks to blend into their environment and suggested that individuals might actively select microhabitats that facilitate camouflage. Such colour-matching might be accompanied by intermittent locomotion, which can serve to confound predators (see Kramer & McLaughlin, 2001). Under this escape strategy, other performance traits, such as acceleration (e.g. Husak & Fox, 2006), may be more important than sprint speed. Alternatively, such low repeatabilities could simply indicate that animals were not performing at their maximum physiological capacity. Performance in lizards has a strong environmental and behavioural component, and factors such as perceived degree of threat (Irschick *et al.*, 2005) and motivation (Losos, Creer & Schulte, 2002) can influence performance. Temperature can have a particularly strong impact. For instance, in the case of New Zealand lizards, which are exposed to low environmental temperatures, the optimal performance temperature range may not be attainable in the field, resulting in a mismatch between preferred and field temperatures (Hare *et al.*, 2007; Gaby *et al.*, 2011).

INTRASPECIFIC VARIATION IN LOCOMOTOR PERFORMANCE

There was a general trend for juvenile robust skinks to attain greater speeds than adults, but models only showed strong support for sub-adult females attaining greater average maximum speeds than adult males. While some studies have recorded juveniles being slower (e.g. Irschick *et al.*, 2000; Miller *et al.*, 2010), juveniles of other lizard species sprint at comparable or faster speeds relative to adult conspecifics (e.g. Husak, 2006; Husak & Fox, 2006; Ekner-Grzyb *et al.*, 2013). These differences could be due to a reduction in mobility with increasing size of adults (K. A. Miller, personal observation) or reflect variation in selective pressures among sexes and age classes (Husak

Table 1. Summary results of the Markov chain Monte Carlo-derived posterior distributions for models investigating the influence of demographic group on sprint speed and diving performance in robust (*Oligosoma alani*) and shore (*O. smithi*) skinks

	Full model				Maximum model			
	Mean	SE	2.5%	97.5%	Mean	SE	2.5%	97.5%
Robust skinks – sprint speed ~								
Intercept (adult female)	0.54	0.11	0.31	0.77	0.68	0.13	0.41	0.95
Snout–vent length	0.03	0.08	−0.14	0.20	0.01	0.10	−0.18	0.21
Ambient temperature	−0.01	0.02	−0.04	0.04	0.02	0.05	−0.08	0.3
Sex (male)	0.1	0.12	−0.13	0.35	0.06	0.14	−0.21	0.35
Age (sub-adult)	0.24	0.20	−0.16	0.65	0.18	0.23	−0.28	0.65
Sex (male) * age (sub-adult)	−0.07	0.27	−0.60	0.45	0.10	0.31	−0.52	0.74
Shore skinks – sprint speed ~								
Intercept (not gravid female)	0.76	0.03	0.70	0.82	0.96	0.04	0.86	1.05
Snout–vent length	0.02	0.01	−0.01	0.05	0.04	0.02	−0.01	0.09
Ambient temperature	0.06	0.01	−0.04	0.09	0.06	0.02	0.02	0.10
Demographic status (gravid female)	−0.04	0.04	−0.12	0.04	−0.12	0.06	−0.25	0.01
Demographic status (male)	−0.03	0.01	−0.10	0.03	−0.14	0.05	−0.25	−0.02
Shore skinks – dive duration ~								
Intercept (not gravid female)	144.27	16.09	112.20	175.93	180.59	21.33	137.51	221.75
Snout–vent length	18.97	7.75	3.77	34.10	25.28	10.77	4.28	46.53
Water temperature	−8.89	7.19	−22.91	5.61	−15.87	10.07	−35.48	4.04
Demographic status (gravid female)	−45.84	21.62	−88.23	−3.18	−49.82	28.84	−105.69	8.08
Demographic status (male)	−30.52	18.79	−67.26	6.5	−40.06	25.28	−89.203	10.70

& Fox, 2006). For instance, predators are likely to impose stronger selective pressure on juveniles than on their larger, adult counterparts (Husak, 2006). Indeed, survival has been linked to sprint speed in juvenile collared *Crotaphytus collaris* (Husak, 2006) and tree lizards *Urosaurus ornatus* (Miles, 2004). Juveniles may also sprint at speeds that are closer to their maximum capacity (Irschick *et al.*, 2005). Husak & Fox (2006), for example, found that despite having slower maximum speeds under laboratory conditions, yearling collared lizards ran faster than adults in the field and used a greater percentage of their maximum sprinting capacity. Thus, selection may not act on absolute sprint speed but rather on the proportion of maximum capacity used.

In this study, adult males displayed slower sprint speeds than all other groups, which could imply that male robust skinks are less reliant on speed than females. It is possible that sprinting capacity varies on a seasonal basis, possibly related to testosterone, in males (Peterson & Husak, 2006). Alternatively, males are often bolder (*sensu* Michelangeli, Chapple & Wong, 2016; Michelangeli, Wong & Chapple, 2016; Moule *et al.*, 2016) and might not perceive the stimulus as threatening. Finally, since dietary niche (Vanhooydonck, Herrel & Van Damme, 2007) and habitat use of lizards can produce evolutionary shifts in performance (Goodman *et al.*, 2008), the divergence

in sprint speed could reflect intersexual differences in fine-scale habitat use or foraging behaviour. For example, males might spend more time in microhabitats that favour other performance traits over speed (e.g. acceleration: Husak & Fox, 2006, which may be particularly important for capturing evasive prey: Vanhooydonck *et al.*, 2007), or alternatively, that require them to flee longer distances to escape predators. Indeed, Jayne & Ellis (1998) found that *Uma scoparia* lizards require relatively long distances to attain maximum sprint speeds (e.g. >3 m for some individuals). Under such situations, burst speed would be less biologically meaningful than speed determined over greater distances.

Contrary to our predictions, sprint speed among male, pregnant female and non-pregnant female shore skinks did not differ. This is surprising given the additional load imposed on pregnant females (Shine, 2003), with many studies reporting impaired locomotor performance in pregnant or gravid squamates (e.g. Jayne & Bennett, 1990; Miller *et al.*, 2010). Why, then, did pregnant females in our study run at comparable speeds to non-pregnant females and males? It is plausible that they compensate for their lower sprint capacity by using comparatively more effort to attain similar speeds (e.g. Irschick *et al.*, 2005; Husak & Fox, 2006). Pregnancy could also incur an endurance cost rather than a cost in sprint speed (Chapple & Swain, 2002), which may enable individuals
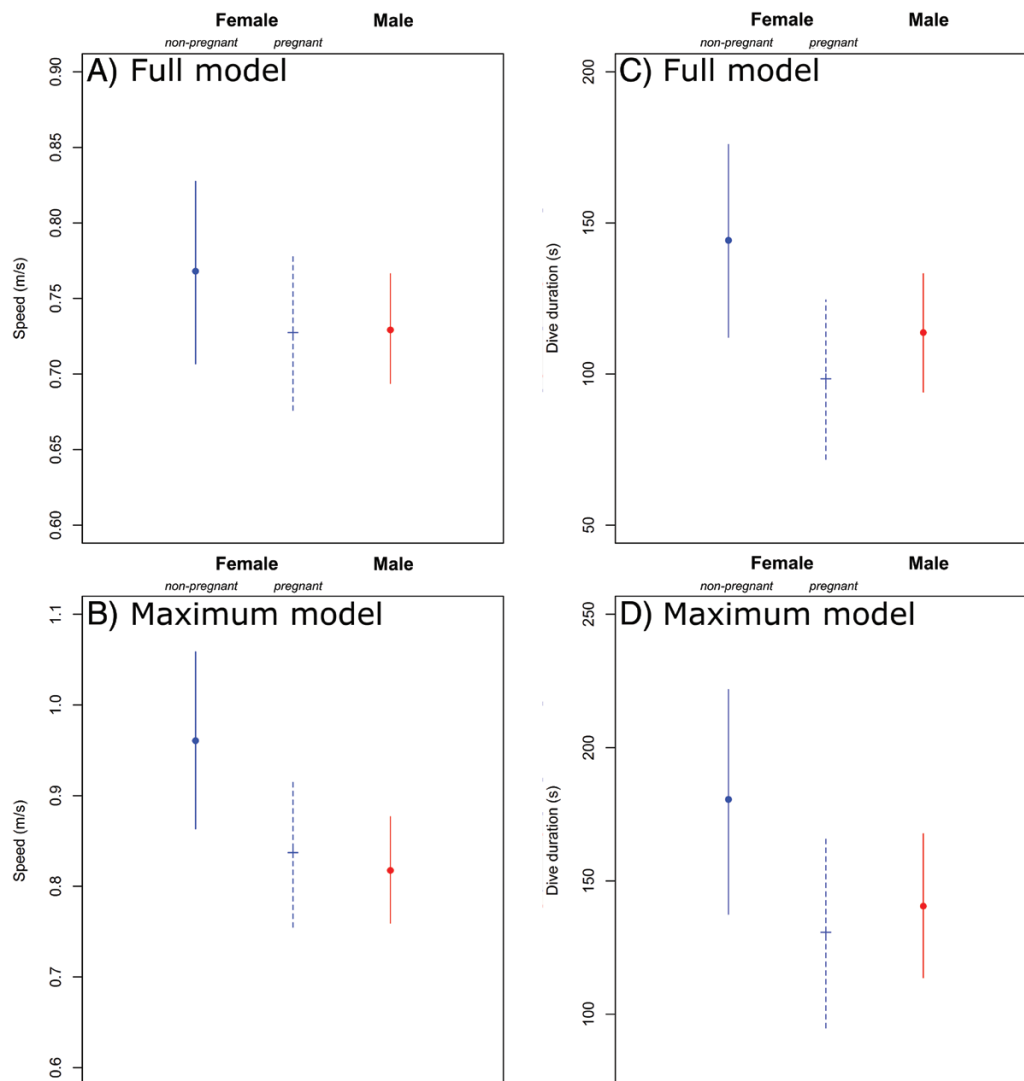
Figure 2. Comparison of the maximum recorded sprint speeds and dive durations in shore skinks (*Oligosoma smithi*), averaged across all trials (speed – A, dive duration - C) and including only the fastest speed recorded between trials (speed – B, dive duration – D). Means ± 95% CI are shown.

to maintain high speeds over short distances. In both of these instances, we would expect lower dive durations, a measure of endurance, in pregnant females. However, although there was a general trend towards shorter dive durations in pregnant females, support for this in dive duration models was weak.

Diving offers individuals an alternative predator-escape tactic for eluding terrestrial predators (Pianka & Vitt, 2003). Hare & Miller (2009) suggested that pregnancy does not impede diving in shore skinks and provides pregnant females with a more effective means of reaching safety. As predicted, our results are consistent with this finding. In contrast, gravid egg-laying skinks (*O. suteri*) have been reported diving for longer durations than males. This was attributed to compensation by gravid females for their slower sprint speeds (Miller *et al.*, 2010). However, we found no sexual difference in any aspect of locomotor performance in shore skinks.

NO TRADE-OFF BETWEEN SPRINT SPEED AND DIVE DURATION IN SHORE SKINKS

In keeping with our predictions, we did not find a negative relationship between sprint speed and dive duration in shore skinks. This supports the findings of several studies on squamates that have shown no trade-off between speed and stamina (e.g. Garland Jr., 1988; de Albuquerque *et al.*, 2015). Trade-offs are unlikely when performance traits are not coupled with the same underlying morphological features. Sprint

speed and dive duration may therefore be independent of each other in shore skinks. Indeed, sprint performance is related to the proportion of fast-twitch muscle fibres (Esbjörnsson *et al.*, 1993), while dive duration is influenced by lung volume and oxygen consumption rate (Andersson & Shagatay, 1998). It is possible that had we used an alternative measure of endurance (e.g. by running lizards on a treadmill: Vanhooydonck *et al.*, 2001), we might have found a different relationship.

CONCLUSION

In summary, we found that sprint speed in robust skinks was repeatable, whereas in shore skinks, both sprint speed and dive duration had low repeatability. The faster average maximum sprint speed of juvenile female robust skinks relative to adult males was accompanied by slower maximum speeds in adult males. In the case of juveniles, this is probably a result of running closer to their maximum capacities than adults, while the slower speed of males may reflect intraspecific ecological or behavioural differences. Sprint speed in shore skinks was similar among classes, and given that pregnancy often impedes locomotor performance, this implies that pregnant females perform closer to their maximum capacities. The lack of intersexual difference in dive duration suggests that pregnancy does not hamper dive duration. There was no trade-off between sprint speed and endurance in shore skinks, indicating that the two performance traits operate independently of each other. The ability to interpret our results is hindered by the paucity of data on the biology and ecology of both skink species; research into these, and how they vary ontogenetically and between sexes, is required to further elucidate the relationships observed in our study.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Morphometric and demographic details for all robust (*Oligosoma alani*) and shore (*O. smithi*) skinks used in the performance trials carried out for this study.

Table S2. Summary results of the combined posterior distributions for models investigating the relationship between sprint speeds and diving performance in shore skinks (*Oligosoma smithi*).

Figure S1. Estimated relationship between sprint speed and dive duration in shore skinks (*Oligosoma smithi*), accounting for temperature during trials. If there was a relationship between the two variables, we should expect the line to deviate significantly from zero. The solid line represents the mean estimate and the shaded region shows the 95% confidence intervals.