



Beyond black and white: divergent behaviour and performance in three rapidly evolving lizard species at White Sands

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Determining which traits enable organisms to colonize and persist in new environments is key to understanding adaptation and ecological speciation. New environments can present novel selective pressures on colonists' morphology, behaviour, and performance, collectively referred to as ecomorphology. To investigate ecomorphological change during adaptation and incipient ecological speciation, we measured differences in morphology (body shape and size), behaviour (startle response), and performance (sprint speed) in three New Mexican lizard species: *Holbrookia maculata*, *Sceloporus undulatus*, and *Aspidoscelis inornata*. Each species is represented by dark morphs, cryptic on the brown adobe soils of the Chihuahuan Desert, and white morphs, cryptic on the gypsum substrate of White Sands. For each species, we then determined the effects of morphology and startle response on sprint speed on matched and mismatched substrate. For two of the three species, white morphs had larger body size and longer limbs. However, we found no statistical evidence that these morphological differences affected sprint speed. Colour morphs also exhibited different escape responses on the two substrates: in all species, dark morphs were less likely to immediately sprint from a simulated predator on white sand. As a result, escape response had a significant effect on sprint speed for two of the three species. Not surprisingly, all lizards sprinted faster on dark soil, which was probably due to the lizards' more immediate escape response and the higher compaction of dark soil. The relationship between escape response and sprint performance across the dark soil and white sand habitats suggests that behavioural differences may be an important component of adaptation and speciation in new environments. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **111**, 169–182.

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INTRODUCTION

Determining the morphological and behavioural traits that enable organisms to successfully colonize and persist in novel environments is crucial to understanding both adaptation (Losos, Warheitt & Schoener, 1997; Reznick & Ghalambor, 2001) and ecological speciation (Orr & Smith, 1998; Rundle & Nosil, 2005; Schluter, 2009). The three main aspects of ecomorphology – morphology, behaviour, and per-

formance – affect the survival of an organism through interactions with the surrounding environment (Galis, 1996; Irschick, 2002). Morphology and behaviour interact to influence performance in different habitats (Arnold, 1983; Galis, 1996; Calsbeek & Irschick, 2007), which in turn can strongly affect fitness (Arnold, 1983). As such, performance is an important and ecologically relevant link between the phenotype and the environment (Irschick, 2003).

Squamates have been the focus of many ecomorphological studies because of their impressive ecological, morphological, and behavioural diversity (Garland & Losos, 1994). Results from field and

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laboratory experiments on squamates typically support a link between morphology, performance, and habitat use. For example, in phrynosomatid, lygosominid, and anoline lizards, longer-limbed individuals sprint faster (Bonine & Garland, 1999) especially in open habitats (Melville & Swain, 2000) and on broad perches (Losos, 1990). Similarly, limb reduction and elongated bodies have evolved multiple times in squamates and are correlated with increased speed through dense vegetation (Wiens, Brandley & Reeder, 2006). However, some studies show that morphology does not always correlate predictably with performance in different habitats: although certain morphological traits appear to have evolved for habitat-specific performance, phylogenetic analyses sometimes fail to support particular adaptive hypotheses (Jaksic, Nunez & Ojeda, 1980; Vanhooydonck & Van Damme, 1999).

Behavioural shifts can play a crucial role during adaptation to new environments. On entering a new habitat, behavioural changes often precede morphological adaptations (West-Eberhard, 1989). Microhabitat selection, for example, can buffer organisms from environmental changes that otherwise would exert strong selective pressure on morphology (Bogert, 1949; Coyne, Bundgaard & Prout, 1983; Huey, Hertz & Sinervo, 2003; Duckworth, 2009), which is known as behavioural inertia (Huey *et al.*, 2003). Behavioural shifts can also expose organisms to novel selective environments, a process termed behavioural drive (Mayr, 1963). When behaviours are heritable, behavioural drive can promote evolutionary change in morphological, physiological, or ecological traits (Bateson, 1988; Wcislo, 1989; West-Eberhard, 1989) and may even contribute to speciation (Duckworth, 2009).

Certain behaviours may be especially important for the success of colonists in new environments. Different anti-predator strategies adopted by colonists can determine whether they survive post-colonization (Schwarzkopf & Shine, 1992; Vanhooydonck & Van Damme, 1999). For example, lizards will avoid habitats in which they perform poorly (Irschick & Losos, 1999) and alter anti-predator behaviour depending on their immediate surroundings (Vanhooydonck & Van Damme, 1999). Although the most common escape strategy for a startled lizard is to move towards a refuge (Greene, 1988), its behaviour and morphology may prevent detection altogether, for example through substrate matching (Losos *et al.*, 2002; Schulte *et al.*, 2004b). For lizards already detected by a predator, the inability to flee may be fatal. As such there can be strong selection for the fastest individuals that immediately respond to a predator by sprinting (see Husak, 2006). Because sprint speed is often heritable and can influence fitness (e.g. Miles, 2004;

Husak, 2006; Husak *et al.*, 2006), it is frequently used to measure performance in different habitats.

The geologically and ecologically unique White Sands dune field in New Mexico provides a setting for the integrated study of recent and ongoing selection on morphology, behaviour, and performance. White Sands formed approximately 6000 years ago (Kocurek *et al.*, 2007) and represents a novel habitat for three lizard species (*Holbrookia maculata*, *Sceloporus undulatus*, and *Aspidoscelis inornata*). The White Sands populations evolved from lizards inhabiting the surrounding Chihuahuan dark soil desert scrubland, and there is dramatic divergence in dorsal colour between White Sands and dark soil individuals (Rosenblum & Harmon, 2011). All three species have evolved blanched coloration on White Sands, which presumably allows them to better match their surrounding white substrate (Rosenblum *et al.*, 2010). Additionally, two of the three species (*H. maculata* and *A. inornata*) show parallel directional shifts in body shape with white morphs having longer legs and broader heads (Rosenblum & Harmon, 2011). These morphological shifts may be a result of selection in a novel habitat with different microhabitat and substrate characteristics (Des Roches *et al.*, 2011). Soil compaction, for example, affects the speed of sprinting animals, and lizards, among other species, will often evolve longer limbs to increase performance on looser soils (Ding *et al.*, 2011). Finally, dark and white morphs show divergence in certain behavioural characteristics (e.g. Robertson & Rosenblum, 2010). Most relevant to the current study are differences in anti-predator response with white morphs of *S. undulatus* being more wary (i.e. they retreat more) but less vigilant (i.e. they allow the approaching observer to get closer before retreating) than dark morphs (Robertson *et al.*, 2011). Nevertheless, previous research has not examined these putative morphological and behavioural differences in the context of the performance of the different colour morphs.

We compared aspects of morphology, escape behaviour, and sprint performance between dark and white morphs of the three species from the dark soil desert and White Sands, respectively. First, we examined morphological differences between dark and white morphs. We expected our findings to correspond in general with the findings of Rosenblum & Harmon (2011); specifically, white morphs having longer legs in both *H. maculata* and *A. inornata*, but not *S. undulatus*. Second, we conducted an experiment in natural conditions to determine whether startle response behaviour and sprint performance differed between morphs on matched and mismatched substrate. In terms of startle response, we formulated two hypotheses based on the finding that white and

dark morphs have diverged in behavioural characteristics in different habitats (Robertson & Rosenblum, 2010). If lizards are aware of their level of substrate matching, matched lizards will remain still, apparently cryptic to a predator, whereas mismatched lizards will sprint immediately from a simulated predator. Alternatively, we hypothesize that matched lizards may be more familiar with their native background, and sprint immediately. In terms of performance, we hypothesize that selection has led to optimal performance for all lizards in their native habitats. As a result, matched lizards will in general sprint faster than mis-matched lizards on either substrate. Finally, we tested whether morphological differences and/or startle response behaviour were predictive of sprint performance. We hypothesized that if white *H. maculata* and *A. inornata* had longer legs, this morphology would allow them to sprint faster in general, and specifically on white sand substrate (Ding *et al.*, 2011). Furthermore, we hypothesized that larger lizards would sprint faster, regardless of species and substrate. We also hypothesized that startle response would strongly influence performance in terms of sprint speed, with individuals that immediately sprint when startled achieving a greater speed. By simultaneously examining morphology, behaviour, and performance of three different species that have undergone parallel evolution, we provide an example of replicated ecomorphological change in a new environment.

MATERIAL AND METHODS

SAMPLING

We captured lizards in New Mexico from 12 May to 9 July 2010 between 07:30 and 13:30 h. We collected 20 dark *S. undulatus* and 19 dark *A. inornata* from a blue-gramma grassland and yucca–mesquite scrubland at Jornada Long-term Ecological Research Station, Doña Ana County. We collected 15 dark *H. maculata* from a similarly vegetated Bureau of Land Management site north-east of the White Sands Missile Range, Otero County. We collected 15 white *H. maculata*, 18 white *S. undulatus*, and 18 white *A. inornata* from the White Sands National Monument, Otero County. We alternated collecting efforts between dark soils and White Sands sites to control for possible seasonal changes. Because we were not comparing ecomorphology among the species, we tested one species at a time, each within the span of up to 2 weeks. We used only adult male lizards, which we collected by hand or with pole and slipknot noose, with the exception of two dark *A. inornata* we obtained from pitfall traps. We performed trials the day following capture after all lizards were housed in

controlled temperature and light conditions overnight. We returned all lizards to the capture site the day following the trials. Because soil density affects the speed of sprinting animals (Ding *et al.*, 2011), we measured soil compaction at dark soils and white sands sites using a pocket penetrometer (Korff & McHenry, 2011). The results from 20 random compaction measurements at each site demonstrated that soil compaction did not differ significantly between dark soils and white sands (Wilcoxon rank sum test: $Z = 1.82$, $P = 0.07$ from 100 000 random permutations of the data); however, there was a trend toward white sand having lower compaction.

MORPHOLOGY

We measured the following morphological characteristics for each lizard: body weight (using a Pesola spring scale), snout–vent length (SVL), interlimb length (from posterior insertion of forelimb and anterior insertion of hindlimb), pelvic width, fore and hindlimb length (from shoulder to tip of longest toe), rear toe length (from heel to tip of longest toe), and tail length (only individuals with intact tails were included) using a clear plastic ruler, and pelvic width using handheld calipers. We first compared morphological traits unadjusted for allometric differences in SVL between dark and white morphs using Welch's *t*-tests. We then compared traits between morphs controlling for the effect of SVL by performing analyses of covariance (ANCOVAs) on the trait of interest against SVL, colour morph, and the interaction between SVL and colour morph. In all cases, measurements were ln-transformed prior to analysis. We performed all statistical tests in R (R Development Core Team, 2012).

ESCAPE BEHAVIOUR

To test escape response behaviour of the two colour morphs on different substrates, we constructed an outdoor racetrack on the edge of the dune fields of White Sands National Monument. Racetracks are frequently used to measure escape behaviour and performance of lizards (Bauwens *et al.*, 1995; Robson & Miles, 2000; Vanhooydonck & Van Damme, 2001) and other vertebrates (e.g. Huey *et al.*, 1981; Llewellyn *et al.*, 2010) because ecological variables (such as substrate) can be manipulated, animals can be confined, and conditions can be made similar to the natural environment. The racetrack, which we made from 47-cm aluminium flashing, consisted of two side-by-side sections, each approximately 0.3 m wide by 2 m long. We dug the track into the ground and lined it with plastic sheeting to prevent intermixing of the treatment substrate with the local substrate. One

section contained dark soils and one contained white gypsum sand (approximately 15 cm deep) collected from dark soil and White Sands sites, respectively. We ran trials on the day following capture between 08:30 and 12:00 h when ambient temperatures were 30–35 °C. We tested lizards on each substrate, alternating which they performed on first. Individuals had an interval of at least 30 min between trials, during which time we kept them at constant temperature in plastic cages in indirect sunlight. Before each trial, we recorded each individual's internal body temperature using a cloacal probe to ensure they were within their normal active temperature range. The active body temperature ranges of for our focal species are: *H. maculata*, 30–39 °C (Dixon, 1967; Sena, 1978; Hager, 2000); *S. undulatus*, 30–40 °C (Crowley, 1985; Pinch & Claussen, 2003); *A. inornata*, 37–39 °C (Medica, 1967; Schall, 1977).

For each trial, we induced a single lizard to run from one end of the racetrack starting from standstill. Because sudden movements initiated by a human observer can elicit a startle response in reptiles (Cooper, Hawlena & Perez-Mellado, 2009), we rapidly moved a feather duster behind each lizard to simulate a predator. We recorded all trials using a Canon VIXIA HFR10 HD video camera mounted perpendicularly on a tripod over the racetrack. We later determined startle response from the video recordings. We defined startle response as the initial behaviour within the first 3 s of the duster first coming in to view of the camera. Although some studies use a simple dichotomous categorization of response (e.g. flee or fail, Fuiman & Cowan, 2003), others categorize a variety of responses relevant to natural escape behaviour in the field (Bauwens & Thoen, 1981). Still others account for differences between fleeing towards or away from a refuge, or remaining immobile (Amo, Lopez & Martin, 2003). For each lizard, we categorized startle response as one of the following: fail (did not move), intermediate (moved slowly or in bursts), or sprint (sprinted immediately, in any direction). We used chi-squared tests to determine whether dark and white morphs differed in startle response on dark soil and white sand substrate.

SPRINT SPEED

After recording initial startle response, we measured lizard sprint speed using the same experimental set-up described above. However, we excluded failed individuals from analysis of sprint speed only if they did not generate useable sprint data, which decreased our sample size for *H. maculata* and *S. undulatus*. We placed measuring tape in the track so that at least 1.5 m was visible in the viewfinder and videotaped all

trials at 30 frames s⁻¹. For each trial, we startled the lizard with the duster at one end of the track until it ran the full length at least five times or tired, a standard procedure for small reptiles (Huey *et al.*, 1981; van Berkum, 1986; Losos, 1990). Because some lizards only sprinted once, we used only the first full sprint over approximately 80 cm. We used ProAnalyst software to compute maximum sprint speed, which we calculated as the furthest distance covered over a specified time interval of two frames, or 0.06 s (e.g. Martin & Avery, 1998). Our procedure is comparable to methods using spaced photocells to record sprint speed, which measure the shortest time interval taken by an individual to move across a certain distance (Losos, 1990; Kohlsdorf *et al.*, 2004). We calibrated the program with the centre-most 10 cm of the measuring tape in the racetrack. We then manually tracked the tip of each individual's nose through the field of view, which generated movement data across an *x-y* field. We calculated the resulting speed by dividing the distance between two (*x,y*) coordinates over two frames by the elapsed time (= 0.06 s). The maximum sprint speed for each individual was the largest displacement within two frames (see Martin & Avery, 1998). To determine whether lizards performed better on 'matched substrate' (i.e. white morphs on white sand, dark morphs on dark soil), we used two-way analyses of variance (ANOVAs) to test for the effects of colour morph and/or substrate on sprint speed.

Finally, for each species, we evaluated the effects of morphology and response behaviour on sprint performance of the two colour morphs on the two substrates. First, we used general linear models to test the effects of morphology on sprint speed, including colour morph and substrate as fixed effects. Here, we only tested morphological variables that were significantly different between colour morphs after controlling for SVL. Second, we tested the effects of startle response on sprint speed including colour morph and substrate as fixed effects. Because body temperature can strongly affect sprint speed (Pinch & Claussen, 2003), and we used the same individuals for trials on both substrates, we ran all linear models including body temperature as a covariate and individual as a random effect. However, because neither of these variables significantly influenced the outcomes of our models, we have presented our results without these variables.

RESULTS

MORPHOLOGY

Overall, we found that white morphs were significantly larger in two of the three species (*H. maculata*

and *A. inornata*). Once adjusting for SVL, some morphological traits remained significantly different. Specifically, dark *S. undulatus* had longer rear toes and forelimbs, and white *A. inornata* had longer rear toes and hindlimbs. We outline these results separately for each species below.

Either body size, shape, or both differed between colour morphs for each species. White *H. maculata* morphs were significantly larger than dark morphs in terms of both SVL and weight. White morphs also had longer hindlimbs, and larger pelvic width, but were not significantly different from dark morphs in forelimb, interlimb, and rear toe length. Hindlimb length and pelvic width scaled with size, and were no longer significantly different between colour morphs when we controlled for SVL in the model. Forelimb, rear toe, and interlimb length all scaled with SVL but did not differ between colour morphs. Finally, dark morphs had longer tails than white morphs, even when controlled for SVL (all results presented in Table 1).

Dark and white *S. undulatus* were not significantly different in size in terms of either SVL or weight. Dark morphs had longer hindlimbs and rear toes but were not significantly different from white morphs in forelimb length, interlimb length, and pelvic width. Hindlimb, rear toe, and forelimb length correlated with SVL, and were still significantly longer in dark morphs when we controlled for SVL. Interlimb length and pelvic width also correlated with SVL, but remained non-significant after controlling for SVL. As with *H. maculata*, dark morphs had longer tails when controlled for SVL; however, in this species tail length did correlate with body size (Table 1).

White *A. inornata* were significantly larger than dark *A. inornata* in both SVL and weight. They also had longer hindlimbs, rear toes, and forelimbs, and larger interlimb length and pelvic width. Forelimb, interlimb length, and pelvic width scaled with body size and did not remain significantly different between morphs when we corrected for SVL. Although hindlimb and rear toe were significantly correlated with SVL, they were still significantly larger in white morphs when we controlled for SVL. Tail length was not significantly different between colour morphs of *A. inornata* from the two habitats and was not correlated with SVL (Table 1).

ESCAPE BEHAVIOUR

Startle response to a simulated predator varied depending on species, substrate, and colour morph. On dark soil substrate, sprint was the most common response for all lizards, regardless of species, and did not differ significantly between colour morphs (Fig. 1; chi-squared test: *H. maculata*: $\chi^2_2 = 5.45$, $P > 0.05$; *S. undulatus*: $\chi^2_2 = 0.034$, $P > 0.05$; *A.*

inornata: $\chi^2_1 = 0.47$, $P > 0.05$). On white sand substrate, however, startle response varied depending on species and colour morph. For *A. inornata*, dark and white morphs did not differ significantly in startle response, with nearly all individuals sprinting immediately after being stimulated (Fig. 1F; $\chi^2_1 = 1.34$, $P > 0.05$). However, for both *H. maculata* and *S. undulatus*, colour morphs exhibited significantly different startle responses (Fig. 1; *H. maculata*: $\chi^2_2 = 7.25$, $P = 0.03$; *S. undulatus*: $\chi^2_2 = 8.07$, $P = 0.02$). Specifically, on white sand substrate nearly 50% of dark morphs of *H. maculata* and *S. undulatus* failed to move from their starting position. The tendency for dark morphs to remain immobile on white sand substrate was particularly notable because the same individuals would respond by sprinting when tested on dark soil substrate. In some cases, these failed dark morphs eventually sprinted on white sand substrate and we were able to record their maximum speed.

SPRINT SPEED

For all three species, maximum sprint speed was significantly correlated with substrate and colour morph. In general, lizards sprinted faster on dark soil substrate (Fig. 2; two-way ANOVA: *H. maculata*: $F_{1,51} = 15.17$, $P > 0.001$; *S. undulatus*: $F_{1,57} = 6.87$, $P = 0.01$; *A. inornata*: $F_{1,70} = 4.19$, $P = 0.04$). Colour morph also influenced sprint performance. Both white *H. maculata* and *A. inornata* sprinted faster than their dark counterparts (Fig. 2A, C; *H. maculata*: $F_{1,51} = 4.11$, $P = 0.047$; *A. inornata*: $F_{1,70} = 7.57$, $P = 0.008$). In *H. maculata*, this effect was driven mainly by superior performance on white sand substrate (Fig. 2A). On the other hand, dark *S. undulatus* sprinted faster than white individuals, especially on dark soil substrate (Fig. 2B; $F_{1,57} = 4.28$, $P = 0.04$). In all cases, there were no significant interactions between substrate and colour morph (all $P > 0.05$).

We found no evidence that morphological differences between colour morphs influenced sprint speed in any species when our models included colour morph and substrate. In *H. maculata*, only SVL differed between morphs (see above) but there was no significant relationship between SVL and sprint speed (general linear model: SVL effect: $F_{1,47} = 0.61$, $P > 0.05$; substrate effect: $F_{1,47} = 14.95$, $P < 0.001$; morph effect: $F_{1,47} = 4.74$, $P = 0.03$; all interactions: $P > 0.05$). In *S. undulatus*, hindlimb, rear toe, and forelimb differed between colour morphs but did not affect sprint speed (morphological characters' effect: $F_{3,45} = 1.26$, $P > 0.05$; substrate effect: $F_{1,58} = 7.78$, $P < 0.01$; morph effect: $F_{1,58} = 0.82$, $P > 0.05$; all interactions: $P > 0.05$). Likewise, in *A. inornata*, SVL,

Table 1. Differences in morphological traits between lizards from White Sands and dark soils sites both not controlled (raw measurements, using Welch's *t*-test) and controlled (using ANCOVA) for snout-vent length (SVL)

Species	Morphological trait	<i>t</i> -test		ANCOVA					
		Raw measurement		SVL effect		Variable effect		Interaction effect	
		<i>t</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Holbrookia maculata</i>	SVL	-3.5	0.001	n/a	n/a	n/a	n/a	n/a	n/a
	Weight	-2.8	0.008	92.3	<0.0001	0.0003	1.0	0.09	0.8
	Forelimb length	-1.8	0.08	55.1	<0.0001	1.6	0.2	0.08	0.8
	Hindlimb length	-2.0	0.05	46.6	<0.0001	0.3	0.6	0.0001	0.10
	Rear toe	-0.5	0.6	11.1	0.002	1.2	0.3	0.1	0.7
	Pelvic width	-3.9	0.001	92.5	<0.0001	1.2	0.3	3.4	0.07
	Interlimb length	-1.3	0.2	16.0	<0.0001	0.4	0.5	0.05	0.8
	Tail length	3.0	0.007	1.5	0.2	11.2	0.002	0.002	1.0
<i>Sceloporus undulatus</i>	SVL	-0.11	0.9	n/a	n/a	n/a	n/a	n/a	n/a
	Weight	1.1	0.3	185.8	<0.0001	8.7	0.006	6.5	0.02
	Forelimb length	1.4	0.2	43.6	<0.0001	4.6	0.04	1.2	0.3
	Hindlimb length	2.6	0.02	51.0	<0.0001	16.8	<0.001	5.3	0.03
	Rear toe	3.2	0.002	6.0	0.02	12.7	0.001	2.4	0.1
	Pelvic width	0.7	0.5	37.9	<0.0001	1.1	0.3	1.2	0.3
	Interlimb length	-0.5	0.6	52.8	<0.0001	0.4	0.5	0.1	0.7
	Tail length	1.9	0.07	11.5	0.003	5.5	0.03	0.9	0.4
<i>Aspidoscelis inornata</i>	SVL	-4.6	<0.001	n/a	n/a	n/a	n/a	n/a	n/a
	Weight	-7.1	<0.001	65.7	<0.0001	20.4	<0.0001	0.02	0.9
	Forelimb length	-3.2	0.003	25.0	<0.0001	0.06	0.8	0.08	0.7
	Hindlimb length	-6.7	<0.0001	26.2	<0.0001	15.7	0.0004	2.4	0.1
	Rear toe	-8.3	<0.0001	14.9	0.0005	31.9	<0.0001	3.1	0.09
	Pelvic width	-4.8	<0.0001	76.2	<0.0001	1.8	0.2	1.1	0.3
	Interlimb length	-4.9	<0.0001	44.8	<0.0001	2.9	0.09	1.3	0.3
	Tail length	-1.4	0.4	1.2	0.3	0.3	0.6	n/a	n/a

All measurements were natural log transformed. Negative test statistics denote the trait of interest was larger in White Sands morphs. Two-way interactions for *Aspidoscelis inornata* tail length could not be calculated as several lizards lacking tails were excluded from the analysis.

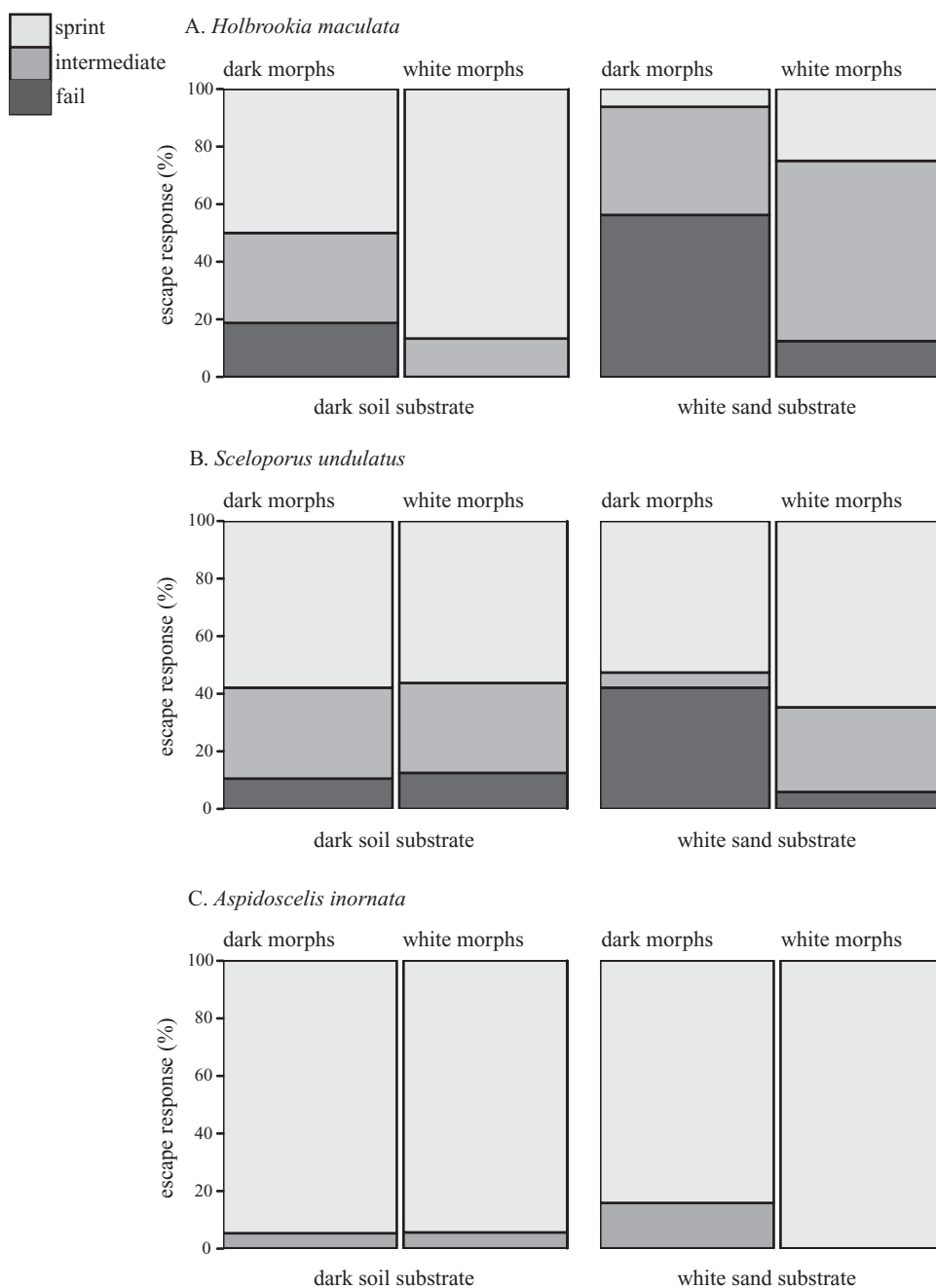


Figure 1. Differences in startle response for three species presented with a simulated predator: A, *Holbrookia maculata*; B, *Sceloporus undulatus*; C, *Aspidoscelis inornata* on dark soil (left) and white sand (right) substrate. Within each panel, response of dark and white morphs are shown on the left and right, respectively.

hindlimb, and rear toe length differed between colour morphs, but had no effect on sprint speed (morphological characters' effect: $F_{3,58} = 0.31$, $P > 0.05$; substrate effect: $F_{1,58} = 4.67$, $P = 0.03$; morph effect: $F_{1,58} = 2.02$, $P > 0.05$; all interactions: $P > 0.05$).

Sprint speed was significantly influenced by startle response in *S. undulatus* and *A. inornata*, but not in *H. maculata*. In the first two species, startle response

affected speed but did not interact with colour morph or substrate (Table 2, *S. undulatus*, response effect: $F_{2,49} = 15.1$, $P < 0.0001$; *A. inornata*, response effect: $F_{1,67} = 4.50$, $P = 0.04$, all interactions: $P > 0.05$). In both *S. undulatus* and *A. inornata*, individuals that exhibited the response sprint achieved a greater sprint speed than those categorized as either intermediate or fail (which did not significantly differ

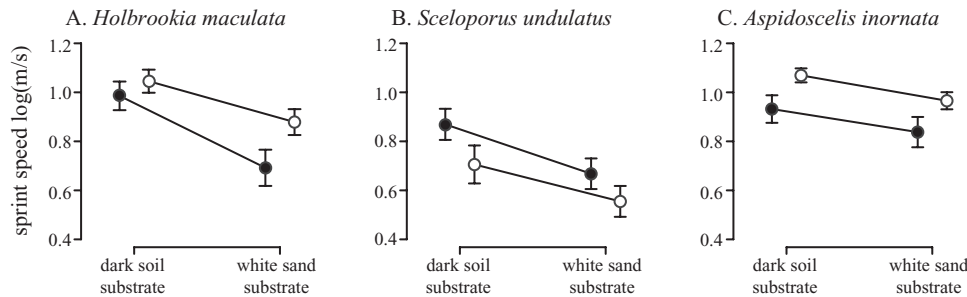


Figure 2. Average maximum sprint speed for three species: A, *Holbrookia maculata*; B, *Sceloporus undulatus*; C, *Aspidoscelis inornata* on dark soil (left) and white sand substrate (right). Within each panel, dark and white circles represent average sprint speed for dark and white morphs, respectively. Points are connected to illustrate the parallel trend for all species to sprint faster on dark soil substrate. Error bars represent standard error of the mean.

Table 2. The effects of morphology and escape behaviour on sprint performance for dark and white colour morphs of three species on dark soil and white sand substrates

Species	Test used	Substrate effect	Colour morph effect	Morphology effect†	Behaviour effect
<i>Holbrookia maculata</i>	Two-way	15.17***	4.11*	NA	NA
<i>Sceloporus undulatus</i>	ANOVA	6.87*	4.28*	NA	NA
<i>Aspidoscelis inornata</i>		4.19*	7.57**	NA	NA
<i>Holbrookia maculata</i>	ANCOVA	14.10***	4.74*	0.063	NA
<i>Sceloporus undulatus</i>		7.78**	0.82	1.26	NA
<i>Aspidoscelis inornata</i>		4.67*	2.02*	0.31	NA
<i>Holbrookia maculata</i>	Three-way	7.88**	1.90	NA	1.28
<i>Sceloporus undulatus</i>	ANOVA	11.83**	5.89*	NA	15.10***
<i>Aspidoscelis inornata</i>		2.98	4.91*	NA	4.50*

The results of a two-way ANOVA describe the combined effects of substrate and colour morph on sprint speed. The results of an ANCOVA and three-way ANOVA show the effects of morphology and startle response, respectively, on this relationship. †Only morphological characteristics that differed between white and dark morphs were tested: SVL for *Holbrookia maculata*; forelimb, hindlimb, and longest toe for *Sceloporus undulatus*; SVL, hindlimb, and longest toe for *Aspidoscelis inornata*.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

from one another). In *H. maculata*, however, startle response did not significantly affect the relationship among sprint speed, colour morph, and substrate (three-way ANOVA: response effect: $F_{2,44} = 1.28$, $P > 0.05$; all interactions: $P > 0.05$). Within each species, initial body temperature did not vary greatly. Furthermore, in all cases where we included initial body temperature as a covariate, it did not significantly affect sprint speed.

DISCUSSION

The parallel phenotypic evolution of the White Sands lizard species provides an opportunity to study comparative ecomorphology during rapid adaptation. Our current and previous work (Rosenblum & Harmon, 2011) demonstrate divergence in body size and shape

between dark and white lizard morphs inhabiting the dark brown quartz soil desert and gypsum White Sands dunes, respectively. However, we found no evidence of these morphological differences affecting sprint performance on dark soil and white sand substrates in an experimental context. Instead, we found that behavioural differences had important consequences on performance. Specifically, startle response to a simulated predator differed between dark and white morphs on different substrates and was predictive of maximum sprint speed in two species. Our results underline the link between behaviour and performance post-colonization of novel habitats.

MORPHOLOGY

The most notable difference in morphology between dark and white lizards was in body size of

H. maculata and *A. inornata*. In both species, white morphs were significantly larger in SVL and body weight. Most other traits (limb length, pelvic width, interlimb length) scaled allometrically with body size, and thus were larger in white morphs. Differences between the morphology of colour morphs may be a result of drift in small isolated populations, phenotypic plasticity, or natural selection on heritable traits, as discussed below.

Phenotypically plastic responses to ecological, physiological, or life-history pressures may explain differences in morphology between morphs. First, because size is indeterminate in these species, white lizards may be larger because they are older (Shine & Charnov, 1991). Specifically, reduced predation in White Sands (Des Roches *et al.*, 2011; Robertson *et al.*, 2011) may allow lizards to live longer (e.g. Sebens, 1987). Second, higher resource availability could promote faster development (Stamps, Mangel & Phillips, 1998) and lower interspecific competition at White Sands (Des Roches *et al.*, 2011; Robertson *et al.*, 2011). Increased body size resulting from competitive release has been shown for the brown anole, *Anolis sagrei*; individuals in areas of higher resource availability and lower species richness grow faster and are larger than those from adjacent resource-poor areas (Schoener & Schoener, 1978).

Morphological differences between morphs could also be due to natural selection, given the dramatic differences between dark soils and White Sands habitats. For example, some trait differences between morphs remained significant even after correcting for body size. It is possible that such traits have adaptive significance if they are heritable. For *S. undulatus*, white morphs had shorter forelimbs and hindlimbs, and longest rear toes. Natural selection for shorter limbs in white *S. undulatus* may follow from our observation that this species uses a wider variety of perches at White Sands (Des Roches *et al.*, 2011). In studies of both *Anolis* and *Sceloporus* species, reduced limb size allows for increased 'surefootedness' on an increased variety of perches (Losos & Sinervo, 1989; Sinervo & Losos, 1991). Conversely, we observed longer hindlimbs and longest rear toes of white *A. inornata*. We expect this difference is correlated with different ecological strategies in the two species (i.e. shorter limbs for surefootedness in the arboreal *S. undulatus* and longer limbs for speed in the terrestrial *A. inornata*). However, our data do not provide evidence that longer limbs in *A. inornata* correlated with faster speed in either habitat (see discussion below). Finally, white morphs of both *H. maculata* and *S. undulatus* had shorter tails, irrespective of body size. Various studies have shown that tail length affects locomotion; for example, better climbers often have longer tails (Jaksic *et al.*, 1980)

and better sprinters often have shorter tails (Li *et al.*, 2011). Yet, the relationship between locomotion and tail length is not as well established as it is with other morphological traits (Buckley, Irschick & Adolph, 2010). Some researchers have argued that tail length is more variable and easily affected by external influences, such as temperature (Buckley *et al.*, 2010). In both *Sceloporus* (Buckley *et al.*, 2010) and *Lampropholis* (Qualls & Shine, 1998), individuals incubated at higher temperatures had shorter tails, and a larger body size. Interestingly, this is similar to the trend we observed in our study, where lizards from the cooler White Sands habitat were also more likely to be larger with shorter tails (see Hager, 2000). More research is needed to discern whether morphological shifts at White Sands are due to heritable change and how they affect performance and fitness.

Our study focused on paired comparisons between one White Sands and one dark soil population for each species. Differences among studies in which specific dark soil populations were sampled may explain the minor discrepancies between our study and previous morphological comparisons that pooled samples from different localities by habitat type (Rosenblum & Harmon, 2011). Future work with broad sampling across many dark soil sites will provide a more general understanding of morphological variation at this spatial scale.

STARTLE RESPONSE

The most unexpected result of our study was the variation of startle response between dark and white morphs. Specifically, we found that many dark *H. maculata* and *S. undulatus* sprinted on dark soil substrate but failed to sprint on white sand substrate where they were mismatched. Our result is surprising because substrate-matched species such as sculpin (Houtman & Dill, 1994) and sit-and-wait lizard foragers (including *H. maculata* and *S. undulatus*) commonly adopt an immobile strategy to enhance crypsis when faced with a predator (Huey & Pianka, 1981). Other species such as the yellow-legged frog (*Rana muscosa*) will exhibit more alert behaviour when they are mismatched, and quickly escape to cover when threatened, (Norris & Lowe, 1964). In our study, lizards that stood out against the white sand background remained motionless when stimulated. Surprisingly, the same individuals would sprint immediately when startled on dark soil substrate, as would white individuals on white sand substrate. It is possible that physical differences between dark soil and white sand substrates influence escape response. For example, gypsum has a lower thermal capacity (Weast, 1986). Another intriguing possibility

is that the observed differences in startle responses reflect a change in sensory perception in White Sands due to the higher reflectivity of gypsum. Geckos (*Sphaerodactylus macrolepis*) from populations inhabiting dark habitats better detect motion in dimmer light, whereas those from light habitats perform better in brighter light (Nava, Conway & Martins, 2009). Similarly, differences in light conditions between White Sands and dark soil habitats, for example the higher reflectivity (Wheeler *et al.*, 1994) of the former, may have led to evolved differences in visual acuity in the lizard species. Regardless of the specific mechanism underlying the response differences, failure of mismatched lizards to sprint could be maladaptive when faced with a predator. These behavioural shifts may have played an important role during adaptation to the new White Sands environment. Indeed, appropriate startle response behaviour may have been a crucial adaptation preceding morphological adaptation. Further work is needed to determine the relevance of this response in a natural setting and whether it represents an actual genetic change under selection.

SPRINT SPEED

Our prediction that sprint speed would be different on white sand and dark soil substrates was met. In general, for all species and both colour morphs, performance was better on dark soil substrate. Our results were not surprising considering that other studies have shown a relationship between sprint performance and substrate type (Kohlsdorf *et al.*, 2004; Ding *et al.*, 2011). Our test of soil compaction demonstrated a trend towards looser soil at White Sands, which has also been shown in other studies (Hager, 2001). The limbs of a running lizard sink deeper into loose substrate, such as sand. The larger the foot surface area, the less penetration and more propulsive force (Ding *et al.*, 2011). Thus, evolution of longer feet or toes is a common adaptation for sprinting in sandy habitats (Melville & Swain, 2000; Kohlsdorf, Garland & Navas, 2001; Ding *et al.*, 2011). However, even lizards that are loose sand specialists, such as the Zebra-tailed lizard (*Callisaurus draconoides*), still sprint faster on harder ground (Ding *et al.*, 2011).

Our data also supported our prediction that the two colour morphs would show differences in sprint speed. However, the patterns we observed were not parallel across species. In the two more 'terrestrial' species (rarely observed on vegetation), *H. maculata* and *A. inornata*, white morphs sprinted faster than their dark counterparts. For *H. maculata*, this effect was driven mostly by white morphs being faster than dark morphs on white sand substrate. For *A. inornata*,

white morphs were faster than dark morphs on both substrate types. In the more arboreal species, *S. undulatus*, dark morphs were faster sprinters, but only significantly so on dark soil substrate. Although there are alternative, non-adaptive mechanisms (e.g. phenotypic plasticity or genetic drift) for increased sprint speed in the more terrestrial White Sands species, one possibility is that natural selection for faster sprint speed has been stronger in *H. maculata* and *A. inornata* because they spend more time foraging and basking on the exposed substrate than does *S. undulatus* (Medica, 1967; Hager, 2001).

Our results did not provide evidence for a relationship between sprint speed and morphology. Research in other systems has shown that morphological adaptation in lizards is often related to performance in specific habitats (Losos, 1990; Bonine & Garland, 1999; Melville & Swain, 2000; Kohlsdorf *et al.*, 2001; Goodman, 2009), yet morphological change does not always accompany ecological divergence (Jaksic *et al.*, 1980; Vanhooydonck & Van Damme, 1999). For example, in our study, white *H. maculata* and *A. inornata* were faster sprinters, but greater speed was not associated with their larger body size or longer limbs. If morphology is related to performance at White Sands, there are several reasons why we may not have uncovered this link. It is possible that morphological variation is related to a performance trait that we did not measure, for example endurance (e.g. for anoles, Calsbeek & Irschick, 2007). It is also possible that we may have lacked power to detect subtle effects of morphological variation on sprint speed (considering the reduced sample size after we removed failed individuals). Finally, differences in running kinematics, such as stride length, speed (Irschick & Jayne, 1999), and muscle physiology (Garland *et al.*, 1995) may explain the subtler relationship between morphology and sprint performance. Further research using a larger sample size of lizards induced to run longer distances, and including direct measurement of kinematics and muscle physiology may elucidate the less apparent effects of morphology on performance.

Although we had no evidence that sprint speed was correlated with morphology, sprint speed was predicted by initial startle response. In both *S. undulatus* and *A. inornata*, individuals that failed or walked initially were slower sprinters. In these species, individuals that exhibited the response sprint achieved a greater speed. However, startle response did not significantly influence sprint speed in *H. maculata*, perhaps due to low statistical power after removing failed individuals. As discussed above, lizards can adopt alternative anti-predator strategies such as crypsis or sprinting (for a comparison of these strategies see Schwarzkopf & Shine, 1992). Studies of

other species including the keeled earless lizard (*Holbrookia propinqua*) and the water skink (*Eulamprus typanum*) demonstrate that individuals avoid sprinting (Cooper, 2003) and adopt crypsis (Schwarzkopf & Shine, 1992) as an anti-predator tactic when their running is impeded (i.e. they have lost tails or are gravid). Although the lizards in our study did not have such extreme morphological impediments, running may be more difficult on white sand substrate and thus lead to shifts in anti-predator tactics. Future work in the White Sands system will be needed to understand the link between initial escape tactic and running performance in both experimental and natural contexts.

Interactions among morphology, behaviour, and performance have been studied in a diversity of animals, including insects (e.g. Betz, 2002), fish (e.g. Huber *et al.*, 1997), mammals (e.g. Aguirre *et al.*, 2002), and lizards (e.g. Vanhooydonck & Van Damme, 2001; Schulte *et al.*, 2004a; Irschick *et al.*, 2005). The White Sands system, colonized recently and independently by three lizard species, provides an opportunity to study these ecomorphological interactions in a comparative framework. Our results underline the relationship between behaviour and performance across the White Sands ecotone, while de-emphasizing the importance of morphological differences post-colonization of a new habitat. More generally, the results of our study underline the importance of future research that integrates analysis of adaptive morphology, behaviour, and performance in the study of organisms invading and persisting in new habitats.

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