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Ecological release and directional change in White Sands lizard trophic ecomorphology

S. Des Roches · M. S. Brinkmeyer · L. J. Harmon · E. B. Rosenblum

Abstract A species' trophic ecomorphology can change drastically following the colonization of a new environment. Resource shifts may result in dietary change of colonists and therefore, the evolution of ecomorphological adaptations such as changes in bite force, head, and body size. To understand the drivers and dynamics of ecomorphological change after colonization we studied prey availability, diet, performance, and morphology in three lizard species (*Aspidoscelis inornata*, *Holbrookia maculata*, and *Sceloporus cowlesi*) in the ecologically distinct environment of White Sands, New Mexico. White Sands, which formed within the last 6,000 years, was most likely colonized by nearby "dark soils" populations. Therefore, for each species we compared White Sands individuals to conspecific inhabiting the surrounding Chihuahuan Desert habitat. The White Sands habitat had higher prey morphospecies richness, increased breadth of prey orders, and a higher percentage of hard-bodied prey than the dark soils habitat. Differences in prey availability in White Sands and dark soils habitats were reflected in lizard diets. Specifically, morphospecies richness and percentage of hard bodied prey were higher in the diet of White Sands lizards compared to dark soils lizards. These similarities in resource use across the three species in two habitats indicated parallel responses to a shared environment. Although some dietary shifts in the three species were predictable and reflected prey availability, differences in performance and morphology traits indicated different ecological responses in each species. In general, average prey hardness was higher in the two White Sands species that had stronger absolute bite force and larger absolute head size. While White Sands lizards generally also included a larger proportion of hard prey in their diets, had higher absolute bite-force, head size, and body size than dark soils lizards, the magnitude of these differences varied across species.

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Introduction

Colonization of novel ecosystems can provide a rare glimpse into patterns of rapid ecological and evolutionary change in new environments. When multiple colonist species encounter a novel, shared environment, how they interact with their new surroundings may be as variable as the species themselves. Colonists' ecomorphology—the interactions among morphology, performance, and the environment (Galis 1996; Irschick 2002)—may determine whether they survive, persist, and adapt to their new ecosystems. If colonists persist, phenotypic plasticity and natural selection may result in ecomorphological change. The direction and magnitude of this change will depend on factors including resource availability and presence of other species.

Both the ecological and evolutionary history of colonists will influence their likelihood of effectively exploiting resources and surviving in a new environment (Simberloff 1978; Parsons 1982; Lodge 1993; Reznick and Ghalambor 2001). Directional selection can lead to the evolution of different mean trait values that optimize fitness in the new resource environment (see Thompson 1998). Alternatively, lack of antagonist species (competitors and predators) and thus the availability of additional resources in a novel environment may result in reduced selective pressures and thus ecological release (Losos and De Queiroz 1997; Yoder et al. 2010). Ecological release is likely to allow increased variation of resources used, which may or may not translate into an evolutionary increase in the variance of trait values (Lister 1976a, b; Bolnick et al. 2007). Finally, phenotypic plasticity of traits (e.g. Aubret et al. 2007; Irschick and Meyers 2007; Aubret and Shine 2009) related to resource acquisition may result in very little evolutionary change in the ecomorphology of colonist species.

Natural selection on morphological and performance traits that influence diet can determine how colonists interact with a new resource base. Performance traits, such as bite force, provide a link between morphological traits—like head shape—and fitness (Arnold 1983; Galis 1996; Calsbeek and Irschick 2007; Irschick et al. 2008). In some cases, selection acts directly on trophic morphology as a result of dietary change of colonists (e.g. Schluter and Grant 1984; McPhail 1993; Herrel et al. 2008). In lizards for example, individuals with larger heads have a more powerful bite and take less time to handle hard-bodied prey items like beetles and ants (Herrel et al. 1999, 2001; Verwaijen et al. 2002; Kaliontzopoulou et al. 2012; Sales et al. 2012). Although large-headed individuals may be able to incorporate bigger and harder prey in their diet (Herrel et al. 1999, 2001; Verwaijen et al. 2002), they may experience trade-offs in prey capture velocity (Herrel et al. 1999). In other cases, selection acts indirectly on trophic morphology. For example, head size often scales allometrically with body size (e.g. Meyers et al. 2002; Herrel and O'Reilly 2006), which itself can be under selection (Calsbeek and Smith 2007). Furthermore, head size and bite force can be influenced by sexual selection. For example, increases in intra-specific competition between males for mates may select for larger head size and stronger bite force (Lappin and Husak 2005; Husak et al. 2006). Finally, ecomorphological change that occurs as a result of phenotypic plasticity may be similar to that brought about by natural selection (Irschick and Meyers 2007). Even when changes in head size and bite force are due to sexual selection or plasticity, they can still influence prey acquisition and thus diet.

Here, we focus our attention on three lizard species that coexist in the unique gypsum dune field of White Sands, New Mexico (Rosenblum 2006). The three species, *Aspidoscelis inornata* (the Little Striped Whiptail), *Holbrookia maculata* (the Lesser Earless lizard), and *Sceloporus cowlesi* (the Southwestern Fence Lizard, formerly *S. undulatus*, Wiens et al. 2010) are the most abundant reptile species inhabiting the sparsely vegetated dunes. These three species have broad distributions across the Chihuahuan desert and are only distantly related to each other. In the 6,000 years since the White Sands dunes formed (Kocurek et al. 2007), the three species have established dense local populations (Des Roches et al. 2011). The most striking convergently evolved adaptive trait exhibited by all three species at White Sands is cryptic blanched colouration. However, previous research has demonstrated differences in behaviour (Robertson et al. 2011), performance (Des Roches et al. 2014), habitat use (Des Roches et al. 2011), body shape and size (Rosenblum and Harmon 2011) between White Sands lizards and their conspecifics in the surrounding Chihuahuan scrubland. The differences in body size and shape between White Sands and dark soils lizards suggest that morphological shifts could be related to differences in resource availability and resource use in this novel environment. Although diet has been previously quantified in White Sands lizards (Dixon and Medica 1966), it has never been compared to that of dark soils lizards.

We examined differences in trophic ecomorphology for the three lizard colonist species of White Sands compared to their dark soils counterparts. Because differences in resource availability between dark soils and White Sands habitats may have caused ecomorphological divergence, we began by first measuring arthropod prey community composition and lizard diet in the two habitats. Specifically, we recorded available arthropod morphospecies richness, niche breadth, and proportion of hard, intermediate, and soft-bodied prey in both dark soils and White Sands habitats. We then recorded these same metrics for the diet of the three species in each habitat. To determine if significant differences in relevant ecomorphological traits exist between lizards from the two different habitats, we then recorded absolute lizard bite force, head size, and body size.

We predicted differences in prey availability between dark soils and White Sands habitats and correlated differences in lizard diet and ecomorphology. We expected several alternative changes in ecomorphological traits, including the possibility that evolution by natural selection did not produce detectable differences between dark soils and White Sands lizards. First, if directional selection led to ecomorphological change at White Sands or if newly available prey are preferred, we expected shifts in diet and in morphological and performance traits towards one extreme (e.g. a higher proportion of harder-bodied prey, stronger absolute bite force and larger absolute head size). Second, if ecological release (i.e. relaxed selection) led to ecomorphological change at White Sands, we expected an expansion in lizard diet to include a greater variety of prey types and potentially a greater variance in ecomorphological traits. Finally, if natural selection did not drive ecomorphological shifts in White Sands lizards, we expected to observe either stochastic change, or a lack of change, in performance and morphological traits relative to resource use. Phenotypic plasticity (Aubret et al. 2007; Irschick and Meyers 2007; Aubret and Shine 2009) could also have contributed to ecomorphological change. Analyzing the relationships among prey availability, diet, performance, and morphology in multiple species in a shared novel environment provides an integrative approach to understanding the dynamics of ecomorphological change after colonization of a new environment.

Materials and methods

Sampling

We collected lizards in New Mexico from White Sands and dark soils habitats from 12 May to 9 July 2010. For each habitat, we had three different collection sites. In White Sands Sites A, B, and C were all located at the White Sands National Monument, Otero County. In Dark Soils, Sites D and E were located at a blue-gramma grassland and yucca-mesquite scrubland at Jornada Long-term Ecological Research Station, Doña Ana County, and Site F was located at a similarly vegetated Bureau of Land Management site northeast of the White Sands Missile Range, Otero County. In White Sands, we collected 18 white *A. inornata* from Site A and B, 15 white *H. maculata* at Sites A and B, and 18 white *S. cowlesi* from Sites B and C. We collected 19 dark *A. inornata* from Site D, 20 dark *S. cowlesi* from Site E, and 15 dark *H. maculata* from Site F. We used only adult male lizards to control for variation in developmental stage and sexual dimorphism. We captured all lizards by hand or with pole and slipknot noose, with the exception of two dark *A. inornata* that we obtained from pitfall traps. Because we were more interested in ecomorphological differences between conspecific morphs than differences across species, we conducted trials on one species at a time during a 12–15 day period, alternating between collection at dark soils and White Sands habitats. We returned all lizards to the capture site the day following their capture.

Prey availability and diet

To estimate prey availability, we trapped primarily terrestrial arthropods in all specific locations where we sampled lizards. We placed eight pitfall traps in 1 m intervals along a transect in Sites A through C in White Sands habitats and D through F in dark soils habitats. We dug 50 mL Falcon tubes into the ground and filled them with one part non-toxic anti-freeze (propylene glycol), one part water, and 1–2 mL of biodegradable detergent (to reduce surface tension on the arthropod; see Verwaijen et al. 2002). We collected all traps after leaving them continuously open for 3 days and froze them at −4 °C. We then filtered each pitfall sample with distilled water and excluded very large insects (camel crickets, darkling beetles) that exceed the gape size of our focal species and were therefore too large to be included in the diet (DeMarco et al. 1985). Because we collected each dark soils lizard species from one site only (either D, E, or F), we summarized prey availability data for each dark soils species from eight pitfall traps. In White Sands, however, we collected each species from two sites, thus prey availability data for each species in this habitat was summarized from sixteen pitfall traps.

To obtain samples of lizard diet, we stomach flushed all caught individuals according to standard methods (Legler and Sullivan 1979). We used a flushing instrument consisting of a 75 mm × 16 g curved stainless steel dosing cannula (Harvard Apparatus, Holliston, MA, USA) attached to a 5 mL plastic syringe. We stimulated each lizard to open its jaws, which we propped open with a small plastic ring cut from a Pasteur pipette. While securing the animal in one hand, we slowly inserted the metal cannula through the digestive tract. We flushed the entire stomach contents with tap water (at the lizard's body temperature) and stored stomach contents in ethanol.

We used pitfall and stomach content samples to estimate the arthropod morphospecies richness, niche breadth, and hardness of available prey and lizard diet. To obtain a rough estimate of morphospecies richness, we recorded the number of morphologically distinct

species in each sample. We subsequently dried specimens from each sample in a drying oven for approximately 24 h at 37 °C and weighed them to the nearest 0.001 g. We recorded total stomach content sample weight for each lizard as the summed weights across each order. Finally, we calculated niche breadth as the inverse of Simpson's Diversity Index:

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2}$$

where B is niche breadth, N is the sample size, p is the proportion, and i is the resource category, in this case, arthropod order (Edwards et al. 2013). We then identified arthropods from pitfall traps and stomach contents to order and separated these out for each sample, while grouping all unidentifiable pieces as "unknown". Because the force required to crush prey can limit which arthropods are consumed by lizards (Herrel et al. 2001; Verwaijen et al. 2002; Kaliontzopoulou et al. 2012; Sales et al. 2012), we categorized arthropod orders into three hardness categories following previous studies (Herrel et al. 1999; Aguirre et al. 2003): "hard" (Coleoptera, Hymenoptera, Chilopoda), "intermediate" (Hemiptera, Orthoptera), or "soft" (Diptera, Lepidoptera, Isoptera, Aranae, Thysanoptera, larvae of any order, and other rare orders). Although these methods can underestimate the proportion of soft-bodied prey, which may digest faster in lizard stomachs, we used the same techniques for all species and all morphs thus minimizing any bias. Because hardness may be less important for smaller prey items, we further categorized the length of each prey item in each order by size class: extra-small (<2 mm), small (2–6 mm), medium (6–12 mm), and large (>12 mm). In instances where only a portion of an arthropod remained, we estimated the total length based on previously observed prey items. We approximated maximum and average prey hardness per lizard stomach content using the following equations, which estimate overall prey hardness based on length and hardness category (Herrel et al. 1999; Aguirre et al. 2003):

Hard : $\log_{10}[\text{prey hardness}] = 1.582 * \log_{10}[\text{prey length}] - 1.365$
Intermediate : $\log_{10}[\text{prey hardness}] = 1.780 * \log_{10}[\text{prey length}] - 1.942$
Soft : $\log_{10}[\text{prey hardness}] = 0.997 * \log_{10}[\text{prey length}] - 1.379$

with prey hardness measured in Newtons (N) and prey length in millimeters (mm).

Like many studies that examine lizard prey availability and diet (Verwaijen et al. 2002; Aguirre et al. 2003; Kaliontzopoulou et al. 2012), our results are restricted to a one-time sampling point. Seasonality in prey abundance and yearly variation in prey diversity may influence lizard diet considerably and can also shape the evolution of specialized trophic morphology (Robinson and Wilson 1998). Our experimental design cannot reveal temporal variation in prey availability and lizard diet as drivers of ecomorphological evolution. However, our approach of concurrent sampling over a short window of time allows us to make comparisons among the three species and between the two habitats.

Performance and morphology

We measured lizard bite performance across all three species from the two habitats using a bite force meter (Herrel et al. 1999, 2001, 2006). We maintained the lizards at their optimal activity temperature (*A. inornata*: 37–39 °C, *H. maculata*: 31–34 °C, *S. cowlesi*: 33–36 °C, see Dixon 1967) in a "basking tank" and recorded their body temperature using a cloacal thermometer before measuring bite force. Despite cloacal temperature varying by up to

3 °C within each species, it did not significantly affect our results when habitat and species were included in the model (three-way ANOVA effect of temperature: $F = 0.053$, $P > 0.05$) and was not included in subsequent analyses. We used an isometric Kistler force transducer (type 9203, Kistler Inc.) connected to Kistler charge amplifier (model 463A, PCB Piezotronics Inc., New York, NY, USA) to measure bite force (see Herrel et al. 2001, 2006). We stimulated each lizard to bite down on two metal plates connected to the transducer. While *S. cowlesi* individuals exhibited a typical threat response and opened their mouths to bite without provocation, we had to encourage *A. inornata* and *H. maculata* lizards to open their mouths with a blunted toothpick placed at the edge of their jaw. Once the lizards opened their mouths, they would continuously bite down on the metal plates. For each individual we recorded the maximal value (in Newtons) from five sequential bite force readings.

We measured morphological characteristics for each lizard on the same day as capture, prior to stomach flushing. We measured total body weight (in grams) using a Pesola spring scale and snout-vent-length (SVL), using a clear plastic ruler. We measured three metrics of head shape (in millimetres) using handheld calipers: head depth (highest part of the skull, midway above eye to below jaw), jaw length (tip of snout to behind lower jaw), and head width (at widest point) using handheld calipers. We condensed these three measures of absolute head shape into one metric, "head size," which we calculated as the cube root of the product of head depth, jaw length, and head width (Mosimann 1970; Kaliontzo-poulou et al. 2012). We also calculated bite force and head size adjusted for body size by taking the residuals of a linear regression of the natural log-transformed values of head size on body size.

Statistical analysis

We compared morphospecies richness and niche breadth between habitats (dark soils vs. White Sands) and prey base (availability vs. diet) using two-way ANOVAs. We then used a two-way MANOVA to test the effects of habitat and use on the percentage of hard, intermediate, and soft-bodied arthropod orders consumed. We used Welch's t tests to determine pairwise differences between availability and diet, and between dark soils and White Sands habitats for morphospecies richness, niche breadth, and percentage of hard bodied-prey only. To compare the effect of habitat on the different aspects of diet (mor-phospecies richness, percent hard-bodied prey, and maximum diet hardness) among the three different species, we used two-way ANOVAs. Finally, to examine the effects of habitat on the pairwise differences in mean and variance of diet hardness, performance (bite force), and morphology (head and body size) we used Welch's t test and Levene's test, respectively. To meet assumptions of normality, we natural log transformed all data, except proportions of hard, intermediate, and soft-bodied prey, which we arcsine trans-formed. We performed all analysis in R (R Development Core Team 2013).

Results

Prey availability and diet

All metrics of arthropod availability—morphospecies richness, niche breadth, and per-centage of soft, intermediate, and hard-bodied prey—differed between dark soils and White Sands habitats for both availability and diet. Specifically, arthropod morphospecies

richness and niche breadth were significantly higher in White Sands than in dark soils ($P < 0.01$ for sites where each of the three species were collected; Table 1; Fig. 1). The percentages of hard, intermediate, and soft-bodied prey were also significantly different between White Sands and dark soils habitats for *A. inornata* and *H. maculata* (all $P < 0.05$; Table 1; Fig. 2). However, in sites where *S. cowlesi* was collected, the percentages of hard, intermediate, and soft-bodied prey were only marginally different between habitats ($P = 0.07$; Table 1; Fig. 2).

In both habitats and across all three species, we found differences between prey availability and diet. For percentage of hard, intermediate, and soft-bodied prey, diet was significantly different from availability in each species (all $P < 0.001$; Table 1; Fig. 2). For morphospecies richness, diet differed significantly from availability only for *A. inornata* where morphospecies richness was higher for White Sands individuals ($P < 0.01$; Table 2; Fig. 1). For niche breadth, diet differed significantly from availability only for *H. maculata* where niche breadth was larger in White Sands ($P < 0.01$; Table 2; Fig. 1). We also found interaction effects between habitat (dark soils vs. White Sands) and prey use (available vs. diet) in two of the species. For *A. inornata,* available morphospecies richness was significantly higher than diet morphospecies richness, but the magnitude of this difference was more extreme in dark soils ($P = 0.02$; Table 1; Fig. 1). For *S. cowlesi,* lizards did not differ significantly in diet breadth between habitats overall ($P = 0.01$; Table 1; Fig. 1); however, there was a significant interaction between use and habitat ($P \ll 0.001$; Table 1; Fig. 1) indicating higher available niche breadth in White Sands than dark soils habitat. These particular contrasts are reflected in the pairwise comparisons below.

Pairwise comparisons for morphospecies richness, niche breadth, and percentage of soft, intermediate, and hard-bodied prey revealed similarities and differences between dark soils and White Sands habitats in both availability and diet. Available niche breadth of arthropod orders and percentage of hard-bodied prey were significantly higher at White Sands across all sites (all $P < 0.05$; Table 2; Figs. 1, 2). All White Sands species included higher morphospecies richness in their diets than their dark soils counterparts (all $P < 0.05$; Table 2; Fig. 1). However, niche breadth was only significantly higher in White Sands *H. maculata* ($P = 0.005$; Table 2; Fig. 1), and percentage of hard-bodied prey was significantly higher in White Sands *A. inornata* and *S. cowlesi* (both $P < 0.05$; Table 2; Fig. 2) when compared to their dark soils counterparts. Finally, available morphospecies richness was only significantly higher at White Sands at *H. maculata* sites ($P = 0.01$; Table 2; Fig. 1).

Finally, we found that different diet characteristics varied among the three different species in the two habitats. Specifically, habitat type (dark soils or White Sands) significantly affected diet morphospecies richness ($F_{1,88} = 17.8$, $P \ll 0.001$) and percentage of hard bodied prey ($F_{1,89} = 7.2$, $P = 0.009$), regardless of species. Specifically, both morphospecies richness and percentage of hard bodied prey were both higher in the diet of White Sands lizards (Figs. 1, 2). On the other hand, species but not habitat significantly affected maximum prey hardness ($F_{2,91} = 96.9$, $P = 0.002$). In particular, *S. cowlesi* consumed the hardest prey, followed by *A. inornata*, and then *H. maculata* (Fig. 3). There were no significant interactions between habitat and species on any diet characteristics.

Performance and morphology

Pairwise comparisons between dark soils and White Sands lizards diet demonstrated that while average prey hardness was higher only in White Sands *A. inornata* ($P < 0.01$; Table 3; Fig. 3), absolute bite force was higher in both White Sands *A. inornata* and *H.*

Table 1 Results of a 2-way ANOVA (morphospecies richness and niche breadth) and MANOVA (% H.I.S bodied = hard, intermediate, and soft bodied arthropod prey) on the effect of use (availability vs. diet) and habitat (dark soils vs. White Sands) and the interaction of these two variables on the morphospecies richness, niche breadth, and the proportion of hard-bodied arthropods for all three species

| Response	Covariate	A. inornata			H. maculata			S. cowlesi		
		R^2	F	P	R^2	F	P	R^2	F	P
Morph. richness	Habitat	0.34	14.1	<0.001	0.15	10.5	0.002	0.11	6.7	0.01
	Use		9.4	0.003		0.04	0.8		1.2	0.3
	Habitat*use		5.3	0.02		0.08	0.7		0.8	0.4
Niche breadth	Habitat	0.19	7.0	0.008	0.31	20.3	<0.001	0.15	6.6	0.01
	Use		1.6	0.08		10.7	<0.01		1.8	0.5
	Habitat*use		2.5	0.05		0.1	0.7		6.5	0.01
% H.I.S. bodied*	Habitat	NA	4.2	0.01	NA	3.3	0.03	NA	2.5	0.07
	Use		9.5	<0.001		12.8	<0.001		7.9	<0.001
	Habitat*use		1.9	0.1		1.9	0.1		1.7	0.2
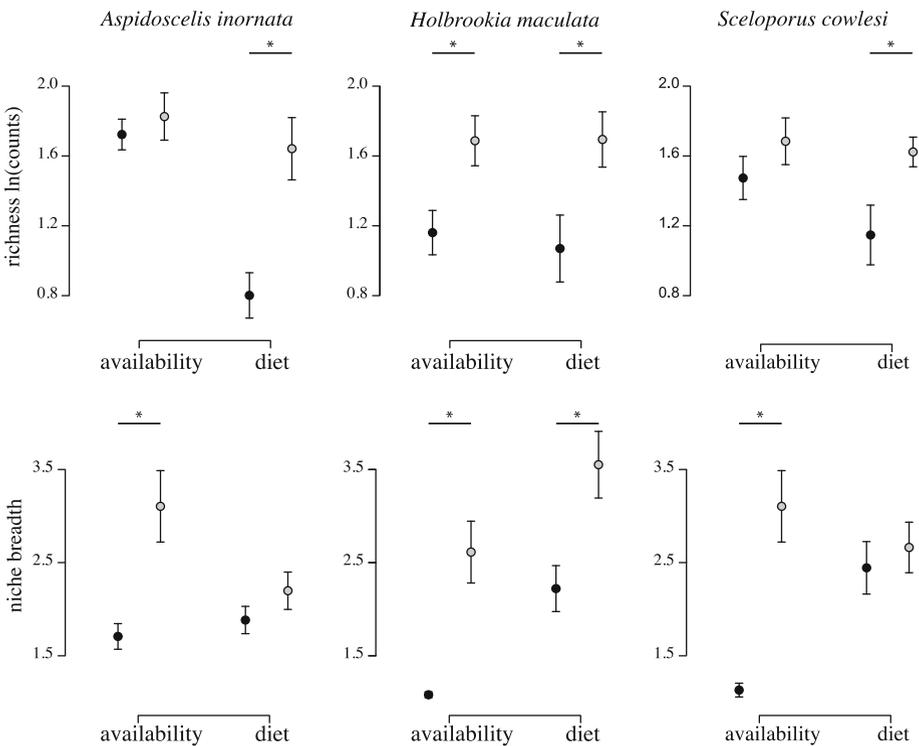
Fig. 1 Prey availability versus prey use (diet) in the three White Sands lizard species for two metrics of arthropod diversity. The top row shows arthropod morphospecies richness (number of "morphospecies") and the bottom row (shows arthropod diversity (1/Simpson's diversity index). *Dark and light shapes* represent mean values from dark soils and White Sands habitats, respectively. Error bars represent standard error of the mean. Results of statistical analysis are displayed in Table 1. *Denotes significant pairwise comparisons
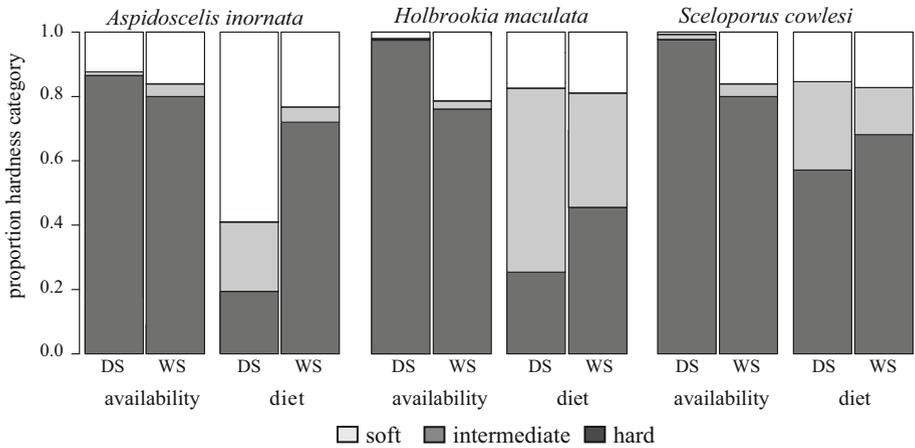
Fig. 2 Mean percentage of hard, intermediate, and soft prey availability and diet in the three White Sands lizard species. *Dark grey, light grey, and white shading* correspond to hard, intermediate, and soft-bodied prey, respectively. Results of statistical analysis are displayed in Table 2

Table 2 Mean (μ) and standard error (s.e.) and results of pairwise differences in means (Welch's *t* test) between habitats (dark soils vs. White Sands) for both availability and diet in (ln transformed) morpho-species richness, niche breadth, and (arcsine transformed) percentage of hard-bodied prey for all three species

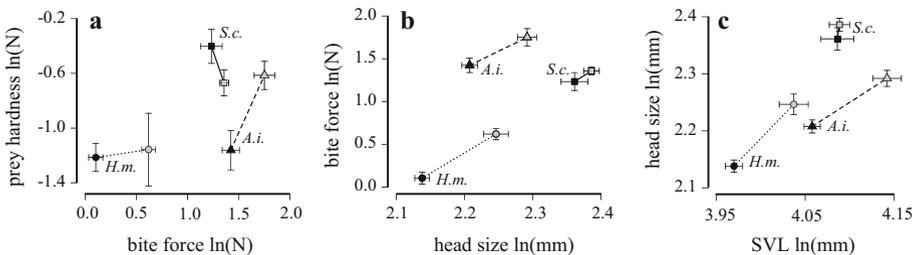| Response	Pairwise comparison	A. inornata		H. maculata		S. cowlesi	
		t	P	t	P	t	P
Morph. richness	Availability	−0.5	0.6	−2.8	0.01	−1.2	0.3
	Diet	−4.4	<0.001	−2.5	0.02	−2.5	0.02
Niche breadth	Availability	−3.2	0.004	−5.8	<0.001	−6.0	<0.001
	Diet	−1.1	0.3	−3.1	0.005	−0.7	0.5
% hard bodied	Availability	2.6	0.02	3.5	0.003	5.6	<0.001
	Diet	−2.7	0.01	−1.7	0.1	−2.4	0.03

Fig. 3 Relationships between prey hardness in the diet versus bite force (left), absolute bite force versus absolute head size (centre), and absolute head size versus body size (right) in *A. inornata* (triangles, dashed line), *H. maculata* (circles, dotted line), and *S. cowlesi* (squares, solid line). *Dark and light shapes* represent mean values from dark soils and White Sands habitats, respectively. Error bars represent standard error of the mean. Results of statistical analysis are displayed in Table 3

maculata ($P < 0.05$; Table 3; Fig. 3). Furthermore, both *A. inornata* and *H. maculata* had larger absolute head size ($P < 0.0001$; Table 3; Fig. 3) and larger body size ($P < 0.001$; Table 3; Fig. 3). Only in *H. maculata* were bite force ($P = 0.003$; Table 3) and head size ($P = 0.004$; Table 3; Fig. 3) still larger in White Sands lizards after adjusting for body size. Although *S. cowlesi* demonstrated a similar trend with White Sands lizards having stronger bite, larger head, and larger body size, they were not significantly different from their dark soils counterparts in these aspects (all $P > 0.05$; Table 3; Fig. 3). Dark soils *S. cowlesi* did, however, show significantly more variation in these performance and morphology characteristics than their White Sands counterparts ($P < 0.01$; Table 3; Fig. 3) but this was not the case for the other two species.

Discussion

By comparing three White Sands lizard species and their dark soils conspecifics, we illustrate different ecomorphological responses to shared environments. In general, we found that the White Sands habitat had higher prey morphospecies richness, increased breadth of prey orders, and a higher percentage of hard-bodied prey than the dark soils habitat. Differences in prey availability in White Sands and dark soils habitats were reflected in lizard diets indicating parallel responses to a shared environment. Variation in performance and morphology demonstrate alternative ecomorphological responses of each species. Overall, White Sands lizards included a larger proportion of hard-bodied prey and had a higher average prey hardness in their diets than dark soils lizards. Although White Sands lizards also had a stronger absolute bite-force, and larger absolute head and body size dark soils lizards, the magnitude of this difference varied among species.

We found important differences in prey availability between White Sands and dark soils habitats. Specifically, White Sands had higher arthropod morphospecies richness, increased breadth of arthropod orders, and a higher percentage of hard-bodied prey. Lower morphospecies richness and diversity of arthropods in dark soils habitats is surprising given that there are more species of vertebrates (Des Roches et al. 2011) and plants (Emerson 1935) than in White Sands. Our sampling of prey availability was, however, limited to a short time interval and only terrestrial arthropods that fell into traps, so therefore likely does not encompass the breadth of diversity in either habitat. Our limited sampling considered, our results do reflect the influence of a high proportion of hard-bodied hymenopterans (i.e. ants), which we collected at the dark soils sites in large numbers.

All three species showed a similar dietary response to higher arthropod diversity in White Sands. In all cases, White Sands species included a significantly higher arthropod morphospecies richness of arthropod morphospecies in their diet than did their dark soils conspecifics (Table 2; Fig. 1). Although there was a similar trend for all lizard species to have a higher dietary niche breadth in White Sands, this difference was only significant in *H. maculata* (Table 2; Fig. 1). Similarly, all White Sands species had a higher average proportion of hard-bodied arthropods in their diets, but this difference was only significant in *S. cowlesi* and *A. inornata*. The increase in hard–bodied prey in lizard diet at White Sands is consistent with our observation of a higher abundance of coleopterans in that habitat (Fig. 2). The difference also may be due to the fact that two species of ants (which are hard-bodied) represented such a large portion of available prey in dark soils. Adult lizards, including those studied here, may avoid certain species of ants, such as invasive and toxic fire ants and not include them in their diets (Robbins and Langkilde 2012; Robbins et al. 2013).

Table 3 Results of pairwise differences in means (Welch's *t* test) and variance (Levene's test) between habitats (dark soils vs. White Sands) in various aspects of diet (diet hardness in N), performance (bite force in N), and morphology (head size and body size in mm) for all three species

Response	*A. inornata*				*H. maculata*				*S. cowlesi*			
	Welch's		Levene's		Welch's		Levene's		Welch's		Levene's	
	t	P	F	P	t	P	F	P	t	P	F	P
Diet hardness	3.1	0.004	0.1	0.7	−0.2	0.8	5.6	0.03	1.7	0.1	1.7	0.2
Bite force	2.5	0.02	0.2	0.6	−5.4	<0.001	0.2	0.6	−1.1	0.3	9.3	0.005
Adj. bite force	−3.1	0.003	1.2	0.3	−1.0	0.3	0.8	0.4	0.4	0.6	0.0	0.9
Head size	−4.6	<0.001	0.1	0.7	−5.2	<0.001	1.4	0.2	−1.1	0.3	15.4	<0.001
Adj. head size	−2.5	0.4	0.0	1.0	−3.0	0.004	0.8	0.4	−1.8	0.09	0.4	0.5
SVL	−4.6	<0.001	0.8	0.4	−3.5	0.001	0.9	0.3	−0.1	0.9	10.7	0.002

Not surprisingly, our results demonstrated that diet, in terms of morphospecies richness and percentage of hard bodied prey, differed between habitats, whereas maximum prey hardness differed among species. These findings further suggest that habitat closely affects diet composition (e.g. Leyte-Manrique and RamÍrez-Bautista 2010), whereas species' ecomorphology, such as bite force and head shape, might influence the selection of prey with certain functional characteristics, such as hardness (Verwaijen et al. 2002; Herrel and O'Reilly 2006; Kaliontzopoulou et al. 2012).

Although similarities in resource use across the three species in White Sands indicated parallel response to a shared environment, important differences emerged in performance and morphological traits. Specifically, differences between White Sands and dark soils lizards in the *average* hardness of prey in their diets, bite-force, and head and body size is consistent with patterns of directional selection (*A. inornata*), ecological release (*H. maculata*) or no change in selection (*S. cowlesi*). Below we discuss patterns observed in each species separately to highlight both shared and unique ecomorphological differences in the lizards of White Sands.

Directional change in diet and ecomorphological traits was most pronounced for *A. inornata*. The diet of White Sands *A. inornata* showed the largest increase in percentage of hard-bodied prey compared to their dark soils conspecifics (Table 2; Fig. 2). Furthermore, only in this species was the average hardness of prey in the diet significantly higher in White Sands (Table 3; Fig. 3). The observation that White Sands *A. inornata* included harder prey in their diet was paralleled by an increase in absolute bite force, absolute head size, and body size. Close ties between diet, performance, and morphology are common in lizards as a stronger bite force is often required for consumption of harder bodied and larger prey (Verwaijen et al. 2002; Herrel and O'Reilly 2006; Kaliontzopoulou et al. 2012). Not surprisingly, head size (and therefore body size) is closely related to bite force, and lizards with larger heads generally have a stronger bite force and feed on harder prey (Verwaijen et al. 2002; Herrel and O'Reilly 2006; Kaliontzopoulou et al. 2012).

Differences in head size between dark soils and White Sands lizards are almost entirely due to differences in body size (i.e. when adjusted for body size, head size is no longer significantly different between dark soils and White Sands lizards, Table 3). Thus, the consumption of harder prey for White Sands *A. inornata* could be due to increased body size (corresponding with larger absolute head size and bite force) and/or increased availability of harder prey. Several other species of *Aspidoscelis* (e.g. *A. exsanguis*, *A. tesselata*,

A. tigris, and *A. uniparens*) live sympatrically with *A. inornata* in dark soils habitats and reach a larger maximum size than *A. inornata*. These congeneric species compete with—and predate on—*A. inornata* outside of White Sands (see Degenhardt et al. 2005). Thus, the directional shift towards larger body and head size and harder prey in the diet of White Sands lizards may be a consequence of relaxed competition and predation pressures from larger individuals of other *Aspidoscelis* species (Dayan and Simberloff 1998). Although the variance was marginally higher in both absolute head size and SVL of White Sands *A. inornata* compared to dark soils *A. inornata*, these differences were not significant. Increasing sample size and sampling individuals from a greater variety of locations may increase our ability to detect change in trait variances that could arise from ecological release.

Of the three species, *H. maculata* demonstrated the most likely case of ecological release in trophic ecomorphology. Like *A. inornata*, *H. maculata* exhibited directional change in ecomorphological traits and had stronger bite force and larger head and body size in White Sands than in dark soils. Mean prey hardness, however, was not higher in White Sands *H. maculata*, but was significantly more variable. Increased variability in this functional aspect of diet is consistent with increase in dietary niche breadth, which was also significantly different between dark soils and White Sands *H. maculata*. Increases in both niche breadth and in the variability of mean prey hardness in the diet in White Sands *H. maculata* are consistent with models of ecological release (see Van Valen 1965; Lister 1976a, b; Losos and de Queiroz 1997; Yoder et al. 2010). Trophic niche expansion could suggest relaxation in selection on White Sands *H. maculata* as a result of absence of competitors (Losos and de Queiroz 1997), predators (Losos and Mahler 2010), and/or increased availability of resources (Roughgarden 1972). Because the White Sands population of *H. maculata* is dense compared to dark soils populations (Des Roches et al. 2011), there may have also been a shift towards increased intraspecific competition with individuals diverging in their resource use to minimize overlap with conspecifics, which is also a key component of ecological release (Van Valen 1965).

In addition to differences in diet, White Sands, *H. maculata* showed a directional change in ecomorphological traits (i.e. stronger bite force, larger head and body size). Whether lizards have shifted to consume harder prey on average, like White Sands *A. inornata*, or expanded their resource use to include harder prey in addition to soft prey, like White Sands *H. maculata*, stronger bite force may still be necessary (Schoener 1969; Wilson 1975). Although increased variation in performance and morphology might be expected with ecological release, prior studies have demonstrated that ecomorphological variation often does not accompany expansion of resource use (Bolnick et al. 2007). Interestingly, *H. maculata* is the only species of the three to have a larger head size in White Sands, even when adjusted for larger body size (Table 3). Considering our finding that these lizards do not consume harder prey on average, head size may have shifted due to genetic drift, phenotypic plasticity (Aubret et al. 2007; Irschick and Meyers 2007; Aubret and Shine 2009) or may be under selection unrelated to trophic ecomorphology (e.g. due to intraspecific competition for mates via male–male aggression, Herrel et al. 1999; Lappin and Husak 2005). Again, like *A. inornata*, the variance was marginally higher in both absolute head size and SVL of *H. maculata* from White Sands compared to dark soils potentially suggesting a morphological response to ecological release. Similar to *A. inornata*, this comparison was not significant and future sampling efforts could increase our ability to detect more subtle differences in trait variances between habitats.

Finally, *S. cowlesi* showed little change in diet between White Sands and dark soils populations, and also did not differ significantly in mean absolute bite force, absolute head

size, or body size. Although differences in diet and ecomorphology between dark soils and White Sands *S. cowlesi* were usually in the same direction as the other two species, they were largely non-significant (Table 3; Fig. 3). Niche breadth did not increase significantly, nor did proportion of hard bodied prey or average prey hardness in White Sands compared to dark soil lizard diet. Either changes in trophic ecomorphology due to selection or plasticity did not lead to significant differences between dark soils and White Sands *S. cowlesi* or we did not detect these differences. Prior research has demonstrated that White Sands *S. cowlesi* has diverged from their dark soils conspecifics in terms of intraspecific communication (Robertson and Rosenblum 2009, 2010), anti-predator behaviour (Robertson et al. 2011), escape behavior (Des Roches et al. 2014), and microhabitat use (Des Roches et al. 2011). However, dark soils and White Sands *S. cowlesi* are not significantly diverged in traits related to ecomorphology (Rosenblum and Harmon 2011; Des Roches et al. 2014), perhaps because this species is a generalist insectivore (Stebbins 1985) and trophic specialization is not selected for. In general, evidence from *S. cowlesi* demonstrates that differences in resource availability following colonization of a new habitat may not necessarily drive ecomorphological change. Interestingly, both absolute head size and SVL were more variable in dark soils *S. cowlesi* than White Sands *S. cowlesi* (Table 3; Fig. 3), a pattern not found in previous work in this system (Rosenblum and Harmon 2011). The significant difference in the variance of morphology between dark soils and White Sands *S. cowlesi* is likely a result of our sampling across a wider range of age classes in the dark soils habitat combined with our limited sample sizes. Further work will be necessary to determine whether there is a robust difference in trait variances across habitats.

When colonizing a new habitat, a population's trophic ecomorphology is influenced by several non-mutually exclusive factors. First, a new resource environment affects which prey are available for colonists to consume. For example, changes in prey species richness or diversity may affect diet and trophic ecomorphology, particularly when predator species are opportunistic generalists (see Leyte-Manrique and RamÍrez-Bautista 2010) and adjust their diet based on availability. Second, species traits—and the potential for evolution of these traits—affect resource use. For example, certain trait values may facilitate the use of particular resources or a greater variety of resources (Verwaijen et al. 2002; Herrel and O'Reilly 2006) in White Sands. Differences in ecomorphological traits between White Sands and dark soils lizards, such as head size and bite force may be the direct target of natural (e.g. Schluter and Grant 1984) and/or sexual (e.g. Lappin and Husak 2005; Husak et al. 2006; Hunt et al. 2009) selection or may evolve as a result of indirect selection on another trait, such as body size (Meyers et al. 2002; Calsbeek and Smith 2007). Ultimately trait evolution can lead to niche evolution, particularly when there is selection for specialized foraging strategies (see Newbold and MacMahon 2009). In addition, phenotypic plasticity can result in ecomorphological change that is difficult to disentangle from the effects of natural selection (Aubret et al. 2007; Irschick and Meyers 2007; Aubret and Shine 2009). Finally, differences in the competitive environment may affect which of the available resources individuals actually consume. For example, presence or absence of other competing species affects whether individuals experience competitive exclusion or ecological release. Up to 35 different reptile species inhabit the dark soils habitat (see Degenhardt et al. 2005), whereas only three reptile species inhabit the heart of the White Sands dune system. Because total density of lizards is comparable between the two habitats (Des Roches et al. 2011) the three species in White Sands are more likely to interact competitively, potentially leading to more pronounced resource partitioning and even character displacement (Schoener 1974). It is plausible that all of these factors (i.e. changes in resource availability, trait values, and competitive environment) have contributed to the

trophic patterns observed, and future research will focus on determining their relative contributions to ecomorphological change at White Sands.

White Sands is a rare case of a system that presents a snapshot of the early stages of community assembly in a novel ecosystem. Some similarities in the diet across the three species are predictable as they reflect a shared environment with a common resource base. Differences in performance and morphology, however, may reflect the constraints of species-specific ecological and evolutionary history. Whether ecomorphological characteristics differ with habitat and/or species may depend on resource availability, presence of antagonists such as predators and competitors, genetic, and ecological constraints. The distant evolutionary relatedness of these three lizard species (Wiens et al. 2010; Rosenblum and Harmon 2011) suggests that differences accumulated over long evolutionary periods can have important impacts on the ecological dynamics of newly assembled ecological communities.

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