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Colour change on different body regions provides thermal and signalling advantages in bearded dragon lizards

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Many terrestrial ectotherms are capable of rapid colour change, yet it is unclear how these animals accommodate the multiple functions of colour, particularly camouflage, communication and thermoregulation, especially when functions require very different colours. Thermal benefits of colour change depend on an animal's absorptance of solar energy in both UV–visible (300–700 nm) and near-infrared (NIR; 700–2600 nm) wavelengths, yet colour research has focused almost exclusively on the former. Here, we show that wild-caught bearded dragon lizards (*Pogona vitticeps*) exhibit substantial UV–visible and NIR skin reflectance change in response to temperature for dorsal but not ventral (throat and upper chest) body regions. By contrast, lizards showed the greatest temperature-independent colour change on the beard and upper chest during social interactions and as a result of circadian colour change. Biophysical simulations of heat transfer predicted that the maximum temperature-dependent change in dorsal reflectivity could reduce the time taken to reach active body temperature by an average of 22 min per active day, saving 85 h of basking time throughout the activity season. Our results confirm that colour change may serve a thermoregulatory function, and competing thermoregulation and signalling requirements may be met by partitioning colour change to different body regions in different circumstances.

1. Introduction

Many terrestrial ectotherms are able to change colour rapidly to modify their temperature [1–5]. All else being equal, 'dark' coloured individuals (i.e. with low reflectance) absorb more solar radiation than 'light' coloured individuals (i.e. with higher reflectance) and the energy absorbed is converted into heat such that dark individuals will heat faster and reach higher steady-state body temperatures [6,7]. However, seldom is 'all else equal' because animals must accommodate multiple, often competing functions of colour such as camouflage, communication and thermoregulation. Quantitative evidence for a thermoregulatory function of colour change is scarce because the potential thermal advantages depend on how the skin reflects solar energy across the ultraviolet (290–400 nm), human-visible (400–700 nm) and near-infrared (NIR) (700–2600 nm) spectrum [8], and it is very rare for all relevant solar radiation wavelengths to be considered or measured. Although the vision of animals is restricted to the UV–visible (UV–vis) range (300–700 nm), more than half of the sun's energy-rich radiation occurs in the NIR [1,9]. Moreover, animal-visible coloration (300–700 nm) is a poor predictor of reflectance of all solar radiation (300–2600 nm [1,6,7]). It is therefore essential to measure changes in both UV–vis and NIR reflectance, and their interaction. For brevity, we refer here to changes in reflectance across the UV–vis and NIR wavelength ranges as 'colour change'.

Although temperature-dependent colour change is anecdotally common in terrestrial ectotherms, only a few studies have quantified the extent of full-spectrum colour change as a result of temperature [1,9–11]. Other studies have documented temperature-dependent coloration extending from the visible into only part (700–1100 nm) of the NIR spectrum [4,12–19]. Moreover, to assess how such changes in skin reflectance (i.e. the proportion of incident radiation reflected by a surface at each wavelength interval) may affect thermoregulation, we need to estimate the thermal benefits of colour because environmental conditions change through the day and seasons, with ensuing fitness consequences. The overall ratio of reflected to incident solar radiation (i.e. integrated over the full wavelength range of direct sunlight, approx. 300–2600 nm) is termed reflectivity (see Material and methods). Changes in reflectivity can influence the rate of radiant heat gain and steady-state body temperature of an animal, which can be estimated using energy balance equations of heat transfer through radiation, convection, conduction, metabolism and evaporation [20–23]. Ideally, such biophysical models should be based on biological and environmental data specific to the animal's native habitat and be validated empirically. Nevertheless, only a handful of studies have estimated potential thermoregulatory consequences of colour change in different organisms using any form of biophysical modelling [24–29], and none of these studies considered colour changes in different body regions.

In this study, we measured temperature-dependent colour change across the majority of the solar spectrum relevant to thermal balance (300–2100 nm) in wild-caught central bearded dragon lizards, *Pogona vitticeps*, held briefly in captivity. This species is well known both for its marked colour change and for colour variation among different populations [14,30,31]. Bearded dragons can change their dorsal coloration from dark grey to bright yellow or reddish orange. Physiological colour change in bearded dragons occurs over a time scale of seconds to minutes as a result of movement of pigments within dermal chromatophore cells—in particular, the dispersion or aggregation of melanin pigment within melanophores (melanin-containing chromatophores) [32,33]. In lizards, the regulation of colour change may be under endocrine control, neural control or a combination of the two [34,35], and may be triggered by a range of environmental cues including temperature, circadian rhythm, background colour and the presence of conspecifics or predators [36].

Importantly, the large size of bearded dragons relative to most lizards makes a thermal benefit from colour change more likely because their thicker boundary layers couple them more strongly to radiative heat exchange than to convection, and their large mass dampens body temperature fluctuations [6,20,37–39]. We assessed the extent and speed of temperature-dependent colour change in these lizards by testing individuals at temperatures commonly experienced in their natural environment (15°C and 40°C), taking reflectance measurements at the end of experiments and time-series photos for the duration of trials. We compared the temperature-dependent colour change to the maximum potential colour change by measuring colour change responses to staged social interactions with conspecifics, and at different times of day or night because bearded dragons show circadian colour change [30]. Lastly, we used biophysical simulations to estimate how the maximum observed reflectivity change affected basking time required to reach active body temperatures at our study site.

2. Material and methods

(a) Study site

Lizards were captured by hand north of Walpeup, Australia (35°08′10″ S, 142°01′30″ E), during the breeding season. The environment comprises semi-arid mallee woodland, dominated by the silver emu-bush (*Eremophila scoparia*) and blue-leaved mallee (*Eucalyptus polybractea*) trees. The climate of this region during the breeding season (austral spring: September–November) is dominated by warm, sunny days and cool nights (temperature range: 0.6°C–44.7°C), with very little rainfall.

Twelve adult male lizards were captured during October 2013 and transported in cloth bags to the Mallee Research Station (Walpeup, Victoria, Australia). We focused on males during the breeding season because they are likely to show the greatest colour change due to sexual and territorial signalling [40]. Each lizard was weighed, measured and housed individually in large white plastic bins (60 cm L × 45 cm W × 20 cm D) with a bark hide, food/water dishes and a heat lamp (during natural daylight hours), providing a thermal gradient of 23.1°C–38.2°C within the enclosure. Lizards were fed live mealworms and chopped leafy green vegetables daily, and released at their site of capture within 14–17 days of capture.

(b) Temperature-dependent colour change

Temperature experiments at the field station were conducted during hours of normal lizard activity in the spring (08.00–17.00 h). In order to test the effect of environmental temperature on lizard skin coloration (in the absence of background matching and the influence of solar radiation), lizards were placed into a temperature-controlled incubator (32 cm L × 36 cm W × 45 cm H; Exo Terra®, Rolf C. Hagen Corp., USA) with a solid white background, constant lighting and tested for 45 min at 15°C and 40°C. The temperatures 15°C and 40°C were chosen because they reflect the upper and lower limits of the minimum and maximum active core body temperatures of these lizards in the wild (electronic supplementary material, table S1), and are within the natural temperature range experienced in this region during the spring. Additionally, lizards of approximately 50–220 g take about 20–30 min to reach a steady-state body temperature [41]; therefore, we ran experiments for 45 min to allow enough time for all lizards to acclimate (range of lizard masses: 169.4–350.1 g). Temperature within the incubator (recorded with a Thermochron iButton data logger suspended inside the incubator; Embedded Data Systems, USA) showed minor fluctuations (mean ± s.e. of cold experiments = 14.74 ± 0.26°C; mean ± s.e. of hot experiments = 40.72 ± 0.44°C). Each lizard was tested at the two temperatures, with the order of treatments alternated between lizards (15°C treatment first or second, lizards were taken out of the incubator and tested at second treatment within 24 h).

Digital photos of the dorsal surface of the lizard were taken every minute for the 45 min of each experiment by a remote operated digital camera (Canon EOS 600D, Canon Inc., Australia) mounted on the ceiling of the temperature-controlled chamber. All photos were taken under the same lighting conditions and camera settings: shutter speed 1/15 s, f 4.0, ISO 200. A photo of a digital grey/white/black card (Shenzhen Micnova Photo Industrial Co., China), with 30% grey reflectance, was taken at the end of each experiment to standardize images (electronic supplementary material). Because digital photos only accounted for dorsal body regions, we also removed the lizard from the incubator at the end of the every experiment and measured the reflectance of three dorsal body regions—top of the head and back (light and dark regions)—and two ventral body regions: the beard (throat) and chest (less than 15 s until first scan; total measurement time of less than 1 min). Measurements were taken using an Ocean Optics dual-spectrometer

system (Ocean Optics, USA) consisting of two spectrometers (USB2000+, 300–1000 nm and NIRQuest, 1000–2150 nm) with two light sources (PX-2 pulsed Xenon light for the UV–vis range and HL2000 tungsten halogen lights for the vis–NIR range) connected with a quadrifurcated fibre optic. The probe on the end of the fibre optic was held in an Ocean Optics RPH-1 probe holder at a constant angle (45°) and distance from the lizard skin (measurement area of 5×3 mm oval). Each measurement was expressed relative to a Spectralon 99% white reflectance standard (Labsphere, USA).

Hue, chroma and luminance values were calculated from linearized and equalized photos (details in the electronic supplementary material) for only the dorsal (head, back and tail) regions for each photo using a custom MatLab (Mathworks, USA) script written by J.A.E. The time-series of photographs enabled us to estimate the speed of dorsal colour change in the 15°C and 40°C temperature treatments (the electronic supplementary material). Although photos only measure colour in the human-visible spectrum (400–700 nm), they provide an indication of the speed of change across the full wavelength range of interest given the strong correlation between visible and NIR reflectance during colour change in bearded dragons [30].

From reflectance spectra, we calculated average reflectance for the UV–visible part of the spectrum (300–700 nm) and the NIR (700–2100 nm), and the standardized difference between them [(NIR–UVvis)/(NIR + UVvis)]. We also calculated reflectivity, which is a function of reflectance and solar irradiance. Specifically, reflectivity, R is

$$R = \frac{S(\lambda)I(\lambda)\,\mathrm{d}\lambda}{I(\lambda)\,\mathrm{d}\lambda}, \tag{2.1}$$

where S is reflectance and I is solar irradiance. Although the spectrum of solar radiation extends to 2600 nm, both skin reflectance and solar radiation reaching the earth's surface is very low above 2000 nm (only 5% of the total solar irradiance); consequently, the portion of the spectrum above 2000 nm has very little effect on reflectivity [8]. Therefore, we calculated reflectivity from 300 to 2100 nm using the ASTM G-173 standard irradiance spectrum for dry air derived from SMARTs v. 2.9.2 [42,43].

(c) Temperature-independent colour change

To compare observed temperature-dependent colour change to its maximum extent, we measured skin reflectance in response to staged social interactions, as well as at different times of day (07.00 h and 23.00 h); this species shows circadian colour change and is darkest and lightest at approximately these times, respectively [30]. For social interactions, each lizard was randomly paired and placed together in large white plastic bins, 60 cm L × 45 cm W × 20 cm D at the field station for 10 min, or until the focal lizard displayed characteristics of either dominant (gaping and circling, head bobbing, beard darkening, push-up) or submissive behaviour (arm waving, fleeing), and its coloration was measured using the Ocean Optics dual-spectrometer system. By pairing males with different opponents, we were able to elicit both 'dominant' and 'submissive' coloration for a given individual. We estimated the maximum extent of colour change for each body region (head, beard, light back, dark back and chest) of each individual as the difference between the highest and lowest total reflectance under any of the circumstances described above.

(d) Statistical analysis

To test whether temperature had an effect on lizard skin reflectance (UV–vis, NIR, standardized differences between them, reflectivity) or colour derived from photos (hue, chroma, luminance), we used general linear mixed models (GLMM; PROC Mixed; SAS v. 9.3, SAS Institute) for each skin reflectance variable with temperature (15°C and 40°C) and body region (head, beard, light back, dark back and chest), and their interaction as fixed factors. Lizard ID was included in all models as a random effect to account for repeated measures on the same individual. To examine significant effects, we conducted post hoc tests for each temperature or body region separately and corrected p-values for multiple tests using false discovery rate [44].

The spectral data from the temperature-independent colour change experiments were analysed in the same manner, except with colour (light and dark) and body region (head, beard, light back, dark back and chest) and their interaction as the fixed factors (and lizard ID as the random factor).

(e) Biophysical simulations of heating rates

We modelled the effect of differences in skin reflectance on warming rate at the study site using the transient heat budget model and microclimate model originally described in [25]. Specifically, the net environmental heat flow to the animal, Q_e, is

$$Q_e = Q_{solar} + Q_{IR} + Q_{conv}, \tag{2.2}$$

where Q_{solar}, Q_{IR} and Q_{conv} are heat flows via solar radiation, infrared radiation and convection, respectively. Following Porter *et al*. [25], we did not include metabolism, evaporation and conduction. Body temperature T_b is the sum of the steady y_p and transient y_c thermal state, $T_b = y_p + y_c$, and is formulated as

$$T_b = \frac{j}{k} + \left(T_b - \frac{j}{k}\right)e^{-kt} \quad \text{and} \quad \frac{\mathrm{d}T_b}{\mathrm{d}t} = j - kT_b, \tag{2.3}$$

where $j = (Q_{sol,abs} + h_c\ A_{tot}\ T_{air} + h_r\ A_{tot}\ T_{rad})/C$. Solar radiation absorbed by the lizard is the sum of the direct, diffuse and reflected radiation absorbed, i.e. $Q_{sol,abs} = \alpha_{liz}(Q_{sol,norm}(1 - p_{diff})A_{sil} + Q_{sol}p_{diff}F_{sky}A_{tot} + \alpha_{sub}Q_{sol}F_{sub}A_{tot})$. The terms α_{liz} and α_{sub} are the lizard and ground solar absorptivity, respectively. We assume that absorptivity is $1 - R$. $Q_{sol,norm}$ is direct solar radiation normal to the direction of the sun's rays, i.e. $Q_{sol,norm} = Q_{sol}/\cos(Z)$, where Q_{sol} is solar radiation reaching flat ground and Z is the zenith angle of the sun. p_{diff} is the fraction of Q_{sol} that is diffuse (here assumed to be 0.15), F_{sky} and F_{sub} are the configuration factors to the sky and substrate (assumed to each be 0.4), A_{tot} is the total surface area of the lizard and A_{sil} is the silhouette area of the lizard to the sun. We computed A_{tot} and A_{sil} using the allometric formulae presented in [25] for the lizard *Dipsosaurus dorsalis*, which has a very similar morphology, and used the equation for A_{sil} normal to the sun. The term $kT_b = T_b(h_c\ A_{tot} + h_r\ A_{tot})/C$, with the time constant $1/k$ accounting for the response time of T_b between steady and transient states that influences heat transfer through the animal depending on individual thermal mass. Here, C is the thermal capacitance (specific heat capacity × mass, assuming a value of 3073 J kg^{-1} C^{-1} for heat capacity), h_c is the convection coefficient and h_r is the radiation coefficient. h_c was computed as the combination of free and forced convection coefficients, where the Nusselt/Reynolds number relation for forced convection was assumed to be $Nu = 0.35\ Re^{0.6}$ as determined by Porter *et al*. [25] and the free convection coefficient was computed using the methods for horizontal cylinders from [45]. The h_r was approximated in our model by a Taylor series expansion $4\varepsilon\sigma((T_b + T_{rad})/2 + 273.15)^3$ with emissivity ε (0.95) and Stefan–Boltzmann constant σ.

These models are now part of the NicheMapR biophysical modelling package (v. 1.0, https://github.com/mrke/NicheMapR/releases) for R (v. 3.2.2; R Foundation for Statistical Computing) and the script implementing them for this study, 'bearded dragon field heating rate.R', can be found at https://github.com/mrke/bearded-dragons.git. We used the NicheMapR microclimate model, integrated with a continent-wide daily weather database [46], which we queried for the study site for all days in the year 2013 to obtain hourly estimates of air temperature and wind

Table 1. Mean (±s.e.) change in UV–vis total reflectance, NIR total reflectance and reflectivity (the ratio of reflected to incident solar radiation over the whole wavelength range of interest, i.e. 300–2100 nm) for the temperature-dependent and temperature-independent colour change ($n = 12$).

	dorsal		ventral	
	mean % change (±s.e.m.)	min – max % change	mean % change (±s.e.m.)	min – max % change
UV–vis				
temperature-dependent	7.0 ± 0.6	0.5–14.4	0.2 ± 2	0.3–19.4
temperature-independent	9.0 ± 0.6	3.2–22.7	16.5 ± 0.09	3.4–29.8
NIR				
temperature-dependent	3.1 ± 0.4	0.1–8.4	0.8 ± 1.1	0.2–12.6
temperature-independent	5.2 ± 0.4	1.4–16.2	8.2 ± 0.7	0.4–14.1
reflectivity				
temperature-dependent	7.4 ± 0.7	0.02–15.0	0.5 ± 2	0.04–19.5
temperature-independent	10.5 ± 0.6	1.1–27.4	16.0 ± 1.6	1.1–30.8

Table 2. The effect of temperature treatment (15°C versus 40°C) and body region (head, light back, dark back, beard, upper chest) on reflectance and reflectivity (the ratio of reflected to incident solar radiation; $n = 12$).

dependent variable	fixed factors	$F_{d.f.}$	*p*-value
UV–vis reflectance	temperature	$17.69_{1,92}$	<0.0001*
	body region	$10.38_{4,92}$	<0.0001*
	temperature × body region	$3.22_{4,92}$	0.016*
NIR reflectance	temperature	$15.58_{1,92}$	0.0002*
	body region	$27.24_{4,92}$	<0.0001*
	temperature × body region	$1.44_{4,92}$	0.23
standardized difference (NIR–UV–vis)	temperature	$17.55_{1,92}$	<0.0001*
	body region	$1.83_{4,92}$	0.13
	temperature × body region	$7.06_{4,92}$	<0.0001*
reflectivity	temperature	$23.05_{1,92}$	<0.0001*
	body region	$13.95_{4,92}$	<0.0001*
	temperature × body region	$3.23_{4,92}$	0.016*

speed at 3 cm above the ground, as well as substrate and sky temperature and horizontal-plane solar radiation, for either full sun or full shade. Previous tests of the microclimate modelling system show that it is capable of accurate prediction of microclimatic conditions across a wide range of environments in Australia [47].

We used the R package deSolve [48] to solve the transient heat budget model through time, using events option to transition between behavioural states, and splining the hourly microclimate output data using the base R function approxfun. We modified the solar absorptivity of the lizard in the biophysical model to represent the highest measured range of reflectivity change (15%) in response to temperature from experiments (table 1; 0.92 and 0.77 absorptivity, equal to 8% and 23% skin reflectivity, respectively, assuming zero transmissivity). We assumed the lizard started the day in full shade, emerged to bask once it had reached a threshold body temperature of 15.1°C and became active at 31.8°C (the lowest and median T_b, respectively, that we observed of emerged animals in the field; $n = 88$ recorded temperatures for 10 individuals; electronic supplementary material, table S1). We assumed that the basking lizard was in the maximum available solar radiation level (accounting for cloud cover), and perpendicular to the sun's rays. Simulations were terminated when the lizard either reached the activity temperature or at 17.00 h (if the activity temperature was never reached). To assess the rate of heating, we calculated, for each reflectivity and on each day, the time taken to reach the activity temperature from the point of emergence, excluding days where the activity threshold was not reached.

3. Results

(a) Temperature-dependent colour change

Lizards showed significant increases in visible (UV–vis) and NIR reflectance at 40°C versus 15°C (tables 1 and 2). The change in UV–vis reflectance was confirmed by digital photos, which showed that lizards had higher chroma (more chromatic yellow) and were lighter (higher luminance) on all dorsal body regions (head, back and tail) at 40°C than

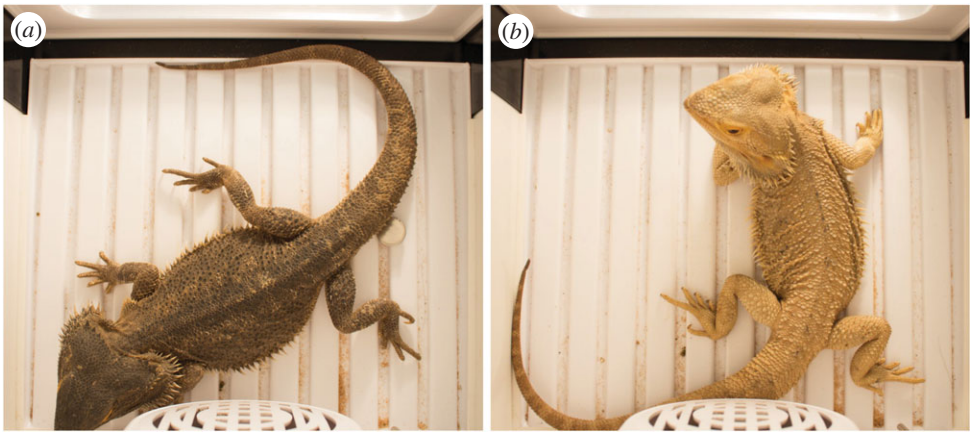

Figure 1. Photographs of the same individual during the (*a*) 15°C and (*b*) 40°C experiments.

15°C (figure 1; electronic supplementary material, figures S1 and S4, and table S2). Furthermore, analyses of the time-series of photographs showed that the average speed of colour change at 15°C was more than twice as fast as at 40°C (electronic supplementary material, table S3 and figure S5), although this difference between temperature treatments was only statistically significant for the speed of change in chroma ($F_{1,11} = 5.68$, $p = 0.04$), but not luminance ($F_{1,11} = 3.02$, $p = 0.11$; electronic supplementary material, table S3).

Reflectance change varied depending on body region (table 2); there was an increase in relative UV–vis reflectance for the dorsal (head, light back and dark back), but not ventral (throat or 'beard' and upper chest) regions (figure 2*a*,*b*). Lizards showed a greater change in the UV–vis spectrum than in the NIR such that there was a significant difference in the standardized difference between them at the two temperatures for dorsal but not ventral body regions (average dorsal: $t_{1,98} = 5.93$, $p < 0.0001$; average ventral: $t_{1,98} = -0.94$, $p = 0.35$). For dorsal body regions, the mean reflectance change between 15°C and 40°C for the UV–vis range was $7.0 \pm 0.6\%$ s.e. compared with $3.1 \pm 0.4\%$ s.e. in the NIR range (table 1).

The reflectance change between the temperature treatments corresponds to a very strong effect of temperature on reflectivity (table 2), with a significant interaction between temperature and body region ($F_{4,92} = 3.22$, $p = 0.016$; table 2). Lizards had significantly higher reflectivity at 40°C than 15°C for dorsal body regions (head: $t_{92} = -4.30$, $p \leq 0.0001$; light back: $t_{92} = -3.40$, $p = 0.001$; dark back: $t_{92} = -2.49$, $p = 0.015$) but not ventral body regions (beard: $t_{92} = -0.40$, $p = 0.69$; chest: $t_{92} = -0.28$, $p = 0.78$). The average difference in reflectivity between the two temperatures for all dorsal body regions combined was approximately 7.4% (40°C: $21.2 \pm 0.8\%$ s.e.; 15°C: $13.8 \pm 0.6\%$ s.e.). However, the extent of temperature-dependent reflectivity change varied substantially among individuals, ranging between approximately 0.02% and 15%. This variation was not explained by body mass ($F_{1,35} = 3.18$, $p = 0.08$).

(b) Temperature-independent colour change

The mean extent of temperature-independent reflectivity change for the dorsal region was $10.5 \pm 0.6\%$ s.e., with some lizards reaching changes of up to 27.4% on the dorsal surfaces (table 1; electronic supplementary material, figure S2*a*). The beard showed the largest difference between light and dark states (figure 3; electronic supplementary material, figure S2*a*,*b*), with a maximum observed change of 30.8% reflectivity between circadian coloration and social interaction. Overall, the average reflectivity change for the ventral region (beard and upper chest) was $16 \pm 1.6\%$ s.e., substantially higher than the $0.2 \pm 2\%$ s.e. reflectivity change due to temperature-dependent stimuli (table 1). During the temperature-independent experiments, 8 of 11 lizards expressed their darkest beard coloration during social experiments, and 11 of 12 lizards expressed their lightest beard coloration at night. Lizards were darkest on their dorsal body regions in the mornings (31 of the 33 dorsal measurements), and lightest on their dorsal body regions either during social experiments (19 of the 33 dorsal measurements) or at night (12 of the 33 dorsal measurements). Temperature-independent colour change was not correlated with body mass ($F_{1,34} = 1.91$, $p = 0.18$).

(c) Biophysical simulations of heating rates

Reflectivity had a substantial effect on heating rates throughout the active season (figure 4), whereby dark lizards (8% reflectivity) reached their activity threshold on average 22 min (range 3–230 min) earlier than light lizards (23% reflectivity). The typical simulated response involved an initial rapid heating rate when first moving into the sun (after the emergence threshold was reached) and then a more gradual rise to the activity threshold as the day heated up (electronic supplementary material, figure S6*a*). In more extreme situations, lizards either emerged into a strong radiation field such that warming was extremely rapid for both reflectivity values (electronic supplementary material figure S6*b*), resulting in little advantage, or into a relatively weak radiation field such that the paler lizard only just reached the activity threshold late in the day (electronic supplementary material, figure S6*c*). In the period between mid-May and late-August, it was generally too cool for simulated lizards to reach the activity threshold temperature (electronic supplementary material, figure S6*d*).

4. Discussion

Our study shows that wild-caught bearded dragons are capable of temperature-dependent colour change of a sufficient magnitude to provide thermoregulatory benefits. Lizards had higher dorsal skin reflectance at 40°C compared with 15°C, with some

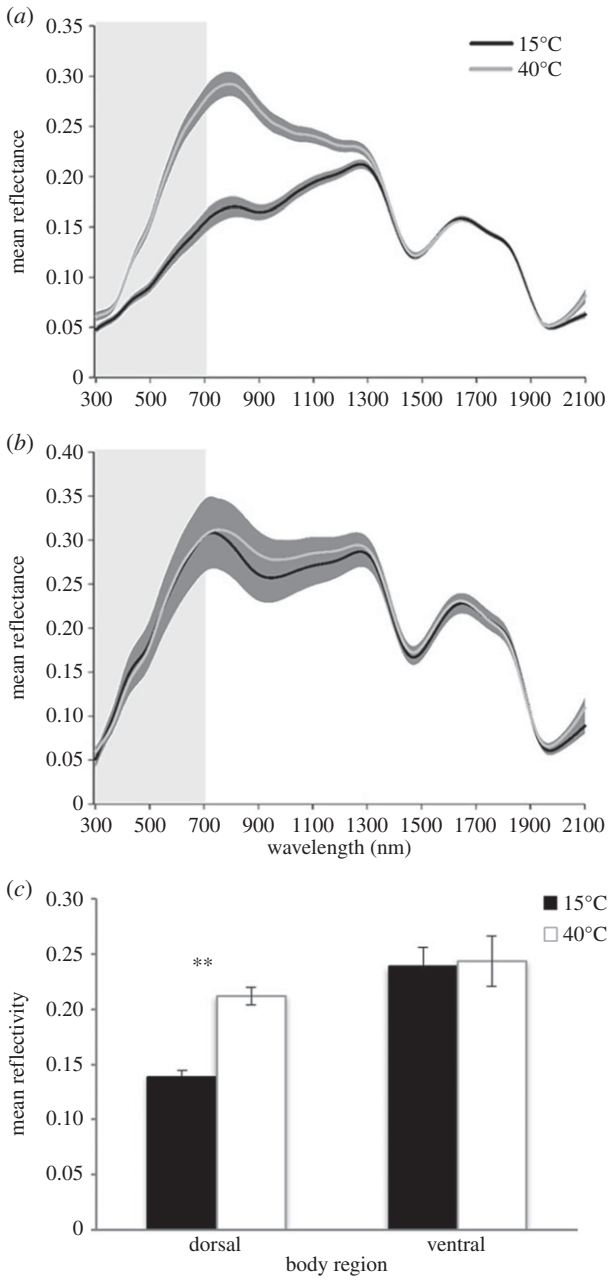

Figure 2. Mean spectral reflectance (±s.e. shown by dark grey shading) of the (*a*) dorsal and (*b*) ventral body regions at 15°C and 40°C, respectively. Light grey highlighted region represents the human-visible spectrum (400–700 nm). (*c*) Mean (±s.e.) reflectivity of the dorsal and ventral body regions at 15°C and 40°C, respectively. The reflectance curves (*a*,*b*), show the proportion of incident radiation reflected by a surface at each wavelength interval while reflectivity (*c*) shows the overall ratio of reflected to incident solar radiation (i.e. integrated over 300–2100 nm).

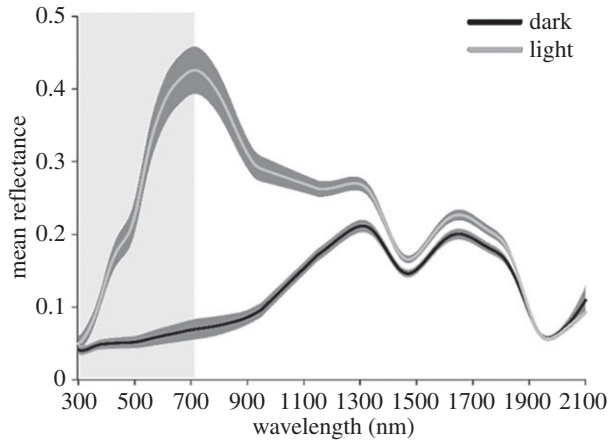

Figure 3. Mean (±s.e. shown by dark grey shading) maximum and minimum spectral reflectance of the beard region for all lizards. Highlighted region represents the human-visible spectrum (400–700 nm; $n = 12$).

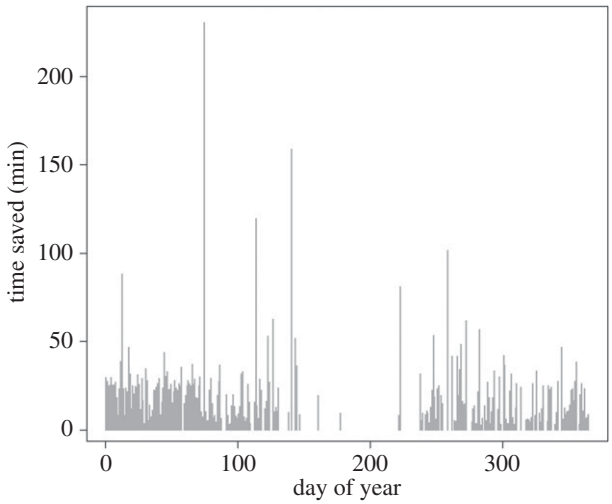

Figure 4. Reduction in basking time per day for a dark lizard (8% reflectivity) compared with a light lizard (23% reflectivity) to reach the activity threshold of 31.8°C from the emergence threshold of 15.1°C. Simulations are based on the climatic conditions at the field site for 2013.

individuals changing dorsal reflectivity up to 15%, with a 14.4% change in UV–vis reflectance over this temperature range, which is similar to the maximum reflectance changes recorded in previous studies of other lizard families [1,17,24]. However, this temperature-based change is less than the observed maximum dorsal colour change (22.7% UV–vis reflectance and 27.4% reflectivity). Furthermore, the capacity for colour change in response to temperature could potentially be greater in the wild and/or in response to greater thermal extremes. Field data confirm that bearded dragons show substantial temperature-dependent colour change in the wild (K.R.S., V.C., J.A.E., M.R.K., W.P.P. & D.S.-F. 2013, unpublished data). In sharp contrast with the dorsal temperature-dependent colour change, there was no UV–vis change on ventral body regions and only minor NIR change in response to temperature. If colour change in response to environmental temperature were merely a physiological response, one would expect that the whole body of the lizard would lighten and darken equally. However, the lack of ventral reflectance change in response to temperature suggests that dorsal temperature-dependent reflectance change has a thermoregulatory function rather than simply being a physiological response to temperature change, because ventral coloration would have little effect on thermoregulation (these lizards usually lie flat against a surface).

Although dorsal reflectance change was substantial, the greatest change occurred on the beard and upper chest (mean 16%, max 30.8% change in reflectivity). Bearded dragon lizards use colour change on their ventral body surfaces as a social signal in dominance, territorial or mating displays, combined with head bobs, push-ups and arm waving [49]. The observation that bearded dragons showed no significant colour change on the chest and beard in response to temperature, despite clearly having the capacity to do so, supports the view that colour change on the ventral surface is exclusively used as a social signal. Thus, our results suggest that these

lizards can partition colour change on different body regions to accommodate competing requirements of thermoregulation and signalling.

Temperature-dependent colour change facilitates a more rapid rise to body temperatures suitable for activity. Average colour change at 15°C was more than twice as fast as the rate at 40°C for changes in both chroma and luminance, consistent with the faster rate of colour change in the Pacific tree frog (*Hyla regilla*) at 10°C than 25°C [50]. Because 15°C is much colder than the bearded dragons' preferred body temperature of 35°C [51,52], lizards may have darkened rapidly under those conditions to increase solar absorption. By contrast, once active, lizards may rely on other forms of behavioural or physiological thermoregulatory mechanisms to cool down (e.g. moving into shade or cardiovascular adjustments) [53]. Free-ranging bearded dragons reach a voluntary maximum core body temperature of 40°C (electronic supplementary material, table S1), which could explain why there is little need for the lizards to rapidly increase reflectivity to prevent overheating at this experimental temperature (40°C). Alternatively, differences in rates of colour change could reflect physiological constraints associated with mechanisms controlling colour change, as in the chameleon grasshopper (*Kosciuscola tristis*), which can change to bright turquoise in 30 min, but can take up to 5 h to change back to their dark phase [18,32,54–56]. However, this seems unlikely in these lizards because they darken and lighten similarly in social interactions (V.C. & D.S.-F. 2014, unpublished data).

All else being equal, the skin's reflectance will influence the amount of solar radiation absorbed, thereby affecting core body temperature [2,6]. Furthermore, under any given set of environmental conditions, reflectivity has a greater effect on steady-state body temperature in individuals with a larger body size, and hence greater thermal inertia and thicker boundary layers [6]. Our biophysical simulations indicate that for an average-sized bearded dragon, darker coloration in the morning could meaningfully reduce the time spent achieving an active body temperature, saving on average 22 min per active day and summing to 85 h across the year 2013. Reaching an active body temperature more rapidly in the morning may be important because individuals must trade off time spent regulating body temperature, and being active to forage, mate, avoid predators and defend territories [57,58]. This is consistent with the observation that the majority of lizards showed their darkest dorsal coloration early in the morning. Colour change may therefore be an important modulator of body temperature, and these lizards probably combine changes in colour with other physiological and behavioural thermoregulatory mechanisms.

Dorsal colour change may also be important for camouflage and social signalling [1,3,32,36,55,59–62], and the requirements of thermoregulation and these other functions of colour may therefore conflict. Our results suggest that bearded dragons minimize the trade-off between thermoregulation and social visual signals by using the dorsal surfaces for thermoregulation and the upper chest and beard for social signalling. However, there could be potential conflicts between colour change for camouflage and thermoregulation on the dorsal surfaces; for example, turning dark to increase heating rate may make a lizard more conspicuous against a lighter background. Thus, there are likely to be interactions between behaviour, camouflage, social signalling and thermoregulation, which could influence the rate, degree and location of observed colour change. Despite such potential trade-offs, it seems that the thermal benefit of colour change for a relatively large lizard like a bearded dragon would be significant under certain conditions, such as when basking to reach preferred body temperatures. Overall, our results suggest that colour change may serve an important thermoregulatory function and that partitioning colour change on different body regions may be a mechanism to accommodate multiple functions of colour.

Ethics. This research was approved by the Department of Environment and Primary Industries, Victoria (permit 10006829) and the University of Melbourne's Animal Ethics Committee (permit 1212547.2).

Data accessibility. Data on experiments and biophysical model simulations are deposited in Dryad (http://dx.doi.org/10.5061/dryad.t34qq)

Authors' contributions. All authors contributed to research conception and design; K.R.S., V.C. and D.S.-F. performed experiments; J.A.E. provided photo analysis methods and software; M.R.K., K.R.S. and W.P.P. contributed to biophysical modelling; K.R.S. processed all raw data; K.R.S. and D.S.-F. conducted statistical analyses; all authors contributed to writing the manuscript.

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