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Rapid divergence of social signal coloration across the White Sands ecotone for three lizard species under strong natural selection

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Animal social signals are important for population recognition, communication, and mate choice. Although natural selection often favours cryptic coloration, sexual selection can underlie patterns of coloration that function in inter- or intrasexual communication. We compared social signal coloration of three lizard species across a substrate colour ecotone in New Mexico. These species exhibit cryptic blanched dorsal coloration on the gypsum dunes of White Sands and dark coloration on the surrounding desert soils. We detected corresponding population divergence in colour used for intra- (*Aspidoscelis inornata*, *Sceloporus undulatus*) or inter- (*Holbrookia maculata*) sexual signalling. Although the magnitude and direction of change in coloration varied among taxa, differences in hue and chroma accounted for more variation in social coloration than for dorsal coloration. The relative conspicuousness of social signals also varied across the ecotone. We discuss the possibilities that divergent signalling colours in this system are the result of: (1) stochastic processes, (2) direct selection, and/or (3) a correlated response to natural selection on dorsal coloration.

ADDITIONAL KEYWORDS: *Aspidoscelis* – ecological speciation – *Holbrookia* – *Sceloporus* – sensory drive – sexual selection.

INTRODUCTION

Social signals are important evolutionary cues for population recognition, intrasexual communication, courtship, and mate choice (West-Eberhard, 1983; Shaw, 1996; Seehausen, van Alphen & Lande, 1999; Masta & Maddison, 2002; Gray & McKinnon, 2007; Ritchie *et al.*, 2007), and often vary among populations and species (Endler, 1973; Endler, 1983; Slatkin, 1985). Diversification of signals among populations can arise via selection when reproductive success is associated with a local phenotype (Anderholm *et al.*, 2004; Andersson & Simmons, 2006). Adaptive social signal divergence may also evolve in response to variable signalling environments (Leal & Fleishman, 2004; Maan *et al.*, 2006; Seehausen *et al.*, 2008) or differences in background substrate (Macedonia *et al.*, 2004; Stuart-Fox, Moussalli & Whiting, 2007). Differences among populations can also arise through non-adaptive stochastic processes (i.e. drift, founder events). A species' ecology, natural history, demographic history, and signalling environment thus provide key insights towards understanding the processes that influence population and lineage divergence (Endler, 1977; Orr & Smith, 1998).

Lizard coloration has been subject to extensive evolutionary and ecological study because colourful, complex displays function in both intra- and intersexual communication as well as population recognition (Rand & Williams, 1970; Losos, 1985; Martins, Bissell & Morgan, 1998; Thorpe, 2002; Martins *et al.*, 2004; Stuart-Fox *et al.*, 2004; Harmon *et al.*, 2005; Thorpe *et al.*, 2008). Sexual dimorphism in colour pattern and behaviour reflect these different sexual selection pressures. Geographic variation of

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*Corresponding author. E-mail: jmrobertson@uidaho.edu stereotyped male behaviours, such as head-bobs, push-ups, and lateral compression, are well documented in iguanid lizards (Ferguson, 1971; Martins *et al.*, 1998). Many taxa expose elaborate coloration on the throat coincident with these stereotyped behaviours, and thus are important for intrasexual communication and competition (Cooper & Burns, 1987; Martins *et al.*, 1998; Baird, 2004). The intensity of these signals often varies with circulating levels of androgens (e.g. testosterone), which, in turn, could effect aggression and dominance (Baird, Fox & McCoy, 1997; Meyers *et al.*, 2006; Husak *et al.*, 2007). Thus, the evolution of male social signals in many taxa occurs primarily through the fitness benefits gained by access to territories and reproductive females rather than through direct female choice (Kwiatkowski & Sullivan, 2002; Baird *et al.*, 2003). Female lizard coloration, however, functions primarily in population or sex recognition, competition, courtship stimulation or courtship rejection (Ferguson, 1969; Sullivan & Kwiatkowski, 2007). For many squamate taxa, female coloration is also a condition-dependent signal that varies with reproductive state, thus playing a role in mate choice (Baird, 2004; Weiss, 2006; Calisi & Hews, 2007).

Ecotonal populations provide an ideal setting to study the potential for population differentiation in lizard social signals and to examine the evolutionary processes that maintain locally adapted phenotypes (Martins *et al.*, 1998; Schemske & Bierzychudek, 2007; Seehausen *et al.*, 2008). Social signal differentiation via sexual selection could lead to reproductive isolation. Thus, examining the mechanisms underlying signal evolution could provide valuable insight into the processes of lineage divergence and ecological speciation (West-Eberhard, 1983; Orr & Smith, 1998; Panhuis *et al.*, 2001; Andersson & Simmons, 2006; Seehausen *et al.*, 2008).

The White Sands of southern New Mexico is a geologically recent formation (approximately 6000 years old) that encompasses 275 square miles of white sand dunes, composed of hydrous calcium sulphate (gypsum). The white sand dunes are adjacent to the surrounding dark adobe soil of the Tularosa basin, creating a dramatic ecotone of white and dark substrates. Despite the relatively young age of the white sand dunes, multiple animal taxa exhibit blanched dorsal coloration on the white sand dunes, including three species of lizards (Rosenblum, 2006). In all cases, the conspecific populations that occur on the neighbouring dark soil are darkly coloured. Presumably, background matching in each habitat evolved through natural selection pressures to escape detection by visual predators (Luke, 1989; Rosenblum, 2006). If recognizing appropriate mates and competitors is important for maintaining locally adapted phenotypes across this ecotone, with strong natural selection, we might expect a concomitant change in signalling colour patches that are important for population recognition (Gray & McKinnon, 2007).

We examined differences in social signals between dark and light-adapted populations of three syntopic lizard species, *Holbrookia maculata* (lesser earless lizard), *Sceloporus undulatus* (eastern fence lizard), and *Aspidoscelis inornata* (little striped whiptail). Previous mate choice experiments of *H. maculata* determined that white sands males (blanched phenotype) prefer white sands females, even when female dorsal coloration is artificially painted to resemble a ‘dark soil’ female (Rosenblum, 2008). These experiments eliminated dorsal coloration as a visual signal used for mate choice and indicate that other signals (e.g. social signals, behaviour, pheromones) underlie mate discrimination in *H. maculata* (Rosenblum, 2008). Although mate choice experiments have not been conducted for *S. undulatus* or *A. inornata*, in all three species, social signals are sexually dichromatic and can be important for inter- or intrasexual interactions. The orange throat patch of female *H. maculata* is a condition-dependent signal that varies with reproductive state and is used for male mate choice (Hager, 2001b). The bright blue coloration of male throat and belly regions of *Sceloporus* lizards are correlated with dominance in male–male interactions (Cooper & Burns, 1987), and thus are likely to be an indicator of male quality. The blue heads of male *A. inornata* is a species-specific trait; male head coloration is associated with aggression and courtship success in other *Aspidoscelis* species (Baird *et al.*, 2003). Moreover, other traits (i.e. body size, shape) are known to evolve through sexual selection in this group (Anderson & Vitt, 1990).

The present study aimed to determine whether ecologically divergent populations (light versus dark) exhibit differences in social signals. Specifically, we examined: (i) the magnitude of population differentiation in social coloration; (ii) the divergence in social coloration relative to cryptic dorsal coloration, and (iii) the relative conspicuousness of each signal to its respective substrate.

MATERIAL AND METHODS

FIELD MEASUREMENTS

Field measurements for *H. maculata*, *A. inornata*, and *S. undulatus* were collected during the reproductive season (May to July) in 2003–2006. All lizards were captured by hand or noose and subsequently released at the site of capture. We sampled four white sands localities and three dark soil populations. All white sands populations were located within White Sands National Monument or White Sands Missile Range (WSMR). Dark soil populations were located within the Jornada Long Term Research Station or WSMR. We quantified and compared coloration among 14 *H. maculata* females (nine white sands and five dark soil), 18 male *A. inornata* (nine individuals from each habitat) and 22 male *S. undulatus* (15 white sands and seven dark soil). Sample sizes were necessarily small as a result of the challenges of collecting spectral data in a field setting during the breeding season. This was particularly limiting for *H. maculata*, where signalling colours could only be measured for receptive and gravid females. Although samples sizes were small, the effects were large (Table 1), indicating reliable interpretation of the results obtained. In the present study, we include only individuals from a single dark soil population for each species because signal colors likely evolve, in part, through conspecific interaction of individuals within populations. Differences in the history and genetic connectivity of geographically subdivided populations could contribute to an overall high variance in signal coloration, obscuring interpretation of the processes mediating population diversification. Thus, we chose not to pool multiple dark soil populations because signal evolution is fundamentally a population level process. Additionally, analyses using larger sample sizes (with lizards from multiple populations pooled by substrate colour) corroborated the conclusions presented here.

Spectrophotometric readings of colour patches were taken with an Ocean Optics USB 2000 spectrophotometer *sensu* Rosenblum (2006). Briefly, a custom made probe-holder was used to orient the probe at 45° and 1 cm away from the body surface (Endler, 1990). The probe opening was approximately equal to the size of the colour patch. A dual deuterium/tungsten halogen light source was used. Each spectral reading was taken in reference to a white standard and consisted of percent reflectance recordings at 0.3-nm intervals. Spectral readings were taken at a similar temperature for all individuals to control for the small degree of physiological colour change with temperature for these species (Rosenblum, 2005). Detailed analyses of population variation in dorsal coloration for all three species are presented in previous analyses (Rosenblum, 2006). In the present study, we included additional individuals and pair dorsal with social signal colour readings. For social signal coloration, we measured signalling patches on the throat (*H. maculata*), head (*A. inornatus*, *S. undulatus*), and belly (*S. undulatus*). For *S. undulatus*, the results obtained from both belly and throat coloration were indistinguishable, and so we report only on belly

Table 1. Social signal and dorsal colour for three species of lizars found in white sands and dark soil habitat

		Social signal colour			Dorsal colour		
Species	Habitat	Brightness	Chroma	Hue	Brightness	Chroma	Hue
Holbrookia maculata	Dark soil	18737.90 (1537.21)	0.30 (0.03)	0.85 (0.05)	5954.60 (106.65)	0.29 (0.03)	0.58 (0.10)
	White sand	20528.30 (6336.13)	0.22 (0.05)	0.67 (0.06)	11682.30 (1770.53)	0.19 (0.01)	0.58 (0.08)
	χ^2, *P*-value	2.35, 0.1252	4.84, **0.0278**	9.00, **0.0020**	8.57, **0.0034**	8.51, **0.0034**	0.02, 0.8836
	Difference	1790.4	0.07*	0.17*	5727.64*	0.10*	0.00
Aspidoscelis inornata	Dark soil	2992.05 (571.40)	0.28 (0.09)	1.06 (0.18)	3946.91 (1029.91)	0.47 (0.08)	0.61 (0.08)
	White sand	5252.63 (1156.59)	0.10 (0.04)	0.76 (0.62)	8527.06 (1417.58)	0.27 (0.05)	0.59 (0.06)
	χ^2, *P*-value	12.78, **0.0003**	12.16, **0.0005**	0.438, 0.5078	12.78, **0.0003**	11.55, **0.0007**	0.32, 0.5660
	Difference	2198.42*	0.18*	0.28	4580.15*	0.20*	0.02
Sceloporus undulatus	Dark soil	7775.41 (1197.09)	0.12 (0.06)	0.22 (0.65)	3966.24 (890.04)	0.32 (0.08)	0.78 (0.14)
	White sand	5039.60 (1647.03)	0.22 (0.08)	−0.43 (0.27)	7548.35 (1451.42)	0.16 (0.02)	0.61 (0.12)
	χ^2, *P*-value	8.55, **0.0034**	5.94, **0.0150**	8.55, **0.0034**	12.677, **0.0004**	12.67, **0.0040**	5.91, **0.0150**
	Difference	2735.8*	0.10*	0.65*	3582.11*	0.15*	0.16*

Reflectance spectrum (400–700 nm) partitioned into three components of: brightness, chroma, and hue for three species of lizard. Wilcoxon nonparametric test of population means (SD) reveal population divergence in both social signal colour and dorsal colour. Significant tests ($P < 0.05$) are shown in bold. For each parameter, the difference between means (Difference) with significance of the *t*-test ($^*P < 0.05$) is given.

coloration. Because *H. maculata* throat coloration changes with reproductive state, we excluded nonreproductive females. Post-hoc analyses of *H. maculata* throat coloration revealed relatively high variance among individuals occurring in white sand populations relative to dark soil populations. However, the high variance in social signal was not attributed to reproductive condition. Spectrophotometeric readings were also taken for substrate colours at each collecting locality.

Social signal coloration

Our first objective was to examine differences in social signal coloration between dark soil and white sands populations. We quantified and compared social signal coloration among populations using multivariate analyses, including discriminant function analyses and nonparametric analysis of group mean differences (Wilcoxon). We averaged spectral reflectance measured in the range 400–700 nm (i.e. the complete visual spectrum) into 95 equal bins by taking the mean of every ten points along the spectra to create 3-nm bins. We used linear discriminant analysis implemented in JMP, version 7.0 (SAS, 2007) to compare spectral data for each individual (across 95 bins) to the group multivariate mean. We generated a classification matrix to quantify the number of individuals correctly assigned and those misclassified to source populations, and tested the significance of individual assignments using Fisher's exact test in R (R. Core Development Team, 2007). This method predicts assignment based on multivariate analysis of variance. We used the segmentation method of Endler (1990) to partition coloration into three components of hue, chroma, and brightness (HCB). Ideally, reflectance data are evaluated with respect to the visual system of the focal taxon, based on visual pigment and oil droplet peak sensitivities (Siddiqi *et al.*, 2004; Carleton *et al.*, 2005; Cummings *et al.*, 2008; Salzburger, 2009). These data are not currently available for our study taxa. Therefore, in light of this limitation, we used the segment divider recommended by Endler (1990) when employing the full visible spectrum, which partitions spectral data into four equal bins, representing the relative intensity of blue (400–475 nm), green (476–550 nm) yellow (551–625 nm), and red (625–700 nm). LM is the ratio of intensity of red to green and MS is the ratio of intensity of yellow to blue. These ratios are used for calculations of hue and chroma (Endler, 1990). Recent studies implement an estimate of hue defined as the midpoint wavelength between the minimal and maximal spectral reflectance (Pryke, Andersson & Lawes, 2001), and have been effective for measures of hue and chroma for coloration that is monochromatic. By contrast, our dataset spans a large spectral range, making Endler's method more appropriate for the present study. We implemented nonparametric analyses (Wilcoxon) in JMP, version 7.0 (SAS, 2007) to determine the component(s) of coloration that differed between light and dark-adapted populations for all taxa.

Ultraviolet (UV) signal reflectance

A microspectrophotemetric study of the visual pigments and oil droplets of Caribbean anoline lizards revealed peak spectral sensitivities in the UV spectrum, as low as 385 nm (Loew *et al.*, 2002). Although our focal taxa are distantly related to anoline lizards, it is possible that signals displayed over 300–400 nm could be transmitted and perceived (Fleishman *et al.*, 1997; Loew *et al.*, 2002). We quantified differences in total brightness for the UV range (300–400 nm), in addition to conducting the same multivariate analyses described above for reflectance data in the range of 300–700 nm.

All focal taxa exhibited some coloration in the UV spectrum, although we detected no peak reflectance in the range of 300–400 nm for any species (Fig. 1). Our analyses revealed no difference between dark soil and white sands populations in total brightness across the UV spectrum for *S. undulatus* ($\chi^2 = 1.64$, $P = 0.1997$). By contrast, we detected more UV reflectance for white sands populations relative to dark soil populations for both *H. maculata* ($\chi^2 = 8.235$, $P = 0.0041$) and *A. inornata* ($\chi^2 = 4.68$, $P = 0.0304$). Despite differences in UV brightness, analyses of HCB that included UV and visible light spectral reflectance (300–700 nm) did not differ from the results obtained that were based only on the visible light spectrum (400–700 nm) for either species. Therefore, we focus the remaining analyses only on colour reflective in the visible light spectrum.

Dorsal versus social coloration

Our second objective was to compare the magnitude of social signal differentiation (i.e. between white sands and dark soil populations) to the differences in dorsal coloration for those same individuals. We calculated individual pairwise Euclidean distances based on the visible light spectrum (400–700 nm) in R for both social signal coloration and dorsal coloration. Euclidean distances based on the full visible light spectrum (95 bins) biases the analyses to detect differences in brightness. Therefore, we also calculated pairwise Euclidean distance based on the three components of coloration (HCB). We used nonparametric

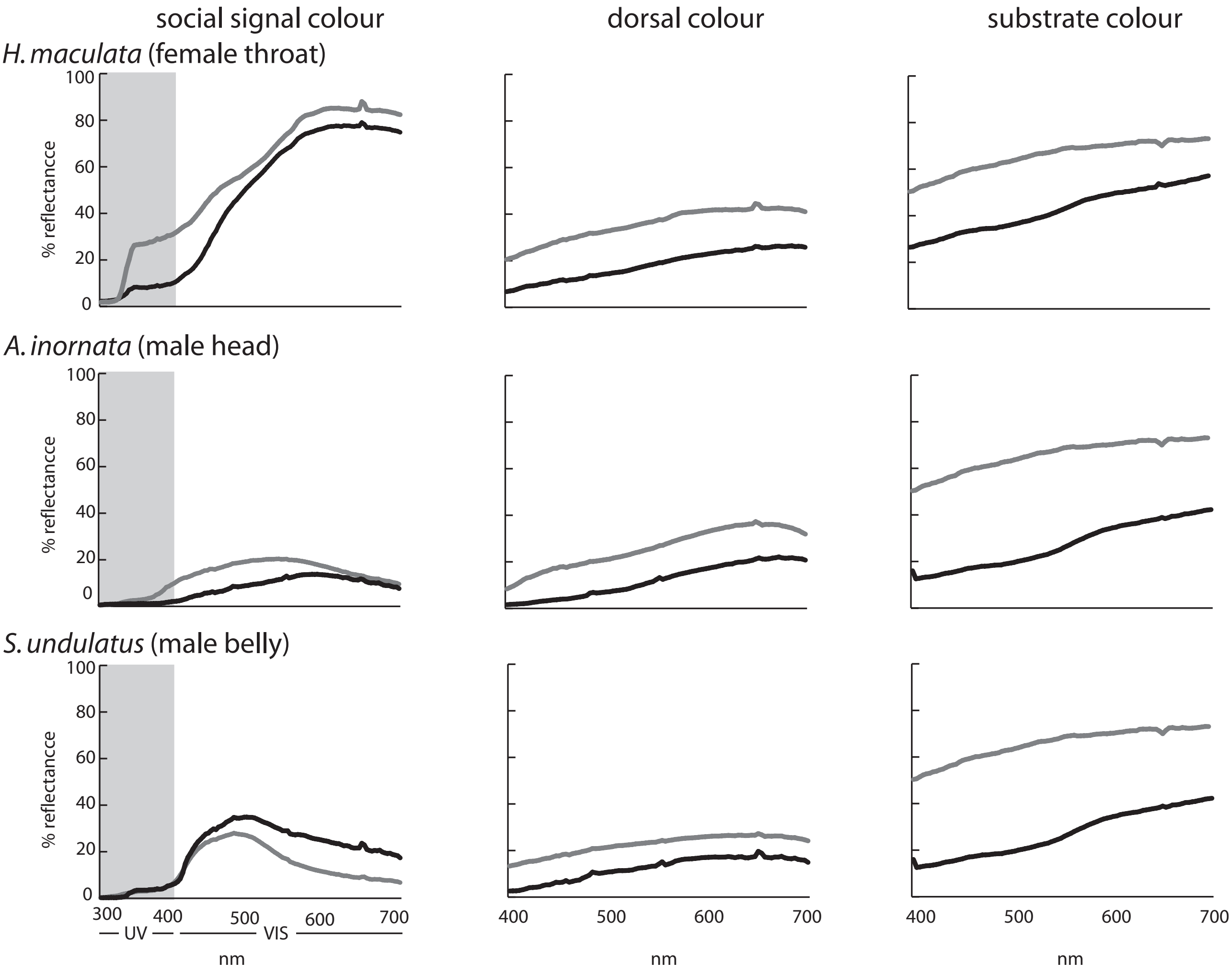

Figure 1. Percent reflectance of social signal colour, dorsal colour, and substrate colour from populations that inhabit white sand (grey line) and dark soil (black line) for three species of lizard, *Holbrookia maculata*, *Aspidoscelis inornata*, and *Sceloporus undulatus*. For social and dorsal coloration, population average (thin line) and standard errors (shaded region) are provided. For social coloration, the spectral range shown includes ultraviolet reflectance (300–400 nm; vertical box shaded grey) and the complete visible light spectrum (400–700 nm).

analysis to determine whether the mean distance in social coloration between dark and light populations was as large as the population differences for dorsal coloration.

SIGNAL CONSPICUOUSNESS ACROSS THE ECOTONE

Lastly, we examined whether social signals could be evolving in response to variation in habitat across the ecotone. We measured the relative conspicuousness of each social signal as the Euclidian distance between signal and local substrate. Euclidean distances were derived two ways: with full spectrum and HCB. We compared our measures of conspicuousness between light and dark populations using nonparametric analyses in JMP, version 7.0. Microhabitats are not the same for all three species (Dixon, 1967; Hager, 2001a). Both *H. maculata* and *A. inornata* spend a large proportion of their time on the ground (sitting and waiting or actively foraging, respectively). However, *S. undulatus* are also commonly found on vegetated microhabitat, displaying from yucca (*Yucca elata*) stalks (Dixon, 1967). Therefore, ground colour *per se* is not always the microhabitat background of greatest relevance for *S. undulatus*. However, phenotypic evolution in response to substrate colour has clearly occurred in this species (Rosenblum, 2008), and substrate colour differences have important effects on the ambient light environments throughout the Tularosa Basin.

RESULTS

Social signal coloration

Social signals varied across the ecotone for all three species. Discriminant analyses reliably distinguished individuals from light and dark habitats in all three species with 100% probability. Fisher's exact tests verified that assignment of individuals to their population of origin could be determined by differences in social signal coloration (*H. maculata*: $P < 0.0001$; *A. inornata*: $P < 0.0001$; *S. undulatas*: $P < 0.0001$).

We detected social signal variation in HCB colour components between light and dark populations (Fig. 1, Table 1). The differences between the means of each group and the statistical significance of *t*-tests show the relative magnitude of differentiation for each parameter (Table 1). Specifically, chroma and hue distinguished female throat patches in *H. maculata*: throat patch coloration of white sands females was less saturated, and the hue was more yellow–orange as opposed to the red–orange hue of individuals on dark soil. Although the magnitude of difference between throat colour patches in light and dark populations of *H. maculata* was not dramatic (Fig. 2), the differences in chroma and hue were statistically significant (Table 1) and sufficient for discrimination among populations with 100% accuracy in discriminant analyses. We detected differences in brightness and chroma for male head colour in *A. inornata*: head coloration of white sands males was brighter but less saturated than conspecific dark soil populations. White sand and dark soil *A. inornata* appeared well-separated with hue on Figure 2 (with white sands individuals appearing more blue–purple, and dark soil individuals more olive–brown), although it is difficult to measure hue reliably for colours with very low saturation (McKenna, Raja & Gong, 1999). Finally, our analyses revealed differences in all three components of colour for male belly patches in *S. undulatus*; belly colour for individuals at white sands was darker, more saturated and more blue (as opposed to more purple) than for individuals on dark soil.

Dorsal versus social coloration

Differences in dorsal coloration across the ecotone were best explained by variation in brightness for all taxa (Rosenblum, 2006). Examination of the HCB components of dorsal coloration for individuals in the present study corroborated the result that populations from white sands were brighter than dark soil conspecifics (Table 1). We also detected differences in chroma between light and dark populations for all taxa. *Sceloporus undulatus* was the only taxon to exhibit differences in hue in dorsal coloration across the ecotone (Table 1).

Patterns of differentiation observed for signalling colour patches differed from those observed for dorsal coloration in several ways. First, as would be expected for a trait under strong natural selection for

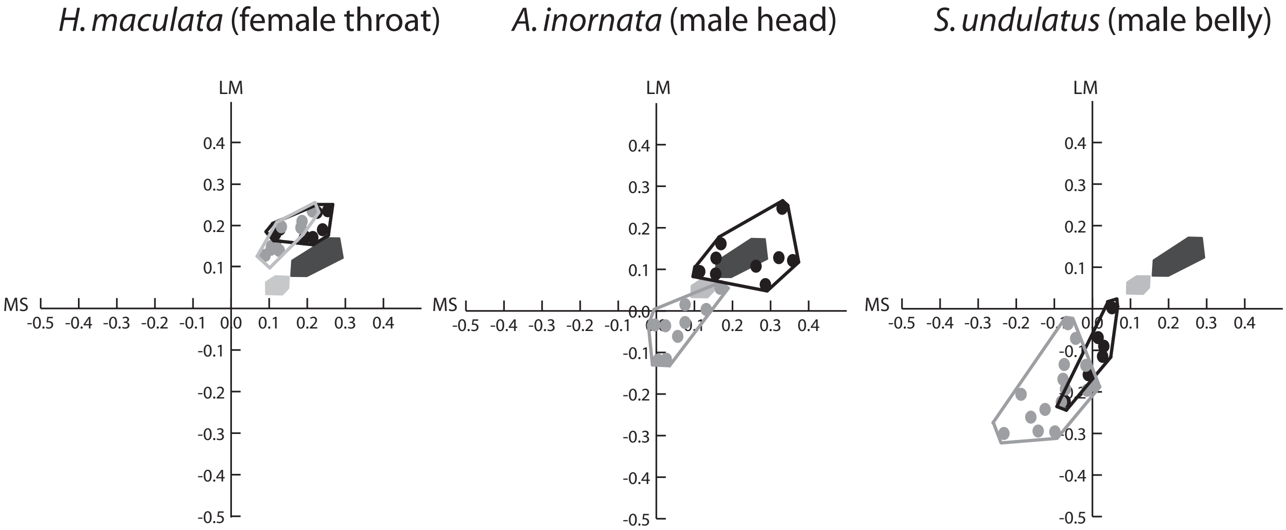
H. maculata (female throat) *A. inornata* (male head) *S. undulatus* (male belly)

Figure 2. Colour space of social signals and substrate reflectance for focal taxa. Minimum convex polygons represent social signal colour space for individuals (open polygons with filled squares) and substrate (solid polygons) on white sands (grey) and dark soil (black). The non-overlapping distribution of polygons illustrates the difference between populations and the conspicuousness of social signals relative background substrate. Differences based on the quantification of hue and chroma for each signal are shown by LM and MS ratios (see text), although differences in brightness between white sand and dark soil populations (significant for all taxa) are not captured in this colour space.

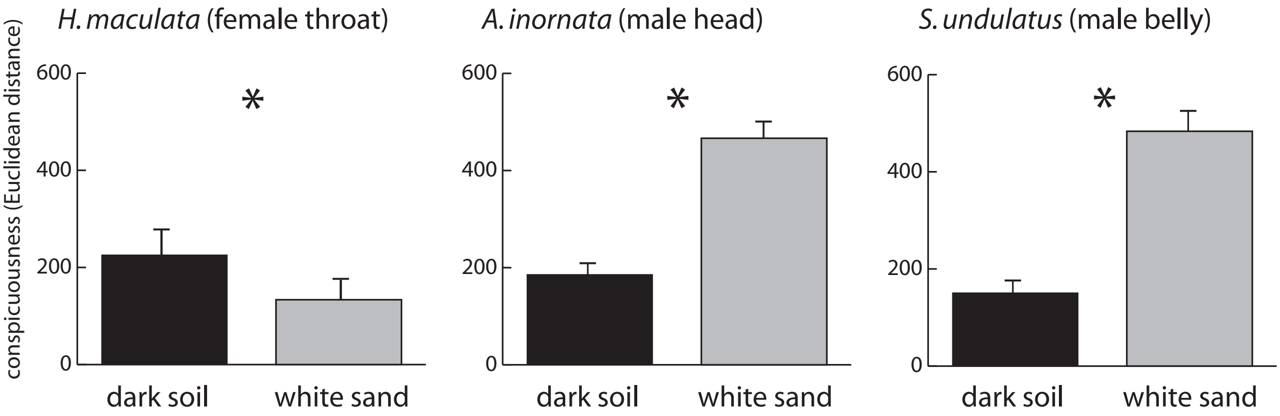

Figure 3. The relative conspicuousness of social signal colour against substrate colour of collecting localities for focal taxa sampled from white sands (grey bar) and dark soil (black bar) populations. The average contrast and standard deviation, based on the Euclidean distance across the 400–700 nm spectrum differed for all taxa (*$P < 0.05$).

crypsis, dorsal coloration tracked substrate coloration over the entire visible spectrum (Fig. 1). The shape of the reflectance curve for social signals, however, differed from the reflectance curves of its substrate, further demonstrating that social signals possibly have not evolved under the same selection pressure for crypsis as dorsal colours have (Fig. 1). Second, differences in dorsal colour between white sand and dark soil populations were primarily the result of differences in brightness in all three species. Indeed, brightness explained 94–97% of all variation in dorsal coloration in this system (Rosenblum, 2006). Conversely, for social signals, brightness explained less, although differences in chroma and hue explained more of the observed variation for all taxa (Table 1). Finally, despite significant differences in social signals between light and dark populations, the magnitude of differentiation tended to be less than the divergence observed in dorsal coloration for all three species. This pattern was statistically significant when using HCB parameters for *A. inornata*: ($\chi^2 = 67.2205$, $P < 0.0001$) and *S. undulatus*: ($\chi^2 = 9.5903$, $P < 0.0020$), but not for *H. maculata* ($\chi^2 = 1.405$, $P > 0.05$), possibly because of the smaller sample sizes in this species. Analyses based on the Euclidean distance across 95 bins spanning the full spectrum yielded similar results.

SIGNAL CONSPICUOUSNESS ACROSS THE ECOTONE

Signal conspicuousness was not uniform across the ecotone for all taxa. Although we detected significant differences in social signal contrast between dark soil and white sands populations for all taxa (*A. inornata*: $\chi^2 = 12.78$, $P < 0.0003$; *S. undulatus*: $\chi^2 = 12.27$, $P < 0.0005$; *H. maculata*: $\chi^2 = 5.48$, $P = 0.019$; Fig. 3), taxa differed with respect to the habitat that their signal was most conspicuous. *Sceloporus undulatus* and *A. inornata* blue male signalling colours were more conspicuous against the white sands than corresponding colour patches were against dark soil substrates, whereas the average orange female throat colour of *H. maculata* was more conspicuous in the dark soil habitat (Fig. 3). The results were unchanged using Euclidean distances derived from measures of HCB.

DISCUSSION

In the present study, we report the rapid evolution of social signalling coloration for three species of lizards in a novel substrate environment of white gypsum sands. Patterns of social colour divergence between populations on white sand and dark soil substrates varied by taxa, which is unsurprising given the differences in signal function among species. *Holbrookia maculata* female throat coloration is an intersexual signal of reproductive condition (Hager, 2001b). *Sceloporus undulatus* male belly coloration is used primarily for intrasexual dominance displays (Cooper & Burns, 1987), and *A. inornata* head coloration is a sexually dimorphic trait that may be important in males for inter and/or intrasexual interactions (Anderson & Vitt, 1990; Baird *et al.*, 2003; Andersson & Simmons, 2006). We found that all three taxa showed strong divergence of signalling colour patches between white sands and dark soil habitats. Divergence of signalling colours was not entirely commensurate with divergence of dorsal colour, with the later almost exclusively being the result of changes in brightness, and not hue or chroma. Finally, we report differences in the relationship between signal and dorsal colour across the ecotone; blue male signalling colours were more conspicuous in white sand compared to dark soil habitats for *S. undulatus* and *A. inornata*, whereas signal conspicuousness was more similar across habitats for *H. maculata*.

Below, we discuss patterns of differentiation for social signalling colours and the mechanisms by which divergence of these signals may have occurred. We consider three nonmutually exclusive hypotheses for the rapid evolution of signal colours. Divergence in signal colours could be the result of: (1) neutral, stochastic processes; (2) divergent selection directly on social signalling coloration in different substrate environments; and/or (3) by-product effects of natural selection on dorsal coloration.

Genetic drift

Genetic drift can induce changes in allele frequencies and lead to divergence in small, semi-isolated populations (Wright, 1946; Slatkin, 1985; Hoffman *et al.*, 2006; Knopp *et al.*, 2007). Given the recent colonization of the white sands formation, it is certainly plausible that differences in signalling colours between dark soil and white sands populations are the result of stochastic 'founder' effects. At least for one of the three species (*S. undulatus*), the genetic data suggest a reduction in population size associated with colonizing the novel white sands environment (Rosenblum, Hickerson & Moritz, 2007) Therefore, differences between populations could be explained, in part, by the non-adaptive consequences of genetic drift in small isolated populations.

However, although genetic drift may contribute to phenotypic change in this system, it is unlikely to be the sole explanation for signalling colour evolution at white sands. Divergence as a result of genetic drift is most pronounced in isolated populations because of the effects of even small amounts of gene flow (Slatkin, 1985; Lenormand, 2002). For all three species, evidence of historical genetic connectivity across the ecotone (Rosenblum, 2006) indicates that colour differences are maintained despite the homogenizing effects of gene flow. This evidence combined with the rapid pace of divergence (occurring in < 6000 years) suggests the role of non-neutral processes in shaping observed colour variation.

Direct selection

Social signals are often constrained because they function in species and population recognition (Rand & Williams, 1970; Losos, 1985). However, social cues can vary among populations (Ferguson, 1971; Martins *et al.*, 1998) as a result of heterogeneity of selective environments (Macedonia, Brandt & Clark, 2002; Macedonia, Echternacht & Walguarnery, 2003; Stuart-Fox *et al.*, 2007; Seehausen *et al.*, 2008). For example, coloration could evolve to maximize transmission in a novel ambient environment (i.e. sensory drive) or as a result of localized sexual selection processes reinforced through assortative mating (Endler & Basolo, 1998; Andersson & Simmons, 2006), or both. In our system, mate choice experiments with *H. maculata* showed that white sands males preferentially mated with local white sands females, even when the dorsal surfaces of these white sands females were artificially painted dark (Rosenblum, 2008). Because female throat coloration was not manipulated in the mate choice experiment, the possibility that differences in sexual signalling colours could be under direct selection remains a plausible mechanism of diversification.

The sensory drive hypothesis predicts that social signals evolve to maximize effective transmission and perception in a particular habitat to conspecifics at the same time as minimizing detection by predators (Endler, 1992; Endler & Basolo, 1998). Colour perception depends on the properties of the signal, light conditions, and the sensory capabilities of the intended receiver (Cott, 1940; Lythgoe & Patridge, 1991; Endler, 1992; Endler & Basolo, 1998). Chameleons (Stuart-Fox *et al.*, 2007), stickleback (Boughman, 2001), and cichlid fish (Maan *et al.*, 2006; Seehausen *et al.*, 2008) provide well-studied examples supporting a sensory drive hypothesis to explain phenotypic differences among populations.

Given the dramatic difference in substrate and ambient light environment between white sand and dark soil habitats, could the sensory drive hypothesis explain the evolution of social signals at white sands? If social signals in this system are important for population recognition or mate choice, might they be under selection for optimal transmission across the ecotone? Superficially, this explanation does not appear to be well-supported by our data. The relative conspicuousness of signal colour to background colour was not static across the ecotone for all focal species (Fig. 3). Specifically, the blue colour patches on *S. undulatus* and *A. inornata* are much more conspicuous in the white sand habitat. The results obtained for *H. maculata* conform better to sensory drive expectations. The overall magnitude of the difference in signal conspicuousness was much lower for *H. maculata* than the other two species.

A number of additional considerations must be formally weighed before rejecting the hypothesis of direct selection and/or sensory drive on social signalling colours in divergent substrate environments. First, understanding the visual system of the white sands lizards will allow a more robust analysis of signal perception (Cott, 1940; Endler & Basolo, 1998; Leal & Fleishman, 2004). Behavioural studies of the visual performance and sensitivity of white sands and dark soil individuals are in progress and indicate both population and sex differences for *S. undulatus* (S. Nava, personal communication). In addition to behavioural studies, microspectrophotometric studies that measure the peak spectral sensitivity of visual pigments and oil droplets are important to better reveal how individuals perceive social signals of local and non-local conspecifics. Studies on the visual system may yet provide evidence in favour of the sensory drive hypothesis.

Additional spectrophotometric data are also important for understanding the signal–environment–perception interaction across the white sands ecotone because conspicuousness can be better contextualized in reference to the micro-environment relevant for displays (Lythgoe & Patridge, 1991). Additional photometric readings would therefore be useful in the white sand and dark soil habitats for: (1) ambient light conditions; (2) display microhabitats; and (3) lizard ventral surfaces. Social interactions for *A. inornata* and *H. maculata* at white sands occur primarily on the gypsum sands. However, *S. undulatus* males frequently display on yucca stalks, and additional spectral habitat data are particularly important for this species. Similarly, for species with discrete signalling patches that are highly contrasted to their overall ventral colour (i.e. *S. undulatus* and *H. maculata*) recordings of nonsignalling ventral colour patches will also be useful.

Finally, it is important to consider possible constraints on selection for optimal signal transmission. Even if there is direct selection to maintain a particular signal to background relationship, necessary phenotypic variation may not exist. Given the pure white substrate colour on the gypsum dunes, it may be impossible for social signalling colour patches to maintain similar contrast ratios across the ecotone. For example, the blue belly of *S. undulatus* and the blue/olive head of *A. inornata* are both dull (in brightness) relative to the extremely bright white sands substrate (Fig. 1). Therefore, colour patches in both species more closely match dark soil habitat. The overall contrast of signal to substrate at white sands is extraordinarily large, resulting in highly conspicuous social signals on the gypsum dunes.

CORRELATED SELECTION

Strong natural selection on dorsal coloration has been demonstrated for all three lizard species (Rosenblum, 2006), with directional selection favouring dorsal blanching on white sands substrate. One intriguing possibility is that changes in social signal colour patches are merely a byproduct of selection for reduced melanin production (Quinn & Hews, 2003). The *Mc1r* gene is a major player in the vertebrate melanin-production pathway, and variation at this gene is responsible for colour variation in a variety of mammals and birds (Eizirik *et al.*, 2003; Mundy *et al.*, 2004; Hoekstra *et al.*, 2006). The *Mc1r* gene is also associated with coloration in all three white sands species (Rosenblum, Hoekstra & Nachman, 2004). Recent functional assays confirmed that the blanched *Mc1r* allele shows reduced basal activity for *S. undulatus* and *A. inornata* (E. B. Rosenblum, H. Römpler, T. Schöneberg & H. E. Hoekstra, unpubl. data), implicating this gene as a major contributor to colour variation in these two taxa. A functional link between genotype and phenotype remains to be made for *H. maculata*.

Reptile coloration is produced by the interaction of multiple cell layers (Bagnara & Hadley, 1973; Morrison, 1995): melanophores contain melanin and produce dark brown/black pigments, iridophores do not contain pigments but produce structural colours, such as blue, through the reflective properties of the cells, and xanthophores are pigment-containing cells that produce yellow/orange colours. Although the exact configuration of these cell types varies taxonomically (Spearman & Riley, 1969; Macedonia *et al.*, 2000), the density and dispersion of melanin in melanophore soma and dendrites can affect the colour of any colour patch. A positive relationship between blue social coloration and dermal melanin density has been demonstrated for *Sceloporus* (Quinn & Hews, 2003) and *Anolis* (Macedonia *et al.*, 2000) lizards. Changes in orange and blue signalling colour patches in the focal taxa could certainly be the result of changes in the xanthophore or iridophore cell layers. It is possible, however, that the reduction in melanin production in white sands lizards has altered the colour of these signalling patches. Histological study is required to determine whether differences in social coloration of the focal taxa are the result of changes in melanin.

If correlated evolution of dorsal and social signalling colours has occurred at white sands, should we expect similar changes in signalling colour across species, as seen for dorsal coloration? Initially, the data obtained in the present study did not demonstrate that social coloration changes in a predictable direction (or in the same direction as dorsal color) across the ecotone. Dorsal coloration was brighter and less saturated for all three species at white sands than for dark soil conspecifics. However, for signalling patches, we detected an increased brightness of white sands populations of *A. inornata* and *H. maculata* but decreased brightness for *S. undulatus*. Similarly, we observed less saturated signalling colour patches for *H. maculata* and *A. inornata* on white sands but higher saturation for *S. undulatus*.

Upon closer examination, however, we see some predictable features of signalling patch colour evolution across the ecotone. Most notably, signalling colour patches for all species demonstrated reductions in long wavelength coloration with increased contributions of short wavelength colour on white sands relative to dark (ancestral) populations (Fig. 1). This shift toward shorter wavelengths could resolve the apparent disparity among species in change in saturation. For example, *H. maculata* throat colour shifted from an orange–red (dark soil) to orange–yellow (white sands) and *A. inornata* head colour was olive–brown on dark soil but blue on white sands. In both cases, the shift to greater contribution of short-wavelength colour resulted in less saturated colour (less pure). On the other hand, the shift towards shorter wavelengths (more blue) of an already blue form, as observed for *S. undulatus*, resulted in greater saturation because of the loss of non-blue long wavelengths.

Additionally, the differences we observed across species and between dorsal versus signal patches were compatible with correlated selection. First, reductions in melanin will have very different effects depending on the contribution of different cell layers to overall patch color. Dorsal coloration in the focal species is determined primarily by melanophores, and so reductions in melanin in white sands lizards have a simple predictable effect (i.e. increased brightness and decreased saturation). However, reductions of melanin in colour patches that have a strong contribution of xanthophore pigments or iridophore structural colours are less predictable because of the interaction among these additional cell layers in producing the perceived coloor. Furthermore, it is not surprising to observe somewhat different phenotypic effects across species, even if reductions in melanin are the result of disruption of the same gene. For example, although *Mc1r* is implicated in dorsal blanching in *S. undulatus* and *A. inornata*, the mutations found in white sand populations were different in the two species and lead to different functional effects (in terms of the mechanism and magnitude of decreased *Mc1r* receptor activity; E. B. Rosenblum, H. Römpler, T. Schöneberg & H. E. Hoekstra, unpubl. data). Therefore, to better evaluate the hypothesis of correlated selection, the precise effect of changes in melanin production on signalling colour patches must first be determined.

CONCLUSIONS

Recent studies provide a number of examples of ecologically diverged populations that also exhibit differences in sexual signals (Endler, 1990; Nosil, Crespi & Sandoval, 2003; Maan *et al.*, 2006; Gray & McKinnon, 2007; Seehausen *et al.*, 2008). These differences in social signals may then serve as reproductive isolating mechanisms to maintain locally adapted phenotypes (Nosil, Vines & Funk, 2005). The interaction between natural and sexual selection can lead to rapid speciation, particularly when traits contributing to assortative mating have evolved as a by-product of natural selection on ecologically important traits (Schluter, 2001; Kirkpatrick & Ravigne, 2002; Gavrilets, 2003; Servedio, 2004). In the present study, we demonstrate social signal divergence in populations of three lizard species that exhibit dramatic local adaptations for background matching. Although additional data are required to determine whether signalling colour patterns are the result of selection for optimal transmission in different light environments or the by-product effects of natural selection on dorsal coloration, this system provides an opportunity to further examine the interplay between natural and sexual selection in lineage diversification.

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