

A comparative study of two agamid lizards, *Laudakia stellio* and *Pseudotrapelus sinaitus*, in southern Sinai

Olivia Norfolk¹, Alice Melotte¹, Francis Gilbert¹, Samy Zalat² & Tom Reader^{1*}

1. School of Biology, University Park, University of Nottingham, Nottingham NG7 2RD, UK

2. El Taiba University, El-Ula, Saudi Arabia

Abstract

The study compared habitat use and behaviour in two sympatric species of agamid lizard, *Laudakia stellio* and *Pseudotrapelus sinaitus*. Despite sharing the same habitat, the two species differed in their utilisation of microhabitats within it. *Pseudotrapelus* spent significantly longer on rocks compared to *Laudakia*. *Pseudotrapelus* showed evidence of heliothermic regulation, spending most of the time in the sun, but moving into the shade in the warmer afternoons. These varying temporal patterns may reflect differential thermoregulatory requirements between the two lizard species.

Pseudotrapelus can change colour rapidly. There was no evidence of any thermoregulatory function in this ability; it is likely to be a form of social communication. Being brightly coloured was associated with behaviours implying increased conspicuousness: blue lizards were alert and vigilant for an average of 93% of each viewing session, compared to just 60% of the time in non-blue camouflaged lizards. The striking nature of the transitory blue colouration suggests it may have evolved for maximum salience, a trait common with signals. We simulated social encounters using blue model lizards and mirrors. Behavioural responses to these stimuli all involved colour changes, and support the social-signaling hypothesis.

Keywords: thermoregulation, colour change, social signalling

Introduction

Theoretically the coexistence of high numbers of related species will result in high levels of interspecific competition. However in reality such competition is minimized because each species has evolved to exploit a distinct niche within the shared environment. Pianka (1969a) studied the diverse ecology of the 40 species of sympatric lizards that inhabit the Australian desert. More complex habitats were associated with more lizard and bird species, suggesting that environmental heterogeneity is key in facilitating niche divergence and thus speciation. A major element of environmental heterogeneity is topography; the climatic variation associated with large altitude variation leads to gradients in vegetation, which creates a wide range of habitats. For this reason mountainous regions often have high biodiversity, with distinct ecosystems operating at different altitudinal clines (Fu *et al.* 2007). Lizards are particularly sensitive to altitude, and species richness can vary over heights of just 50 m (Fischer & Lindenmayer 2005).

Pianka (1969b) analysed the subdivision of habitat and resource-use in *Ctenotus*, Australia's largest genus of lizard. He identified a minimum of three dimensions involved in determining the species niche; habitat, diet and time. All three can be mediated by phenotypic differences such as body size that have knock-on effects on how species utilise the environment, thus can help explain how similar species co-exist in a shared habitat.

Pianka (1969b) stresses the importance of considering time as a dimension of the niche. In environments where resources are replenished frequently, competition can be decreased or avoided entirely if species are active at different times of the day. The time of day will have direct effects on both air and ground temperature, so temporal activity patterns will relate to lizard thermoregulatory ability. Lizards are able to regulate their body temperature by managing the time they spend in the sun and the shade. Huey *et al.* (1977) demonstrated that the number of lizards in the sun is inversely proportional to ambient temperature, and that lizards alter their regulatory behaviour with the seasons in order to maintain constant body temperatures despite climatic differences.

Some lizards have evolved physiological mechanisms of thermoregulation and there is some evidence suggesting that colour change is associated with thermoregulation. Morrison *et al.* (1996) found that the blue pigmented cells of the lizard *Urosaurus ornatus* respond to changes in temperature by reflecting more light at high temperatures and thus aiding cooling. However, in other lizard species such as dwarf chameleons (*Brachypodion* spp), colour change is used primarily for social signaling and has no relevance to temperature (Stuart-Fox & Moussalli 2008). Although traditional taxonomy places chameleons and agamas in separate families, more recent phylogenies suggest they are related. Colour change appears in many species of chameleon and agama (Baha El Din 2006), so may have evolved before the groups diverged. If the shared ancestral lizard primarily used colour change for social signaling, then this may still be the main function in both agamas and chameleons (McKittrick 1993). Chameleon colour change is traditionally associated with camouflage, but social communication could also constitute a selective force (Stuart-Fox & Moussalli 2008). Chameleons can often match the typical background colour of their habitat. Despite some misconceptions, they cannot match all backgrounds, only those of their normal environments: in an unnatural environment against an unfamiliar colour, they cannot blend in. Furthermore, they are known to alter the level of their camouflage when faced with different prey (Stuart-Fox *et al.* 2008).

Chameleons also exhibit a set of more vivid and rapid colour changes for the purpose of display. Here the objective is not crypsis, but to stand out in relation to the background. Quantitative measures show that the colour of these display signals varies predictably in response to the background environment (Stuart-Fox *et al.* 2007), increasing detectability in order to increase signal efficacy. Stuart-Fox & Moussalli (2008) showed that the capacity for colour change in dwarf chameleons is positively associated with the use of elaborate signals in male contests and courtship. They found no evidence that these transitory colour changes were used in camouflage, but concluded they had evolved purely for social communication.

Ultraviolet signals that remain unseen by the human eye are also be an important component of social signaling in lizards. In brightly-lit habitats the dewlaps of *Anolis* lizards contrast strongly in the UV with the colours of the background (Fleishman *et al.* 1993). The dewlap remains hidden except during communication bouts, strongly supporting the importance of UV signals in lizard communication. Ultraviolet signals can be involved in competitive assessment between males, with territorial displays typified by a head-bobbing motion that shows off the UV colourations of the throat or dewlap. Stapley & Whiting (2006) manipulated the UV colouration of male Broadley's flat lizards (*Platysaurus broadleyi*) and monitored the impacts on fighting ability. The outcome of the fights was not affected by UV alteration, but was determined by other asymmetries such as body size. However UV-reduced males showed longer assessment periods and a higher likelihood of escalation. This suggests that bright UV-colouration is a sign of aggression that dissuades competitors from escalating into a fight.

In the agamid *Ctenophorus ornatus*, UV signaling is used in mate choice by males. Females display variable spectral reflectance on their throat and chest, and males show preference accordingly (Le Bas & Marshall 2000). There was no correlation between colour and female fitness, but brightness did correlate with female laying-date, suggesting males might use colour cues to identify receptive females.

The mountainous regions of Southern Sinai support a diverse herpetofauna, with a total of 36 recorded species (Baha El Din 2006). We focus on two of the most conspicuous species of agamids there, the Starred agama, *Laudakia stellio* (Linnaeus 1758) and the Sinai agama, *Pseudotrapelus sinaitus* (Heyden 1827). These fairly large, sympatric species are both insectivorous sit-and-wait predators, and should utilize different niches in order to minimize competition. They differ considerably in morphology, such as size and colour, and we

investigate whether there are associated differences in behaviour and niche utilization. We address differential microhabitat use and compared temporal activity patterns throughout the day. *P. sinaitus* shows rapid colour change from brown to vivid blue. It is known to perch conspicuously on high rocks and display with the distinctive head-bobbing motion. We hypothesized that this colour change is used as a form of social signaling, so performed some preliminary observations and experiments on the adaptive significance of colour change in this species.

Materials & Methods

Fieldwork was carried out over a five-week period in August-September 2008 within the St Katherine Protectorate, South Sinai, Egypt (29°33'N, 33°57'E). South Sinai is a mountainous region interspersed with dried-up riverbeds, or wadis, that dissect the landscape into fragmented habitats (see Gilbert *et al* 2006, Zalat & Gilbert 1998, 2008).

Lizards were observed while walking along paths throughout the study area. When a lizard of the study species was seen, it was observed for 15 min from a minimum distance of five metres. We monitored use of the microhabitat by recording whether the lizard was in the sun or shade, the behaviour and appearance. At the end of the 15 mins we took a GPS reading at the place of the initial sighting. We chose not to try to capture the lizards and mark them, and thus we are unsure of individual identities. The study area was walked repeatedly, so almost certainly the same individuals were seen several times, but because we could not identify individuals, the observations we made were assumed to be independent.

Lizards used their immediate environment in a variety of ways. They could be found perching on boulders, climbing on cliffs or large steep rocks, on man-made walls or running across open ground. The use of microhabitat was recorded descriptively in the field, and subsequently placed into one of four classes for analysis (Table 1).

Lizard behaviour was placed into six discrete categories (Table 2) determined from preliminary observations. It was noted that lizards could perform the same behaviour, but with varying amounts of head-turning: we therefore quantified this degree of head-turning and termed it the 'degree of vigilance' (Table 3). We recorded the duration of each behaviour with associated vigilance for the full 15 mins.

Colour changes were assessed descriptively and by photographs for both species. *L. stellio* individuals all had the same typical colouration (Fig 2). They tend to have a dark grey back, with several yellow-orange stripes down their spine, and a banded tail of the same colours. *P. sinaitus* changed colour very rapidly and displayed a wide variety of shade and intensity. We wrote qualitative descriptions of the colour changes to the best of our abilities and took photographs of the changes. Photographic examples of the extraordinary colour range can be seen in Fig 2. This variability meant that the qualitative data proved hard to analyse, so it was converted into binary data of blue versus not-blue for analysis.

Table 1: Descriptions of the four classes of microhabitat.

Microhabitat	Description
1. Flat	Flat, exposed ground, at least 1m from cover
2. Boulder	Single rocks or boulders, or rocky outcrops
3. Walls	The dry stone-walls made by the Bedouin
4. Cliff	Cliffs or large flat rocks over 6m in size

Fig 1: Examples of behavioural categories of Table 2 - (left to right) ‘lying flat’, ‘sitting up’ and ‘eating’. Photographs by ON.



Table 2: Categorisation of typical behaviours, applicable to both *Laudakia stellio* and *Pseudotrapelus sinaitus*.

Behavioural category	Description
Lying flat	Body pressed against surface; head still or lifted intermittently for glancing (scored on vigilance scale - see Table 3)
Sitting up	Erect posture, belly lifted from ground; head turning according to vigilance scale
Eating	A range of eating behaviours seen: licking ants off rocks, catching flying insects from the air with tongue, and stalking and pouncing on dragonfly prey
Running	Used to describe any speed of running
Head-bob	Distinctive bobbing of the head, but with no associated movement of the body
Press-ups	Bobbing of head with associated pressing of body towards the ground, like a press-up exercise; described by Bedouin as ‘praying’

Table 3. Classes of vigilance, determined by the extent of head movement.

Degree of Vigilance and description	Head turns per 10 seconds
1 Head completely still	0
2 Intermittent glancing around	1-2
3 Frequent glancing	3-6
4 Rapid turning of head	7+

All statistical analyses used SPSS ver. 17.0 with a significance level of 0.05. Means are provided \pm one standard error of the mean. A chi-squared test was used to compare habitat use between the two species. If a lizard was observed in the microhabitat one or more times in a viewing session then it was recorded as positive for the microhabitat for this test, and thus these data were assumed to be independent. Independent sample *t*-tests were used to compare the average length of time spent in each microhabitat per viewing session between the two species. Levene’s test was used to test for equality of variance in the samples, and the appropriate assumptions were made in each *t*-test.

Behaviours such as eating, running and displaying occurred as fast spurts of activity in both species, with similarly short durations, and thus comparisons of durations were not undertaken. However, from observations in the field, vigilance states 1 and 2 were associated with relaxed basking behaviours, whereas the regular head movements of states 3 and 4 were associated with active behaviours such as hunting and territorial displays. Binomial logistic regression analysis was therefore used to look at the frequency of relaxed behaviour (states 1 and 2) versus alert behaviour (states 3 and 4) throughout the day for each species, using time of day as a covariate. The probability of a lizard being relaxed or alert at different times of day was then predicted by back-transforming the logistic transformation, ie by inserting the

estimated model parameters into the formula $p = \frac{e^{-(mx+c)}}{1 + e^{-(mx+c)}}$, where p = probability of being alert, x = time, m = the estimated gradient, and c = the estimated intercept of the fitted model.

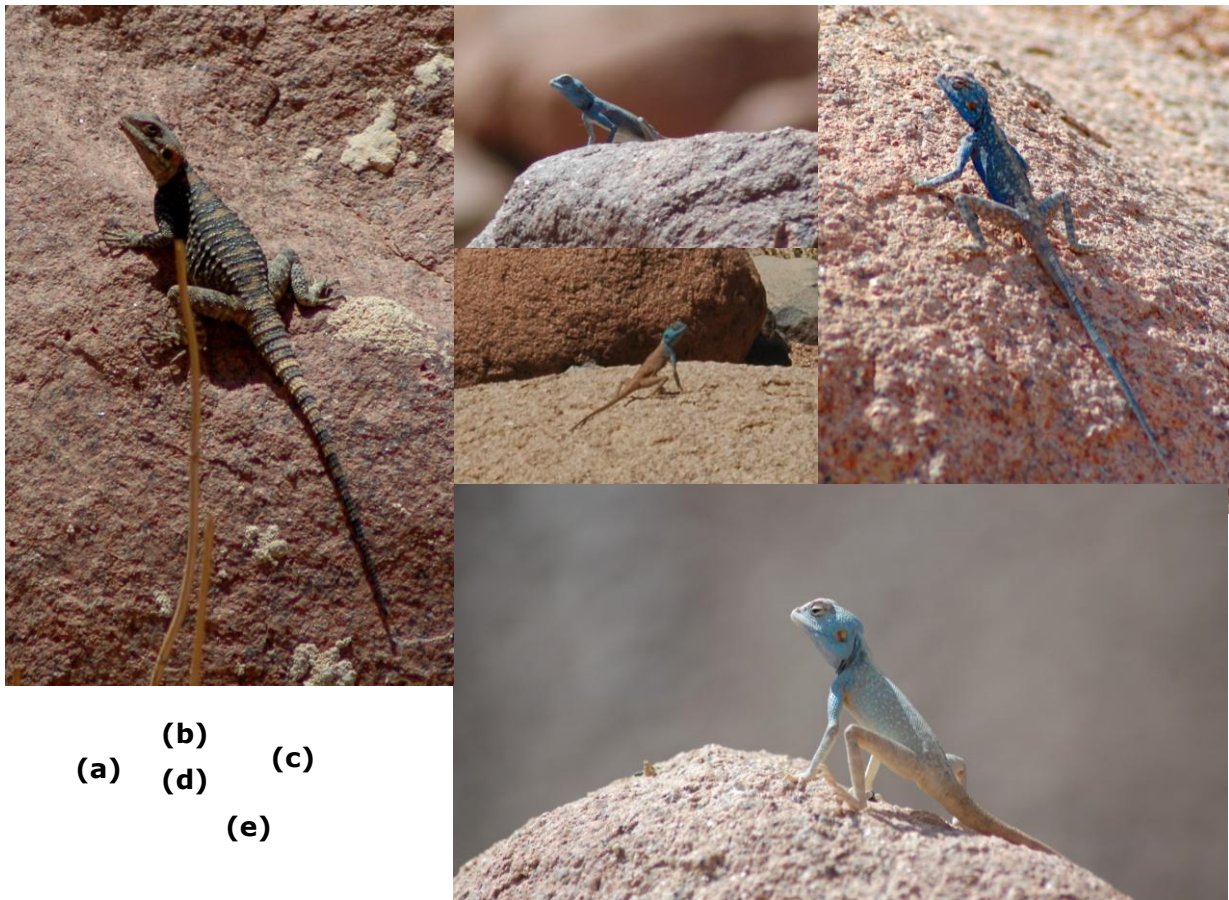


Fig 2: Colours of the two agamids of Sinai. (a) typical colouration of *Laudakia stellio*, with a dark green-grey body with orange bands across the back and tail; (b) *Pseudotrapelus sinaitus* has the ability to turn blue over most of its body; (c) note the deeper blue and speckled appearance of this individual; (d) the blue colour is often most conspicuous on the face, throat and legs. Photos by ON.

Chi-squared tests were used to compare the total number of displays performed within each microhabitat to an expected distribution, and between the species. Head-bobbing and press-ups were pooled together and classed as ‘displaying’. This test was also used to compare how often the two species were found in the sun and the shade. If an individual lizard moved from the sun into the shade (or back) during the viewing session, then it was counted more than once for this test.

Binomial logistic regression analysis was used to examine the utilisation of sun and shade throughout the day. One regression analysis was performed per species. The parameters were then taken from the regression model and inserted into the formula to predict the probability of the lizard being in the shade throughout the day.

GPS Visualiser[®] (Schneider 2009a) was used to convert GPS sightings data into a .kml file compatible with GoogleEarth 5.0, and then used to extract altitude information from the locations (Schneider, 2009b) via the SRTM1 database collected by the NASA Shuttle Radar Topography Mission (Farr *et al.* 2007): these values have an error of ± 90 m. An independent samples *t*-test was used to compare the mean altitudes at which the two species were observed.

The distances between the each lizard sighting were extracted in GoogleEarth and compared between species using a Kruskal Wallis Test.

A chi-squared test was used to see whether lizard colour varied non-randomly with respect to sun and shade. Again independence was assumed, despite certain individuals that changed from blue to not-blue within the viewing session being counted more than once. For *P.sinaitus*, binomial logistic regression analysis was carried out with blue versus not-blue as the dependent variable, and time of day as a factor. In order to test whether colour was associated with relaxed or alert behaviour, two independent samples *t*-tests were used to compare the average time spent per viewing session being 1) relaxed and 2) alert, between blue and non-blue lizards.

To test the social-signaling hypothesis of colour change, two techniques were used in order to simulate social encounters. First, lizards in the field were presented with a vivid-blue cardboard lizard model, and their reactions recorded. Models were initially placed approximately 3 m from the lizard, and then moved to within 40 cm to simulate an escalating level of threat. Second, a captive male lizard in a cage 1.9 x 1.3 x 0.7 m was presented with a mirror, and his responses recorded. An artificial environment was created to mimic the natural habitat, with a stack of rocks at one end that provided shelter and a large rock in the centre that the lizard appeared to use as a lookout point. The mirror was placed at the end of the cage furthest from the shelter, giving him the option to retreat under the rocks if distressed.

Table 4: The number of observations recorded for each test criteria

	N	Microhabitat					Sun/Shade			Displays	Colour	
		1	2	3	4	Total	Sun	Shade	Total		blue	not-blue
<i>Laudakia stellio</i>	32	6	14	19	9	48	137	111	248	58	n/a	n/a
<i>Pseudotrapelus sinaitus</i>	49	18	35	18	2	73	163	38	201	41	35	94

Results

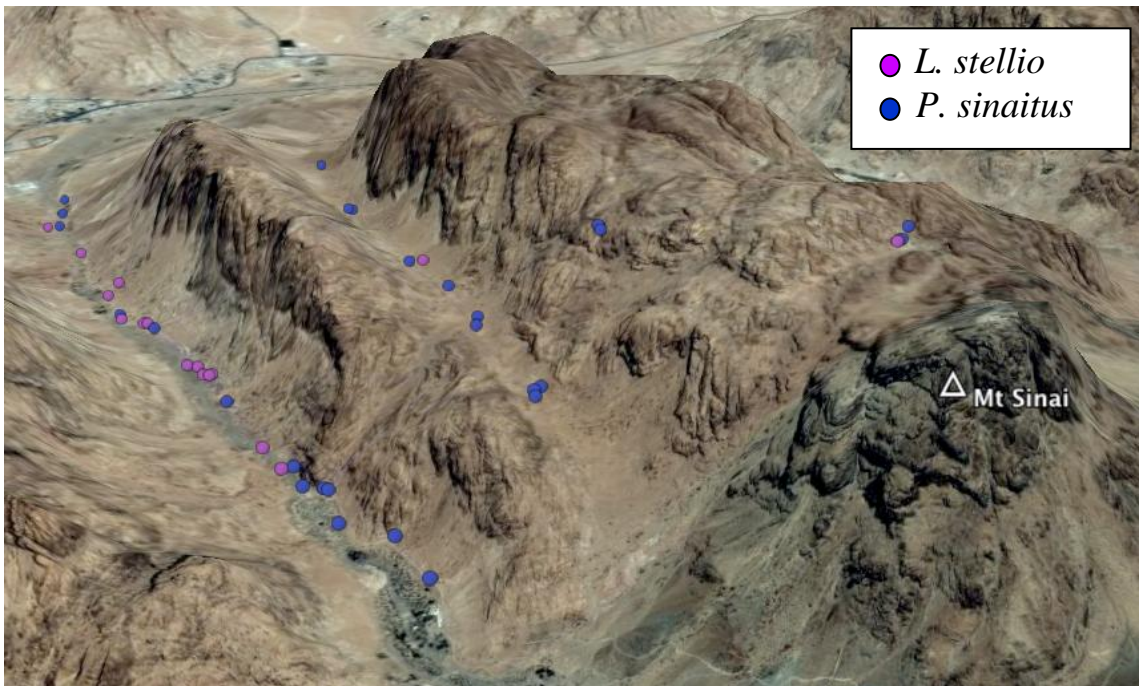
Over the five-week period of August-September 2008 the behaviour of 82 lizards was recorded: there were multiple observations made in each 15-minute time period on each lizard (Table 4). Some of the 82 sightings had incomplete data, due to lizards moving out of sight or behaving in a manner that could not be categorised. The two species overlapped considerably in where they were seen (Figs 3 & 4): *L.stellio* was found at lower average altitude (1780 ± 36 m than *P.sinaitus* (1840 ± 22 m), but the difference is not significant ($t_{81} = 1.5$, ns). There was an average of 370 m between each *Laudakia* sighting, compared to 264 m between *Pseudotrapelus* lizards, but this difference was not significant ($H_1 = 0.0605$, ns)

Utilization of the microhabitats differed between the species (Fig 5): *P.sinaitus* was more frequently seen using rocks and flat areas, whilst *L.stellio* preferred walls and cliffs more. Boulders were the most heavily utilised microhabitat overall, and steep large rocks or cliffs least (only 8% of *L.stellio* and less than 1% of *P.sinaitus*).

Fig 3: The locations where the two lizard species were seen in and around St Katherine



Fig 4: Detailed distribution of the two species in wadis Ferrah and Arbaein



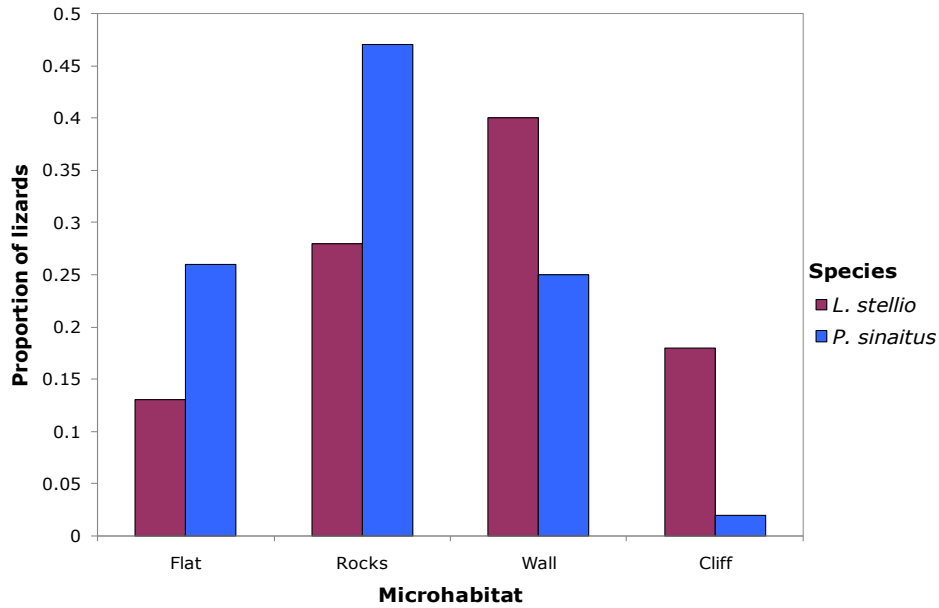


Fig 5: Proportion of observations that occurred within each microhabitat (n = 121) ($\chi^2_3 = 15.0, p < 0.01$).

We had complete data for the microhabitat durations of 32 *L.stellio* and 42 *P.sinaitus*. *P.sinaitus* spent most of the time on boulders, an average of 8.5 minutes per 15-min viewing session. *L.stellio* spent significantly less time in this microhabitat, with an average of just 3.0 minutes per 15-min viewing session (Fig 6: $t_{67} = 3.4, p < 0.001$), instead spending more time on walls and cliffs.

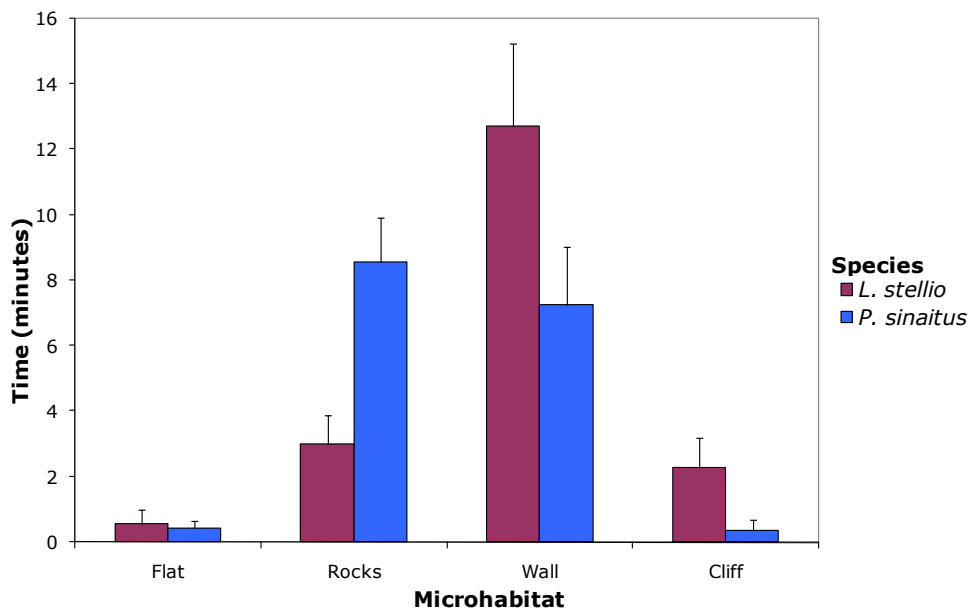


Fig 6: The average time spent by an individual lizard in each microhabitat per 15-minute viewing session (\pm s.e.m.).

The number of displays (head-bobs or press-ups) performed in each microhabitat differed between the two species (Fig. 7). *L.stellio* only displayed when on rocks, walls or cliffs and never on flat open ground. The number of displays in each microhabitat differed from the expected distribution generated from the frequency of being seen in these habitats ($\chi^2_3 = 22.7, p < 0.001$), indicating that display places are selected differently from normal activity. *P.sinaitus*

showed markedly different behaviour, performing 54 out of 58 displays (93%) on rocks or boulders, showing even greater selectivity ($\chi_3^2 = 143.8$, $p < 0.001$).

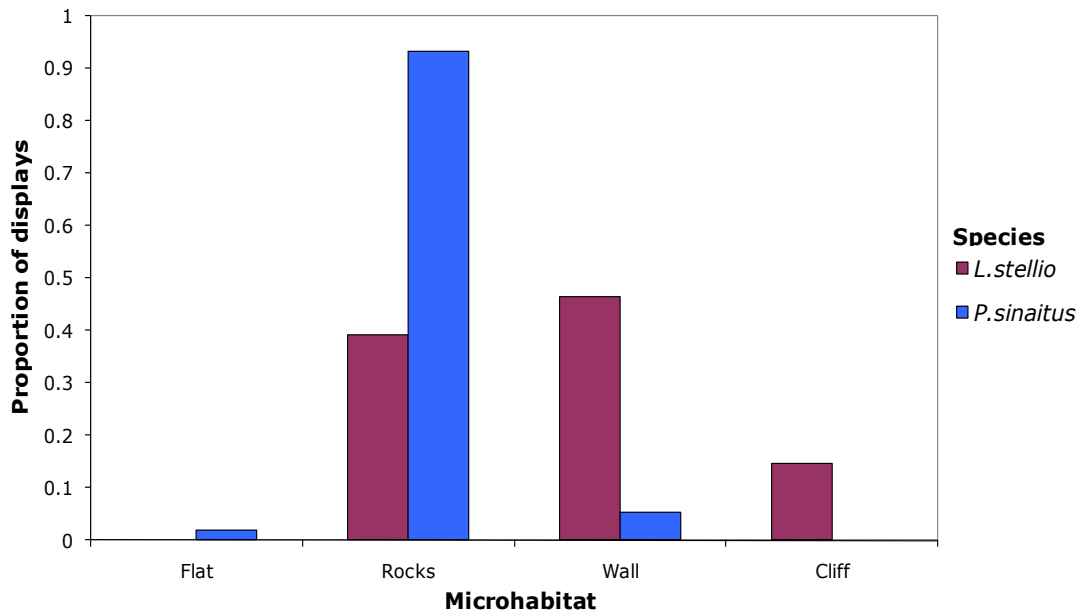


Fig 7: Proportion of all displays (head-bobs and press-ups) performed in each microhabitat between the two species. The two species differ in where they display ($\chi_3^2 = 37.45$, $p < 0.001$)

The number of individuals observed in the sun versus the shade differed between the two species ($\chi_1^2 = 28.6$, $p < 0.001$). *P. sinaitus* was seen in the sun 81% of the time, while *L. stellio* spent more time in the shade (45% in the sun). As the morning progressed, lizards of both species were less likely to be found in the sun. The temperature increased steadily, rising from an average of 23°C in the morning, up to 28°C at the end of the observation period. This means that the likelihood of *P. sinaitus* being in the shade was highest at the hottest times of the day.

We recorded the colour of all 49 individuals of *P. sinaitus*: 18 displayed some degree of blueness. Colour change was observed in both sexes. There was no association between the blue colour and whether the lizard was in the sun or the shade ($\chi_1^2 = 0.004$, ns), nor with time of day (binary logistic regression: $B = 0.002$, $df = 1$, ns). When at rest, lizards tended to be an orange-brown colour that matched the environment. When undergoing colour change, a blue flush first appeared on the neck and throat (Fig 8), spreading onto the face, down the front legs and occasionally onto the back. An entire colour change, from brown to vivid blue could happen very rapidly, within half a minute, though often the change would be slower and more gradual.

When *P. sinaitus* lizards became a more conspicuous blue colour, they tended to display alert, vigilant behaviour. On average, blue lizards spent of 93% of the observation session being vigilant, compared to 60% in non-blue lizards. There was a significant difference between both the levels of alertness ($t_{36.5} = 3.6$, $p < 0.001$) and relaxed behaviour ($t_{35.4} = 4.0$, $p < 0.001$) in blue and non-blue lizards.



Fig 8: Blue colouration first appeared on the underside of the neck (top), leaving the back orange-brown, maintaining camouflage from above (bottom).

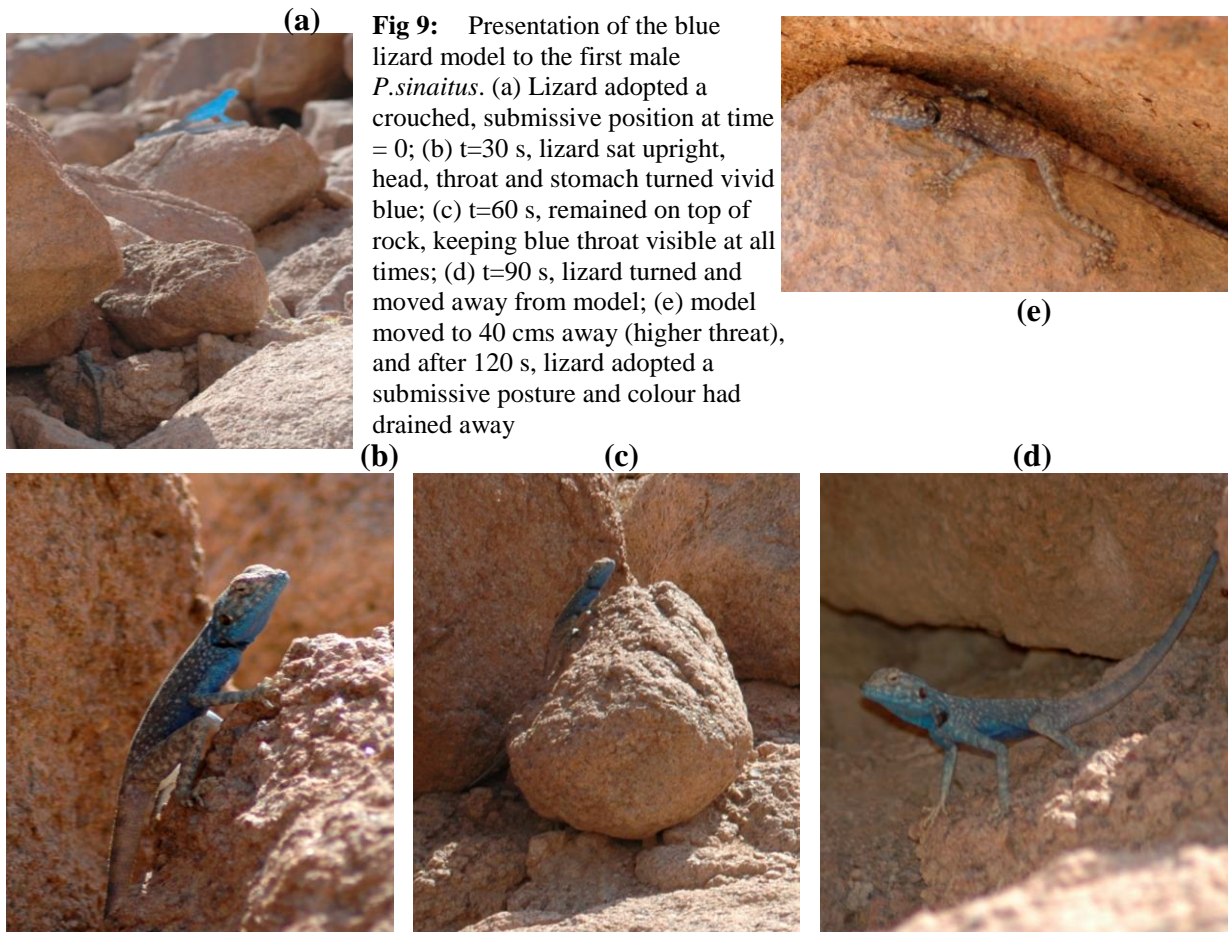


Fig 9: Presentation of the blue lizard model to the first male *P.sinaitus*. (a) Lizard adopted a crouched, submissive position at time = 0; (b) t=30 s, lizard sat upright, head, throat and stomach turned vivid blue; (c) t=60 s, remained on top of rock, keeping blue throat visible at all times; (d) t=90 s, lizard turned and moved away from model; (e) model moved to 40 cms away (higher threat), and after 120 s, lizard adopted a submissive posture and colour had drained away

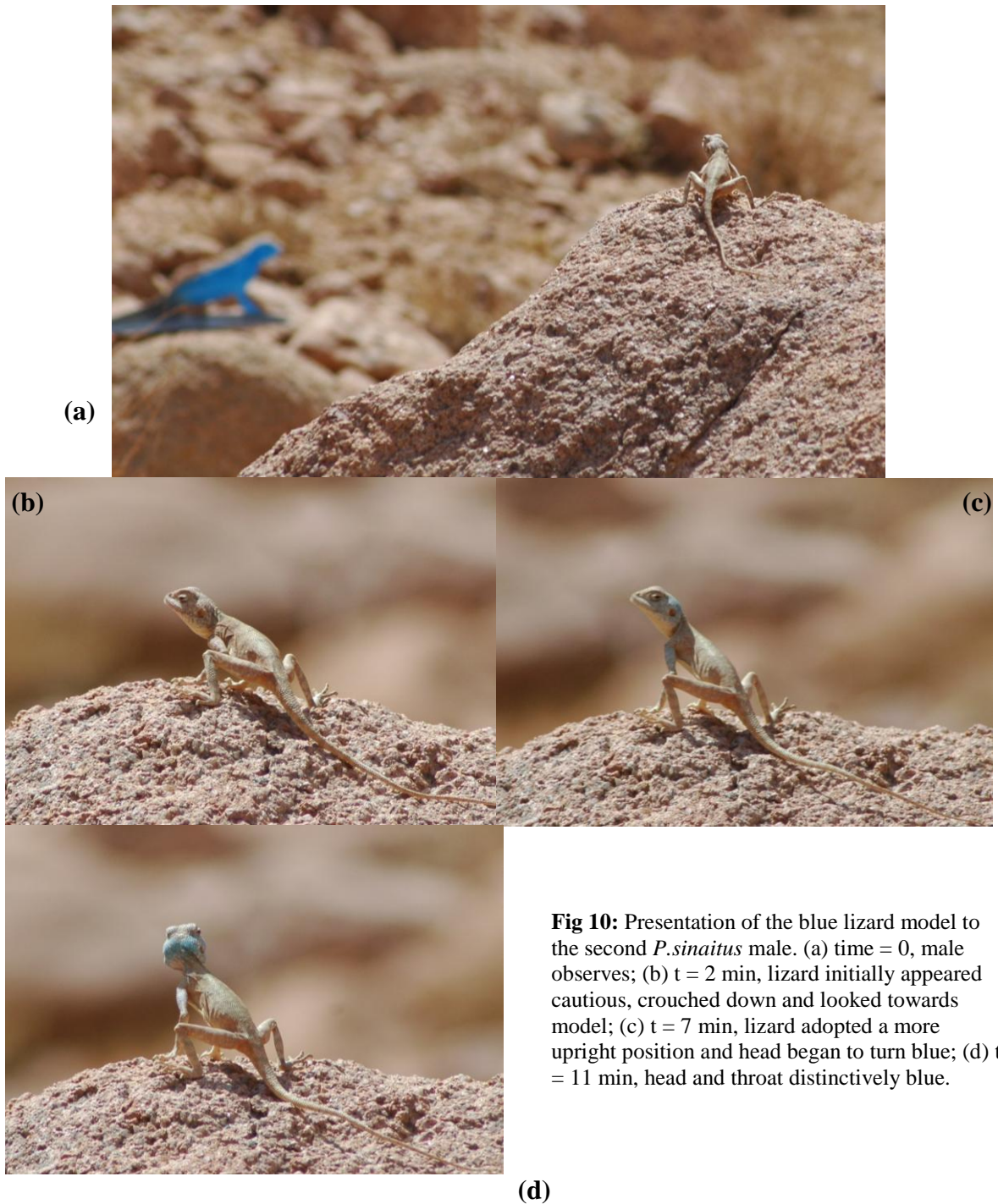


Fig 10: Presentation of the blue lizard model to the second *P.sinaitus* male. (a) time = 0, male observes; (b) t = 2 min, lizard initially appeared cautious, crouched down and looked towards model; (c) t = 7 min, lizard adopted a more upright position and head began to turn blue; (d) t = 11 min, head and throat distinctively blue.

A vivid blue model lizard was presented to two randomly selected *P.sinaitus* in the field. Figs 9 & 10 show a photographic sequence of the events that followed presentation. Both lizards responded with a change in both behaviour and colour (described in the figures).

A captive male *P.sinaitus* was presented with a mirror on three consecutive occasions. The lizard appeared to respond to the reflection, which represented another male entering his territory. His reactions differed on each occasion. On the first, the lizard was initially blue on presentation of the mirror; after looking at his reflection in the mirror, his colour faded; after 10 minutes he went blue again and went very close to mirror, and then tried to escape through the cage netting, near the mirror. On the second occasion (Fig 11), the lizard jumped to back of cage after looking at his reflection, and adopted a flat, submissive position behind a rock; his

colour faded to grey; after approximately 10 minutes, he looked at mirror and his face went slightly blue, and he then turned vivid blue and sat in an upright, apparently dominant position at the top of a rock. On the third try, the lizard remained vivid blue the entire session, and spent much of his time perched on the top of a rock in an upright, dominant position, looking directly at mirror.

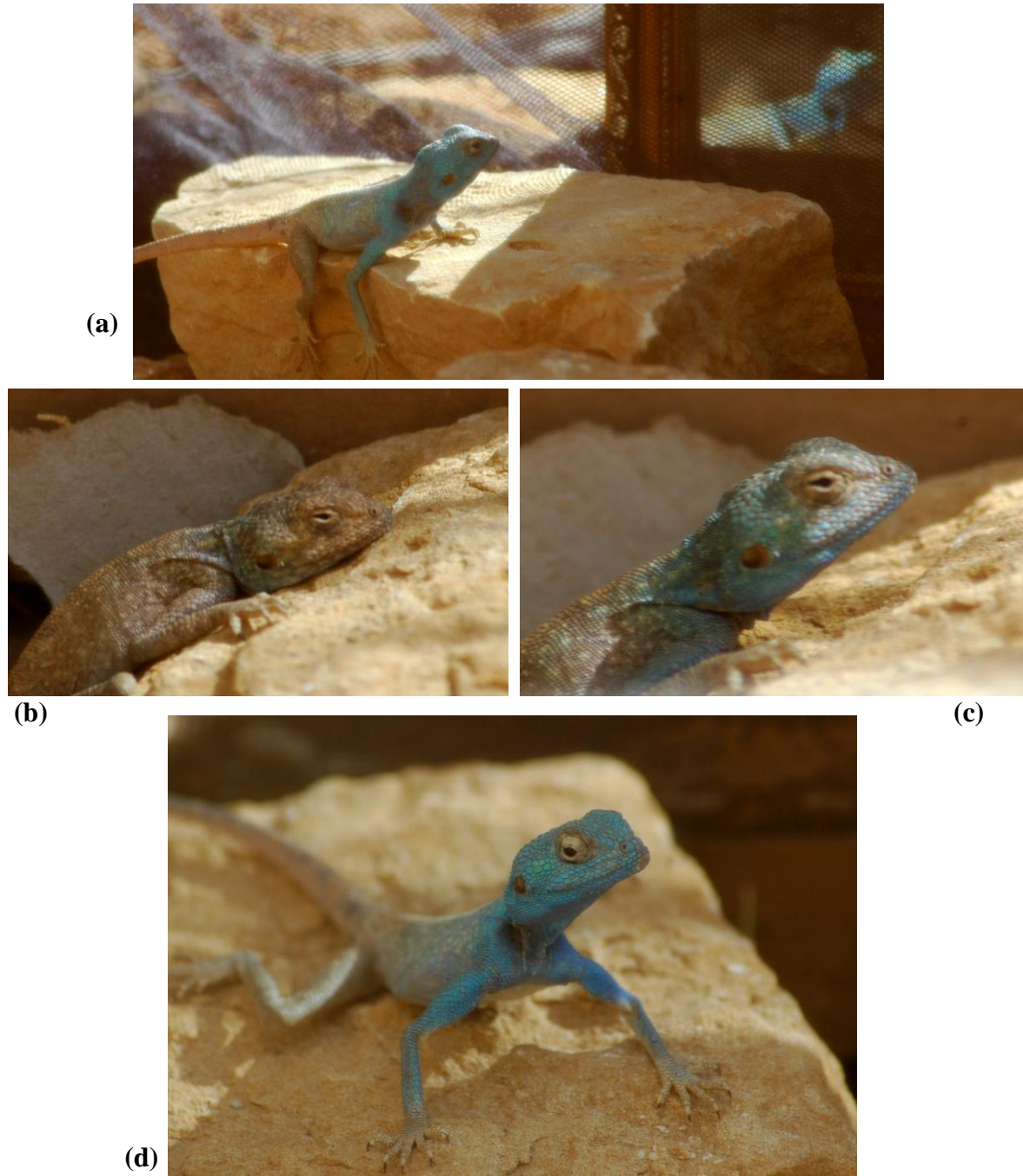


Fig 11: Reaction of a captive *Pseudotrapelus sinaitus* lizard to a mirror. The lizard was blue when the mirror was placed in front of him at time = 0. (a) On looking at the reflection, the lizard jumped to back of cage. (b) $t = 2$ mins, his blue colour faded rapidly and the lizard adopted a crouched, submissive position; (c) $t = 9$ min, the lizard raised his head and throat began to turn blue; (d) $t = 15$ min, the throat, legs and face were a vivid blue and the lizard sat upright at the top of a rock.

Discussion

This is the first comparative study of *Laudakia stellio* and *Pseudotrapelus sinaitus* in the Sinai desert. The results show that the two species differed in their use of the microhabitats within their shared environment, suggesting that these two sympatric species have distinct ecological niches within the Sinai.

Neither species spent more than 30 s per session on flat ground, and were usually observed running at fast pace through this microhabitat. Lizards are more exposed on flat, open ground and this may leave them more vulnerable to predation. During the study period we observed a range of potential predators, including birds of prey, foxes and snakes. When scared or disrupted lizards of both species would retreat to inaccessible crevices in rocks. Al-Johany (1995) reports similar behaviour in *Agama yemenesis*, which avoided feeding on flat exposed ground and used similar retreat techniques to hide from potential prey. Rocky outcrops seemed to offer a safer viewpoint, because they provided the crevices and cracks needed for a quick escape. The suitability of rocks and boulders is supported by the fact that they formed the most heavily utilised microhabitat, being used by approximately half of all observed lizards. The two species differed in the length of time they spent on rocks, with *P.sinaitus* spending significantly longer per viewing session. *P.sinaitus* spent the highest proportion of its time here and was often observed sitting at the very top of large rocks and boulders. *L.stellio* spent an average of six times longer than *P.sinaitus* on cliffs and large steep rocks, but the small sample sizes precluded statistical power.

Baha El Din (2006) stated that *P.sinaitus* are frequently found upon prominent lookouts and attributed this behaviour to male lizards defending their territory. Our results are consistent with his theory, because the vast majority (92%) of all *P.sinaitus* displays occurred on such rocks. These distinctive displays have been attributed to territoriality and mate attraction in other agamas (Al-Johany 1995) and the nature of the displays supports the theory that they are involved in social communication. They occur in short bursts of rapid movement, incorporating repeated head bobs and/or press-ups. The conspicuous and repetitious nature of the displays is crucial in lifting signal salience above background noise, and grabbing the attention of the territory invader or, for example, a potential mate (Fleishman 1992, Johnstone 1997). If display behaviour has evolved as a form of social signaling then it follows that *P.sinaitus* would display on conspicuous, elevated perches. The majority of *L.stellio* displays occurred on rocks (39%) and walls (26%), both microhabitats that combine reasonable visibility to conspecifics with easy access to the safety of crevices.

Temperature increased steadily throughout the day, so lizards were most alert in the hottest parts of the day. This is consistent with what we know about general lizard physiology, because endothermic species are generally more active when their body temperature is higher. Avery *et al.* (1982) showed that lizards reduce their activity levels, but increase their basking rates when sunlight is reduced. The species differed in their utilisation of sun and shade throughout the day with *L.stellio* spending more time in the shade. *P.sinaitus* spent most of the time in the sun, but showed evidence of actively modifying their basking rates throughout the day by moving into the shade in the hot afternoons. The results suggest that heliothermic regulation is occurring in *P.sinaitus*, with lizards controlling their body temperature by adjusting their basking rates. Heliothermic regulation is common in many reptile species with most lizards showing some degree of thermoregulation (Adolph 1990, Bennett 2004) so it is likely to be occurring undetected in *L.stellio*.

As the day progressed the wadis gradually became cast in shadow. In the afternoons the whole valley was often in shade, so lizards lacked the immediate option of accessing sunlit patches. The patterns seen could reflect passive acceptance of environmental conditions and might not reflect the lizards actively seeking the shade in the afternoons. This effect would have been more apparent in *P.sinaitus* because they spent less time in the shade earlier on in

the day. The temperature in Sinai varies throughout the year, typically reaching 25-35°C in the peak of summer and dropping to under 10°C in the winter months. On some occasions they can even experience snowfall (AllSinai, 2004). Lizards might display more obvious thermoregulatory behaviour under these more extreme conditions.

The two species overlapped considerably in their geographical distribution. Both species were found at a mean elevation of around 1800 m and there was no significant difference in the altitudes at which lizards were found. Other studies have found that lizards are highly sensitive to elevation and that species distributions can vary over just 50m (Fischer & Lindenmayer 2005). The altitudinal data used only had a sensitivity of 90 m (Farr *et al.* 2007) so is insufficient to rule out a difference between the species' altitudinal niche. Many observations came from the base of the wadi. This is not a reflection of actual lizard abundance but an artefact of the route walked. The steep terrain imposed restrictions on the route, at times limiting us to paths through base of the valleys. As a result there are insufficient data from high altitudes, so we can make no real inference about the altitudinal preferences of the two species. Though the species undoubtedly overlap it is possible that further work could reveal a difference in the boundaries of their altitudinal niche.

There was no evidence for colour being used as a mechanism of thermoregulation. Colour was not influenced by the time of day or ambient temperature, nor by whether lizards were in the sun or the shade. In closely related lizard species, colour change is predominantly used for social signaling and not as a thermoregulatory mechanism (Le Bas & Marshall 2000, Stapley & Whiting 2006, Stuart-Fox & Moussalli 2008), so the results of this study are consistent with their findings.

When a lizard began to change colour the underside of the throat was the first to turn blue. In some cases the blueness would spread across the whole back, but sometimes would remain limited to the neck and face. The agamid *Ctenophorus ornatus* uses a brightly coloured dewlap for social signaling, but their back remains camouflaged at all times. *P.sinaitus* may use a similar strategy, showing its brightest hues under the neck so it has the option of lying down and becoming cryptic at any moment. Unlike *C. ornatus*, *P.sinaitus* would sometimes turn vivid blue over the majority of the body. Blue is a conspicuous colour from a predation and camouflage perspective, but conspicuousness is the key to an effective form of communication. The maximum contrast of this blue colour against the oranges and browns of the Sinai habitat, suggests that it evolved for optimal salience, a feature common to signals (Stuart-Fox *et al.* 2007).

When lizards were not signaling they showed a high degree of camouflage and were remarkably adept at blending into the background. Like chameleons (Stuart-Fox & Moussalli 2008) they appear to have a range of cryptic colours that match the typical colours found within the environment. The accuracy of their camouflage suggests that there have been strong evolutionary pressures on remaining hidden, implying that there is a risk involved in being a conspicuous colour. The transitory nature of colour change in *P.sinaitus* means that lizards can turn completely blue in order to give maximum impact, for example if a known conspecific is close by, but can quickly return to a safer cryptic colour when the social situation passes. The vigilance levels of blue signalling lizards reflected the conspicuous nature of the colour change, with blue lizards spending 93% of each viewing session on alert, vigilant behaviour. Non-blue camouflaged lizards spent significantly longer on relaxed, non-vigilant behaviours, presumably because they were released from the risk of being seen by potential threats.

The study set up simulated several social encounters, all of which received reactions involving colour changes apparently associated with social signalling. When the blue model was moved closer, the lizard appeared to regard it as a greater threat, and assumed a crouched, submissive position and rapidly lost the blue colour from his throat. Stuart-Fox & Moussalli (2008) found that colour signals are used by dwarf chameleons in male contests, with elaborate signals equating with dominance. If *P.sinaitus* uses blue colouration as a signal of dominance

in territoriality disputes, then it could explain why this lizard rapidly drained of colour when the blue lizard model was moved deeper into his territory.

The reactions to the mirror were more difficult to interpret than with the model lizard, because the lizard and his reflection changed in colour simultaneously. When he became submissive, so did the challenger, and when he then responded by becoming blue, so did the apparent challenger. The limitations of this experiment were that the virtual territory dispute could never escalate, nor could either lizard, real or reflected, back off and admit defeat. The reactions of the captive lizard suggest that he may have learnt that this stranger did not pose a real threat, because on the third presentation of the mirror he assumed a dominant position and vivid blue colour immediately.

Further research is needed to determine the precise role of colour change in the behaviour of *P.sinaitus*. Comparisons to other species suggest that the transitory vivid blues are likely to be used in communication between lizards. The results of the simulated social encounters supported this theory, but the study lacks observations of real interacting lizards in the field. An experimental study which set up social scenarios between captive lizards might prove more successful at determining whether these signals are involved in, for example, territorial disputes or mate-attraction. It would also be beneficial to incorporate UV-spectroscopy into future studies, because UV-colouration plays a crucial role in signaling in other lizard species (Fleishman *et al.* 1993, Le Bas & Marshall 2000, Stapley & Whiting 2006, Stuart-Fox *et al.* 2007).

Acknowledgements

We thank the Teaching Quality Enhancement Fund of Nottingham University for funding the work; the St Katherine Protectorate for permission to work in the Park; Farag Fox and all the staff of Fox Camp for facilities; and Professor Jerzy Behnke for his advice and support.

References

- Adolph SC (1990) Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* 71(1): 315-327
- Al-Johany AW (1995) The ecology of *Agama yemenesis* Klausewitz (Lacertilia: Agamidae) in south-western Arabia. *Journal of Arid Environments* 29:495-503
- AllSinai (2004) Weather: St Katherine. *AllSinai.info*, <http://www.allsinai.info/sites/weather.htm>
- Avery RA, Bedford JD & Newcombe CP (1982) The role of thermoregulation in lizard biology: predatory efficiency in a temperate diurnal basker. *Behavioral Ecology & Sociobiology* 11: 261-267
- Baha El Din SB (2006) *A guide to the Reptiles and Amphibians of Egypt*. The American University in Cairo Press, Cairo.
- Barracough TG & Vogler AP (2000) Detecting the geographical pattern of speciation from species-level phylogenies. *American Naturalist* 155(4): 419-434
- Bennett AF (2004) Thermoregulation in African chameleons. *International Congress Series* 1275: 234-241
- Bryant EH & Meffert LM (1993) The effect of serial founder-flush cycles on quantitative genetic variation in the housefly. *Heredity* 70: 122-129
- Carson HL & Templeton AR (1984) Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annual Review of Ecology & Systematics* 15: 97-132
- Coyne JA (1992) Genetics and speciation. *Nature* 355: 511-515
- Daly BG, Dickman CR & Mathew SC (2006) Selection of habitat components by two species of agamid lizards in sandridge desert, central Australia. *Austral Ecology* 32(7): 825-833
- Farr TG, Rosen PA, Caro E, Crippen R, Duren R, Hensley S, Kobrick M, Paller M, Rodriguez E, Roth L, Seal D, Shaffer S, Shimada J, Umland J, Werner M, Oskin M, Burbank D & Alsdorf D (2007) The shuttle radar topography mission. *Reviews of Geophysics* 45.
- Fischer J & Lindenmayer DB (2005) The sensitivity of lizards to elevation: a case study from south-eastern Australia. *Diversity & Distributions* 11(3): 225-233
- Fleishman LJ (1992) The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *American Naturalist*, 139: S36-S37
- Fleishman LJ, Loew E & Leal M (1993) Ultraviolet vision in lizards. *Nature* 365: 397
- Frost DR & Etheridge R (1989) Phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata) *Miscellaneous Publications: Museum of Natural History, University of Kansas* 81: 65

- Fu C, Mang J, Pu Z, Zhang S, Chen H, Zhao B, Chen J & Wu J (2007) Elevational gradients of diversity for lizards and snakes in the Hengduan Mountains, China. *Biodiversity & Conservation* 16: 707–726
- Galiana A, Moya A & Ayala FJ (1993) Founder-flush speciation in *Drosophila pseudoobscura*: a large-scale experiment. *Evolution* 47(2): 432–444
- Garland T & Losos JB (1994) Ecological morphology of locomotor performance in squamate reptiles. In Wainwright PC & Reilly SM (eds) *Ecological Morphology*, pp 240–302. University of Chicago Press, Chicago
- Gilbert F, Willmer PG, Semida F, Ghazoul J & Zalat S (1996) Spatial variation in selection in a plant-pollinator system in the wadis of Sinai, Egypt *Oecologia* 108: 479–487
- Herrel A, Cleruren J & De Vree F (1995) Prey capture in the lizard *Agama stellio*. *Journal of Morphology* 224(3): 313–329
- Huey RB, Pianka ER & Hoffman JA (1977) Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecology* 58: 1066–1075
- James CD & Shine R (2000) Why are there so many coexisting species of lizards in Australian deserts? *Oecologia* 125: 127–141
- Johnstone R (1997) Chapter 7, The Evolution of Animal Signals. In Krebs JR & Davies NB (eds) *Behavioural Ecology: an evolutionary approach*, 4th Ed. Wiley–Blackwell, Oxford
- Le Bas NR & Marshall NJ (2000) The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus*. *Proceedings of the Royal Society of London B* 267: 445–452
- Losos JB (1990) Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* 60(3): 369–388
- Losos JB & Schluter D (2000) Analysis of an evolutionary species-area relationship. *Nature* 408: 847 – 850
- McKittrick MC (1993) Phylogenetic constraint in evolutionary theory: has it any explanatory power? *Annual Review of Ecology & Systematics* 24: 307–330
- Mayr E (1942) *Systematics and the Origin of Species, from the viewpoint of a zoologist*. Harvard University Press Cambridge
- Morrison RM, Sherbrooke WC & Frost-Mason SK (1996) Temperature-sensitive, physiologically active iridophores in the lizard *Urosaurus ornatus*: an ultrastructural analysis of color change. *Copeia* 4: 804–812
- Muller HJ (1942) Cited by: Orr HA (1995) The population genetics of speciation: the evolution of hybrid incompatibilities. *Genetics*, 139: 1805–1813
- Pianka ER (1969a) Habitat specificity, speciation, and species density in Australian desert lizards. *Ecology* 50: 498–502
- Pianka ER (1969b) Sympatry of desert lizards (*Ctenotus*) in western Australia. *Ecology* 50: 1012–1030
- Sinervo B & Losos JB (1991) Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard populations. *Ecology* 72: 1225–1233
- Schneider A (2009a) Draw a Google Map from a GPS file. *GPS Visualizer*. [http:// www.gpsvisualizer.com/map_input](http://www.gpsvisualizer.com/map_input).
- Schneider A (2009b) Find “missing” elevations with GPS Visualizer. *GPS Visualizer*. [http:// www.gpsvisualizer.com/elevation](http://www.gpsvisualizer.com/elevation).
- Stapley J & Whiting MJ (2006) Ultraviolet signals fighting ability in a lizard. *Biology Letters* 22 (2): 169–172
- Stuart-Fox D & Moussalli A (2008) Selection for social signalling drives the evolution of chameleon colour change. *Proceedings of the Royal Society of London B* 296(1): 25
- Stuart-Fox D, Moussalli A & Whiting MJ (2007) Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration. *American Naturalist* 170(6): 916–930
- Stuart-Fox D, Moussalli A & Whiting MJ (2008) Predator-specific camouflage in chameleons. *Biology Letters* 4(4): 326–329
- Zalat S & Gilbert F (1998) *A walk in Sinai: St Katherine to Al Galt Al Azraq*. Egyptian Journal of Natural History 1: 1–64
- Zalat S & Gilbert F (2008) *Gardens in a sacred landscape: Bedouin heritage and natural history in the high mountains of Sinai*. Illustrated by Ahmed Gheith. American University in Cairo Press, Cairo

الملخص العربي

دراسة مقارنة على نوعين من زواحف أجاميد (حردون ستيليو وحردون سيناء) في جنوب سيناء أوليفيا نورفولك¹، آليس ميلوتي¹، فرانسيس جلبرت¹، سامي زلط²، توم ريدير¹

1. قسم العلوم البيولوجية – جامعة نوتجهايم – المملكة المتحدة

2. قسم العلوم البيولوجية – كلية العلوم والآداب – جامعة طيبة فرع العلا – المملكة العربية السعودية

تناولت الدراسة مقارنة أماكن المعيشة وسلوك نوعين من الزواحف من مجموعة الحرادين وهما: حردون ستيليو وحردون سيناء. وبالرغم من أن النوعين يتشاركان في أماكن المعيشة والتواجد، إلا أن الاستخدام يتم بطريقة مختلفة، حيث يقضى النوع "حردون سيناء" وقت أطول على الصخور مقارنة بالنوع الآخر "حردون ستيليو"، وأيضاً أظهر النوع قدرة أكثر على تنظيم درجة حرارة جسمه حيث كان يقضى أغلب الوقت في الشمس ويتحرك لمنطقة الظل خلال فترة الظهيرة حيث الحرارة العالية، وهذا يوضح أن النوعين يتباينان في احتياجاتهم من الحرارة وكذلك في طريقة تنظيمهم للحرارة داخل أجسادهم.

أظهرت النتائج أيضاً أن حردون سيناء له قدرة عالية وسريعة على تغير ألوان جسده ولم تظهر أي شواهد عن علاقة تغير اللون بدرجات الحرارة ولكن على الأرجح أن تكون مرتبطة بالاتصال مع الأفراد الآخرين (سلوك اجتماعي). وضح أن اللون الفاتح يعني أن الحيوان يزيد من فرص وضوحه، حيث شوهد الحيوان بنسبة 93% خلال فترة المشاهدة مغطى باللون الأزرق الفاقع مع اليقظة التامة مقارنة بلونه البني المشابه للوسط المحيط والذي شوهد بنسبة 60% خلال فترة المشاهدة. ربما يكون التغير المفاجئ من اللون الأزرق الفاقع إلى البني المحاكي للبيئة قد نشأ حتى يساعد الحيوان في الظهور والوضوح بصورة سريعة استجابة لعلامات معينة. ولقد أجرينا تجربة معملية من خلال دراسة استجابة الحيوان لأفراد أخرى من خلال استخدام موديل للحردون تم تلوينه باللون الأزرق الفاقع وباستخدام مرايات عاكسة، وأوضحت التجربة استجابة ايجابية من الحيوان من خلال تغير لونه مما يدعم فكرتنا بأن تغيير اللون يضع فرضية الاتصال الاجتماعي بين الأفراد المختلفة هو الأقرب إلى الحقيقة.