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# Rapid beard darkening predicts contest outcome, not copulation success, in bearded dragon lizards

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Keywords: colour change courtship dominance intersexual selection intrasexual selection male—male competition signalling Rapid colour change is widespread in animals and allows them to respond dynamically to the physical and social environment. However, few studies have examined the information conveyed by dynamic colour signals in different social contexts, such as courtship and rivalry contests. Furthermore, dynamic colour change on different body regions may be subject to different selection pressures and therefore serve different functions. We tested whether male colour or colour change predicts contest outcome in male—male interactions or the likelihood of copulation attempts in male—female interactions in the central bearded dragon, *Pogona vitticeps*. The extent of beard darkening strongly predicted contest outcome, but neither colour (beard, dorsal) nor colour change predicted copulation attempts. Dorsal colour showed little consistent change and did not predict contest outcome or copulation attempts. Previous work shows that dorsal but not beard colour change occurs in response to both background colour and temperature in the laboratory and in the wild. Taken together, these results indicate that dynamic colour change in bearded dragons varies in relation to social context and can serve different functions depending on the body region. Our results add to the growing appreciation of how rapid colour change enables animals to accommodate the multiple functions of colour, including communication to different receivers, camouflage and thermoregulation.

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Dynamic colour change is widespread among animals and allows individuals to adjust rapidly to a changing environment, including the social environment (Hadley & Goldman, 1969; Thurman, 1988; Tolley, 2014). Research on dynamic colour change has tended to focus on potential benefits of colour change to improve crypsis against different habitat backgrounds (Merilaita & Stevens, 2011; Stevens & Merilaita, 2011); however, dynamic colour change could also convey different information in different social contexts, such as contests and courtship. For example, males of some chameleons (Ligon & McGraw, 2013, 2018), Indian rock agamas, Psammophilus dorsalis (Batabyal & Thaker, 2017), stickleback fish, Gasterosteus aculeatus (Hiermes, Rick, Mehlis, & Bakker, 2016) and mourning cuttlefish, Sepia plangon (Brown, Garwood, & Williamson, 2012) all display different colour patterns to male and female conspecifics. Despite these observations, few studies have examined the role of colour change or the information conveyed by dynamic colour signals in different social contexts.

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In species that use dynamic colour change, colour change on different body regions can communicate different information or serve different functions. One of the most dramatic examples is the mourning cuttlefish, in which males can simultaneously display courtship patterns to receptive females on one side of the body and deceptive female-mimicking patterns to a single rival male on the other (Brown et al., 2012). Cephalopods may be unique in this ability; however, more generally, selection on coloration will differ for different body regions, especially for dorsoventrally flattened animals. Specifically, dorsal body regions exposed to direct sunlight should have a greater effect on thermoregulation than ventral body regions which are not exposed; similarly, dorsal regions visible to predators should be more cryptic than ventral regions which are hidden from the predator's view (Stuart-Fox & Ord, 2004). As a consequence, colour change on different body regions in social contexts may entail different costs and follow different evolutionary trajectories. For example, male Indian rock agamas show strikingly different colours during contests and courtship and courtship colours carry a higher predation risk because of the conspicuous red dorsal stripe (Amdekar & Thaker, 2019). Owing to different selection pressures and costs, we might expect colour



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change on different body regions to convey different information or play different roles during social interactions.

Here, we tested whether colour predicts contest outcome or copulation success in central bearded dragon lizards, Pogona vitti*ceps*. Bearded dragons change colour rapidly (seconds to minutes; de Velasco & Tattersall, 2008; Fan, Stuart-Fox, & Cadena, 2014; Smith, Cadena, Endler, Porter, et al., 2016) and dorsal colour change plays a role in both crypsis (Smith, Cadena, Endler, Kearney, et al., 2016) and thermoregulation (Cadena, Rankin, Smith, Endler, & Stuart-Fox, 2017; Smith, Cadena, Endler, Porter, et al., 2016). The entire body (dorsal side) can change from dark grey to bright yellow or reddish-orange, depending on the dominant visual background to which populations are locally adapted (Cadena, Rankin, et al., 2017; Smith, Cadena, Endler, Porter, et al., 2016). Dorsal coloration changes in response to both background colour and temperature in the laboratory and is correlated with both substrate colour and body temperature in the wild to accommodate camouflage and thermoregulation requirements (Cadena, Rankin, et al., 2017; Cadena, Smith, Endler, & Stuart-Fox, 2017; Smith, Cadena, Endler, Kearney, et al., 2016; Smith, Cadena, Endler, Porter, et al., 2016). However, the beard and chest show the most dramatic colour change, from cream to jet black, and this change primarily occurs during social interactions (Smith, Cadena, Endler, Porter, et al., 2016). Males are territorial and survey their territory from elevated perches. During territory defence, they display conspicuous colours (yellow or reddish-orange body and black beard and chest) and may engage in ritualized head-bobbing displays which can escalate to physical contests involving circling and biting (Brattstrom, 1971: Smith, Cadena, Endler, Porter, et al., 2016), Females are similar in size, morphology and colour repertoire to males, but the extent to which they defend home ranges or territories is unknown. Like other agamid lizards, the species is likely to have a polygynous mating system (Hacking, Stuart-Fox, & Gardner, 2018; Qi, Yang, Lu, & Fu, 2013), although there is no definitive evidence that females make mate choice decisions.

We performed behavioural experiments on captive wild-caught lizards from two populations, Alice Springs in central Australia and Mildura in southeastern Australia, representing extremes of body coloration and geographical range of the species. We compared colour change during male—male and male—female interactions for dorsal and ventral (beard) body regions. We tested whether colour, the extent of colour change or specific behaviours predict contest outcome in male—male interactions or the likelihood of copulation attempts in male—female interactions.

#### METHODS

#### Study Species and Husbandry

We captured mature central bearded dragons by hand in September and October 2012 from the Alice Springs region (23°42'S, 133°52'E; 11 males and six females) and the Mildura region (34.18°S, 142.15°E; 10 males and four females). They were transported to The University of Melbourne, Victoria, Australia, where they were individually housed in sand-filled terraria  $(92 \times 77 \text{ cm and } 51 \text{ cm high}; \text{ mean lizard snout-vent length})$ (SVL) = 10.38 cm, mass = 249.7 g) fitted with an ultraviolet (UV) lamp and an incandescent basking lamp for heating, set to a 12:12 h light:dark photoperiod. During the light phase, the temperature inside the terrarium ranged between 25 °C (under the hiding place) and 50 °C (directly under the incandescent light), which allowed for behavioural thermoregulation; these temperatures are within the natural range experienced by bearded dragons in the wild (Smith, Cadena, Endler, Kearney, et al., 2016) and include the range of voluntary active body temperatures in the field (32–40 °C; Smith, Cadena, Endler, Porter, et al., 2016). Each terrarium was also enriched with a hiding place and a natural tree branch for perching. Lizards were provided with water ad libitum and fed a diet of crickets and commercial bearded dragon food (10.04 URS Lizard Food; Ultimate Reptile Supplies, Australia) mixed with chopped green leafy vegetables, carrots and pumpkin, three times a week.

Prior to experiments, we measured SVL to the nearest mm with a ruler and calculated body condition as the residuals of weight regressed against SVL.

#### Ethical Note

This research was conducted in accordance with the University of Melbourne (UoM) Animal Ethics Committee (AEC) approval 1212547.2. Lizards from Mildura were obtained under Department of Sustainability and Environment (DSE) Victoria permit number 10006453. Lizards from Alice Springs were obtained under a Northern Territory Parks and Wildlife Commission (NTPWC) Permit to Take Wildlife for Commercial Purposes number 44582, and a Central Land Council Permit to Enter and Remain on Aboriginal Land number 15396; they were imported into Victoria under DSE Import permit 14237999. At the conclusion of the behavioural trials, the last of several projects involving this captive population, lizards from Alice Springs were humanely killed according to UoM AEC guidelines as required by our NTPWC Permit. The lizards were first anaesthetized with an intramuscular injection of Zoletil (10 mg/kg). Once the animal was no longer responsive, it was killed with an intraperitoneal injection of sodium pentobarbital (80 mg/ kg) and brain death confirmed by absence of breathing, eve twitch. toe pinch and tail flick responses after 5 and 10 min. Ten of these specimens were lodged with the Melbourne Museum and the other seven were lodged with the Museum and Art Gallery of the Northern Territory. Lizards from Mildura were rehomed to licensed institutes and private collectors, approved by the University of Melbourne AEC Animal Welfare Officer.

#### Male-male Interactions

We conducted behavioural trials (N = 32 unique dyadic combinations) between pairs of males from the same source population (Mildura or Alice Springs) in December 2013 during the hours of normal lizard activity at this time of year (0800-1700 hours). We introduced an 'intruder' lizard into the enclosure of a resident lizard because this reliably elicited agonistic behaviour. We recorded the interactions using a Panasonic SDR-H250 digital camera. Trials were run for 10 min, or until there was a clear winner. The mean  $\pm$  SEM duration of male-male trials was  $8 \pm 0.8$  min (including time to first interaction; range 2-18). Each male participated in an average of three trials (range one to five). Residents were not paired with the same intruder more than once. Males were paired by weight (mean  $\pm$  SE body weight percentage difference =  $3 \pm 2\%$ ). To reduce stress, males were not involved in trials more than once a day (mean 3 days, range 1–7 days between trials). Animals were monitored twice daily during the period of behavioural trials and for 1 week after their conclusion; all animals exhibited normal feeding and behaviour during the period of the trials, indicating that they were not adversely affected. Four trials were excluded due to no interaction and in two other trials data from the resident only were removed due to poor spectrometer readings resulting in 54 contestants from 28 trials (26 with data from both participants, two with data from the intruder only) for statistical analysis.

We quantified behaviours from videos using JWatcher ver. 9.0 (Blumstein & Daniel, 2007). We recorded the following behaviours: head bobs, arm waving, bites, circling, throat puffs, chases and

fleeing (described in Table 1). Biting did not constitute an endpoint and never escalated to injury requiring intervention (biting never broke the skin surface). We assigned a winner when one individual (the loser) withdrew from the contest and repeatedly attempted to flee its opponent.

#### Male-female Interactions

Females from the same source population as the host (Mildura/ Alice Springs) were introduced to the male's enclosure. Trials (N = 24) lasted until the male mounted the female or was stopped if there was no copulation attempt within 10 min. The mean duration for male–female trials was  $7 \pm 0.9$  min (range 1–14). Mounted males were removed before they were able to copulate with the female. Each male participated in an average of 1.14 trials (range 1–2); each female was in an average of 2.40 trials (range 1–4). The same behaviours were scored from the videos as in the male–male trials, in addition to the number and duration of attempted mounts. Behaviours were quantified from videos as for the male–male interactions. Of the 24 trials, two were excluded due to no interaction resulting in 22 trials for statistical analysis.

#### Colour Measurement and Analysis

Immediately following each trial, we measured the reflectance of both lizards in the male-male interactions (Fig. 1) or only the male in the male-female interactions. Bearded dragons reveal broad dark dorsal chevrons, on a lighter dorsal background colour, following colour change; thus, we measured a section of each region, which we refer to as 'dark back (DB)' and 'light back (LB)' respectively. An area 1 cm<sup>2</sup> was marked on a light and dark back region with nontoxic marker to ensure measurements were taken from the same location across all trials. As handling stress induces colour change and can affect subsequent behaviour, we only measured colour following the trial to minimize handling before the trial. To estimate colour change, we compared colours measured following behavioural trials to colours measured for the same body regions on the same individuals in an undisturbed state at least 2 days before trials commenced (Cadena, Smith, et al., 2017). We refer to these measures as 'baseline'.

Reflectance measurements were taken of a 5 mm  $\times$  3 mm area, using an Ocean Optics USB2000 spectrometer (Ocean Optics, Largo, FL, U.S.A.) with PX-2 pulsed Xenon light with fibre optics connected to an RPH-1 probe holder, which maintains the light at a constant angle (45°) and distance from the skin surface. Measurements were taken relative to a Spectralon 99% diffuse reflectance stand (Labsphere, North Sutton, NH, U.S.A.). The internal temperature of male lizards was measured following colour measurements using a rectal thermocouple probe.

We summarized spectral reflectance measures by estimating luminance (dL) and chromatic (dS) contrast of the beard (throat) and dark back and light back regions using the receptor noise limited (RNL) model of colour vision (Vorobyev & Osorio, 1998; Vorobyev, Osorio, Bennett, Marshall, & Cuthill, 1998). The RNL model measures colour distance in  $\Delta S$  units where the minimum difference that can be discriminated under ideal viewing conditions (a JND) occurs at  $\Delta S = 1$ , assuming that discrimination is limited only by photoreceptor noise (Vorobyev et al., 1998; Vorobyev & Osorio, 1998). We assumed standard daylight illumination and tetrachromatic vision with spectral sensitivities: LIVS  $\lambda_{max} = 365$  nm, SWS  $\lambda_{max} = 440$  nm, MWS  $\lambda_{max} = 493$  nm and LWS  $\lambda_{max} = 571$  nm, based on the closely related agamid lizards, Ctenophorus ornatus (Barbour et al., 2002) and Ctenophorus decresii visual systems (Yewers et al., 2015). Photoreceptor noise  $(\omega_i)$  for the LWS photoreceptor was set to 0.1 and photoreceptor ratios were 1 UVS: 1 SWS: 3.5 MWS: 6 LWS (Barbour et al., 2002). Luminance contrast was calculated using the sensitivity function for the LWS photoreceptor, assuming  $\omega_i = 0.05$ .

To represent the colour and luminance of lizards at the end of an interaction, we calculated chromatic and achromatic contrasts of specific parts of the body against an achromatic background (uniform 2% reflectance, i.e. black) for each body region. This approach enabled us to measure colour and luminance in the lizard's perceptual space, which is more biologically relevant than calculating hue, chroma and luminance from raw spectra. Here, chromatic contrast (dS) represents the receptor noise model distance from the achromatic centre in a colour space defined by lizard photoreceptor spectral sensitivities, with higher chromatic contrast indicating more chromatic colours (greater spectral purity). Achromatic contrast (dL) relative to 2% uniform reflectance (i.e. black)

#### Table 1

Male bearded dragon behaviours during male-male interactions (winner and loser) and male-female interactions (copulated and no copulation)

Behaviour	Description	Male-male interactions mea	an ± SE (range)	Male-female interactions mean $\pm$ SE (range)		
		Winner	Loser	Copulated	No copulation	
Head bob	Short, rapid, up and down movements of the head. Frequency (head bobs) per min	$2.40 \pm 0.76 \ (0.00 - 20.38)$	$1.43 \pm 0.35 \ (0.00 - 5.48)$	8.40 ± 3.15 (0.00-29.52)	0.90 ± 0.50 (0.00-5.11)	
Arm wave	Slow raising of a single arm in a circular movement. Frequency (arm waves) per min	0.01 ± 0.01 (0.00-0.22)	0.11 ± 0.08 (0.00-1.71)	$0.00 \pm 0.00 \; (0.00 {-} 0.00)$	$0.00 \pm 0.00 \ (0.00 - 0.00)$	
Throat puff	Extension of beard often combined with darkening. Duration (s) per min	16.82 ± 3.61 (0.00-56.54)	8.32 ± 1.77 (0.00-35.03)	5.84 ± 1.85 (0.00-17.01)	$7.55 \pm 5.37  (0.00 {-} 60.00)$	
Circling	Flattening, turning and tilting the body towards the other lizard to increase apparent size. Duration (s) per min	6.49 ± 1.57 (0.00–26.26)	5.23 ± 1.48 (0.00-30.40)	$0.00 \pm 0.00 \ (0.00 - 0.00)$	0.53 ± 0.29 (0.00-2.68)	
Chase	Chasing the opponent or female. Duration (s) per min	$0.27 \pm 0.08 \; (0.00 {-} 1.67)$	$0.28 \pm 0.13 \ (0.00 - 2.77)$	7.46 ± 1.72 (0.00-15.09)	$0.98 \pm 0.59  (0.00{-}6.10)$	
Flee	Fleeing from the opponent. Frequency (flees) per min	$0.32 \pm 0.15 \ (0.00 - 3.19)$	$0.35 \pm 0.12 \ (0.00 {-} 1.97)$	$0.00 \pm 0.00 \; (0.00 {-} 0.00)$	$0.02 \pm 0.02 \; (0.00 {-} 0.19)$	
Bite	Biting the opponent or female. Duration (s) per min	$0.50 \pm 0.54  (0.00{-}3.87)$	0.23 ± 0.08 (0.00-1.83)	1.00 ± 0.40 (0.01-4.62)	0.04 ± 0.03 (0.00-0.36)	

Head bob, chase, flee and bite are expressed as the number (count) of behaviours per min. Arm wave, throat puff and circling are expressed as the proportion of total trial time spent performing the behaviour (male–male trials: N = 54 contestants in 28 trials; male–female trials: N = 22 male participants in 22 trials).



**Figure 1.** Spectral measurements (mean  $\pm$  SE) for three body regions of male bearded dragons following male–male contests: (a) beard, (b) dark back and (c) light back. Mean is of both sites (Mildura, Alice Springs) combined.

provides a measure of perceived luminance where higher luminance contrasts indicate lighter colours. We also calculated contrasts against 'baseline colour' to enable us to assess the degree of colour change. To indicate the direction of change, we assigned negative contrast values to colours that were darker or less chromatic relative to baseline and positive contrast values to colours that were lighter or more chromatic relative to baseline.

#### Statistical Analysis

We tested whether (1) the outcome of male—male competition (win or lose) and (2) attempted copulation in male—female trials (yes or no) could be predicted by (a) chromatic and luminance contrasts relative to a 2% reflectance achromatic background; (b) chromatic and luminance contrasts relative to baseline lizard colour; and (c) behavioural variables. We ran three separate statistical models for each set of trials (male—male or male—female) where each model corresponded to the different sets of predictor variables (six models in total). All statistical models were generalized linear mixed models with a binomial distribution and logit link function, enabling us to predict a discrete outcome (win versus lose or copulation versus no copulation) from a set of continuous, discrete, dichotomous or mixed set of variables (glmer, lme4 package, R; Bates, Machler, Bolker, & Walker, 2015).

The models with colour predictor variables included luminance contrast (dL) for the beard (throat) and dark back and chromatic contrast (dS) for the light back. We did not include chromatic contrast of the beard and dark back as predictor variables because these body regions primarily change in luminance (light grey to black) whereas chromatic contrast of the light back was included as a predictor variable because this body region can change from grey to yellow or reddish-orange. For male-male interactions, the behavioural model included the frequency of head bobs and the duration of biting, time spent with their throat puffed and circling. We did not include arm waves or chasing and fleeing because arm waving was infrequent and chasing and fleeing defined loss of a contest. For male-female interactions, the behavioural model included the frequency of head bobs, time spent with their throat puffed and chasing. Arm waves, circling and fleeing were not included, as these behaviours were infrequent or absent. The highest correlation (Spearman  $r_{\rm S}$ ) between any two predictors in models for male-male interactions was 0.80 (Appendix Table A1) and 0.67 (Appendix Table A2) for male-female interactions. Chases and bites from males were highly correlated during male-female interactions so we ran models with one or the other variable, but not both. We present models with 'chase' because it showed more variation and produced a better model fit. No other variables exceed the cutoff limit of r = 0.70 to warrant exclusion from the models (Tabachnick & Fidell, 1996). All models also included male body condition, body temperature and site (Alice Springs or Mildura) as fixed effects.

We initially ran models with either SVL or body condition but condition consistently explained more variation than SVL, which did not explain a significant amount of variation in any model. We therefore only included body condition in final models. We also checked for a potential effect of time of day by comparing the fit of the top model (see below) with and without time of day as a predictor. Time of day was not significant in either the male—male or male—female interactions, and its inclusion did not improve model fit (see Supplementary Material Table S12). Given the order of magnitude difference between some variables, the predictors were mean-centred and scaled to have a standard deviation of 1. Male ID and trial ID were included as random variables for the male- male trials to account for repeated use of individuals. Male ID and female ID were included as random variables for male—female interactions.

Based on the global models described above, we used Akaike information criterion (AIC) model selection and model averaging to identify the best-fitting final models (dredge, MuMIn package, R; Barton, 2015). Models with < 2 AICc differences ( $\Delta$ AICc) are

considered as good as the best model, but models just above this range should still be considered (Burnham & Anderson, 2004; Richards, 2005; Symonds & Moussalli, 2011). Across the models, the cumulative AICc weights with  $\Delta$ AICc < 2 were between 0.49 and 0.92, equating to 49%–92% confidence that the best model was included in this subset: therefore we considered models with  $\Delta$ AICc < 4 to increase the chance of retaining the best model (this shifted the AICc weights to 0.98–1.00). Where the top model was a subset of another retained model, and the latter did not provide an improvement in log likelihood, we removed the competing model to avoid uninformative parameters receiving undue weight during model averaging (Arnold, 2010; Burnham & Anderson, 2004; Grueber, Nakagawa, Laws, & Jamieson, 2011). Model-averaged coefficients along with 95% confidence intervals and the relative importance of each variable (RIV) were calculated by summing the normalized AICc weights across retained models (Symonds & Moussalli, 2011). All statistics were computed in R 3.4.0 (The R Foundation for Statistical Computing, Vienna, Austria, www.rproject.org).

We examined pairwise correlations between morphological, colour and behavioural variables using Spearman correlations for both the male–male and male–female trials (Appendix Tables A1, A2).

Lastly, we examined the correlation of male colour and colour change between contexts. Since most males were used in more than one male—male or male—female interaction trial, for each male, we first calculated his average colour or colour change for each body region when he was a winner or a loser in male—male contests and when he was in male—female trials. We then examined the correlation between a male's colour or colour change as a winner or loser in male—male contests and his colour in male—female interactions.

#### RESULTS

#### Male-male Interactions

Residency was the strongest predictor of contest outcome in all models with residents winning 21 of 28 contests. In terms of behaviour, throat puff, head bob, circling and bite behaviour were retained in the top models (Table 2; 22 models retained in the top subset); however, none predicted contest outcome (all RIV < 0.42), with residency being the only important variable (RIV = 1.00; Table 2). For the model examining the colour of lizards, in addition to residency, luminance of the beard was included in all top models, with winners more likely to have darker beards than losers (Figs. 1 and 2, Tables 3, 4). All other retained variables had an RIV < 0.52and 95% confidence intervals of parameter estimates spanned zero (Table 4). Winners not only had darker beards, but their beard luminance also changed more relative to baseline colour than in losers (RIV = 1.00; Fig. 2, Tables 3, 4); however, the confidence intervals marginally overlapped zero. All other retained variables in the top models had an RIV below 0.53 (Table 4). Full model averaging tables are available in the Supplementary Material (Tables S1-S9).

Luminance (dL) of the beard and dark back and chromatic contrast (dS) of the light back were all uncorrelated following the contests. The frequency or duration of head bobs, throat puffs, circling, chasing and biting were all correlated with each other, but Spearman  $r_S$  values were all <0.6 (Appendix Table A1). Males that fled their opponent more frequently had lighter 'dark back' regions ( $r_S = 0.31$ , P = 0.023; Appendix Table A1) but no other behaviours were correlated with colour variables in male—male interactions. Neither condition nor SVL correlated with other variables. See Appendix Table A1for all correlations.

#### Table 2

Model-averaged effect sizes and relative importance of variables (RIV) for behavioural variables in models predicting the outcome of male-male interactions (win or lose) and male-female interactions (copulated or no copulation)

Model term	Model-averaged estimate (CI)	RIV
Male-male interactions		
Intercept	-2.202 (-4.921, 0.518)	
Role (Resident)	3.762 (-0.084, 7.607)	1.00
Temperature	0.953 (-0.957, 1.767)	0.43
Throat puff	0.803 (-0.758, 1.432)	0.42
Head bobs	0.686 (-0.837, 1.103)	0.19
Condition	0.821 (-1.157, 1.403)	0.15
Site (Mildura)	-0.630 (-0.774, 0.592)	0.14
Circling	0.160 (-0.296, 0.323)	0.09
Bite	0.172 (-0.288, 0.316)	0.08
Male-female		
interactions		
Intercept	-24.747 (-46.693, -2.801)	
Bite	232.542 (97.214, 367.871)	1.00
Condition	0.123 (-0.169, 0.416)	0.50
Head bobs	0.300 (-1.990, 2.589)	0.08

Model-averaged estimated effect sizes for fixed effects with 95% confidence intervals (CI). Estimates are for the top models ( $\Delta AIC_{c,c}$ 4) corrected for uninformative parameters (Arnold, 2010)N = 54 contestants. Random effects: lizard ID (N = 21); trial ID (N = 29). RIV values of 1.00 (in bold) indicate predictors that were found in all models within the subset of top models. Effect sizes with 95% CIs that do not overlap zero can be considered statistically significant and are indicated in bold.

#### Male-female Interactions

Attempted copulation occurred in 10 of the 22 trials (45.45%). Males that successfully mounted females were significantly more likely to chase the female (RIV = 0.93; Table 5, Supplementary Material Tables S14-S16). Chasing was highly correlated with biting ( $r_{\rm S} = 0.80$ , P < 0.001; Appendix Table A2) and biting also strongly predicted successful mounting in models with biting instead of chasing (RIV = 1.00; Supplementary Material Tables S17–S19). Males chased the female and bit her nape in a mating grip during attempted mounts. Frequency of head bobs and throat puffs were also retained but had low relative importance (RIV = 0.33 and 0.03, respectively; Table 2). Neither the colour at the end of interactions nor the amount of colour change relative to baseline predicted successful mounting (Supplementary Material Tables S10–S13). No variables were retained in the colour model (both when compared to neutral background or lizard baseline values). The variance explained by female ID was low (see Supplementary Material) indicating that results cannot be explained by female state (e.g. some females being receptive or not, or personality differences).

Individuals that bit the female in male–female interactions had darker beards (correlation between biting and beard dL:  $r_S = -0.49$ , P = 0.025; Appendix Table A2). In contrast to male-male interactions, luminance of the beard was negatively correlated with luminance of the dark back ( $r_S = -0.65$ , P < 0.001; Appendix Table A2). Larger males had lighter beards ( $r_S = 0.495$ ; P = 0.022) and males in better condition displayed more throat puffs ( $r_S = 0.457$ , P = 0.33; Appendix Table A2).

#### Comparison of Male-male and Male-female Interactions

The colour of a male's light back was correlated between contexts. The correlation of a male's light back colour (dS) in male–male and male–female interactions was stronger for losers ( $r_S = 0.82$ , P < 0.001) than for winners ( $r_S = 0.608$ , P = 0.036). There was no significant correlation of male beard or dark back coloration between contexts (Appendix Tables A3, A4).



Figure 2. (a) Luminance and (b) luminance change of the beard of male bearded dragons following male—male contests. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers. Luminance is given as the contrast against an achromatic 2% reflectance background; therefore, lower contrast values indicate lower luminance (darker). Luminance changes against baseline were assigned as positive for higher luminance (lighter) and negative for lower luminance (darker) relative to baseline.

 Table 3

 Male colour and colour change relative to baseline for the winner and loser in male-male interactions

Body region,	Colour		Colour change		
contrast	mean ± SE		mean ± SE		
	Winner	Loser	Winner	Loser	
Beard, dL	47.74 ± 2.73	$59.73 \pm 2.41$	-8.00 ± 3.63	$6.57 \pm 3.44$	
Dark back, dL	56.41 ± 1.28	$56.95 \pm 0.92$	-0.21 ± 1.26	$1.88 \pm 1.18$	
Light back, dS	3.02 ± 0.17	$3.10 \pm 0.18$	-0.43 ± 0.57	$-1.49 \pm 0.49$	

dL = luminance contrast; dS = chromatic contrast. N = 54 contestants. Colour is measured as contrast relative to an achromatic black (2%) background. Colour change is measured as the contrast between the lizard's colour at the end of the interaction and its baseline colour.

The amount of colour change (relative to baseline) of all three body regions was correlated between contexts for losers (dL beard:  $r_S = 0.578$ , P = 0.030; dL dark back:  $r_S = 0.604$ , P = 0.022; dS light back:  $r_S = 0.820$ , P < 0.001). For winners, only the amount of colour change for the dark back was correlated between contexts ( $r_S = 0.807$ , P < 0.001; Appendix Tables A3, A4).

#### DISCUSSION

Dynamic colour change could enable individuals to use colour for multiple functions and convey different information to different receivers including potential mates and rivals. However, empirical evidence for colour change associated with different social contexts remains rare (but see Batabyal & Thaker, 2017; Brown et al., 2012; Ligon & McGraw, 2013). Additionally, the information conveyed by such dynamic signals, such as dominance, has rarely been experimentally assessed (but see Ligon & McGraw, 2013, 2018). Here, we have shown that male bearded dragons had darker beards immediately following contests, suggesting that they communicate their dominance by darkening the beard. By contrast, colour or colour change did not predict the probability of successfully mounting a female. Male bearded dragons use a similar repertoire of colours in contests and courtship, as do some other species such as dwarf chameleons (Stuart-Fox, Moussalli, & Whiting, 2007) and sticklebacks (Candolin, 2000). However, we found that male coloration and colour change were much more strongly correlated between contexts (male-male versus male-female) for losers than winners. This suggests that winners and losers may employ different strategies in male-male and male-female interactions. For example, dominant males may use beard colour change to signal their dominance in male-male interactions but rely on a coercive strategy such as chasing and biting in male-female interactions. By contrast, subordinate males may be more likely to rely on signalling in both contexts than on coercion or physical strength, possibly explaining the stronger correlation in colour and colour change between contexts for males that lost fights. Testing this possibility would require evaluating dominance or subordinate status over repeated interactions and examining the relationship with behaviour and colour in male-male and male-female interactions. Single interactions may be poor indicators of dominance given that there is variation among outcomes. Taken together, our results suggest that colour and colour change play a more important role in determining the outcome of male-male than male-female interactions in bearded dragons and may communicate different information in these two contexts.

Beard colour was the strongest statistical predictor of contest outcome, apart from residency. During social interactions, bearded dragons puff out the beard, which becomes black and contrasts with the remainder of the body. Dorsal colour showed little consistent change and did not predict contest outcome or copulation attempts. Dorsal coloration is subject to multiple selection pressures and changes in response to different proximate cues; it changes in response to background colour and temperature (Cadena, Rankin, et al., 2017; Cadena, Smith, et al., 2017; Smith,

#### Table 4

Model-averaged effect sizes and relative importance of variables (RIV) for colour and colour change models predicting the outcome (win or lose) of male-male interactions

Model term	Colour		Colour change		
	Model-averaged estimate (CI)	RIV	Model-averaged estimate (CI)	RIV	
Intercept	3.870 (-1.836, 9.576)		-2.454 (-5.962, 1.054)		
Role (Resident)	3.735 (0.458, 7.012)	1.00	3.653 (-0.927, 8.232)	1.00	
Beard (dL)	-0.118 (-0.216, -0.020)	1.00	-0.100 (-0.216, 0.015)	1.00	
Condition (scaled)	-0.619 (-2.178, 0.940)	0.52	-0.356 (-1.566, 0.853)	0.39	
Temperature (scaled)	0.178 (-0.667, 1.024)	0.28	0.601 (-1.256, 2.459)	0.53	
Site (Mildura)	-0.209 (-1.549, 1.131)	0.21	-0.093 (-1.287, 1.101)	0.17	
Dark back (dL)	0.004 (-0.057, 0.065)	0.06	0.005 (-0.084, 0.094)	0.12	
Light back (dS)	0.010 (-0.300, 0.320)	0.05	0.108 (-0.506, 0.722)	0.29	

dL = luminance contrast; dS = chromatic contrast. Model-averaged estimated effect sizes for fixed effects with 95% confidence intervals (Cl). Estimates are for the top models ( $\Delta$ AICc < 4) corrected for uninformative parameters (Arnold, 2010). N = 54 contestants. Random effects: lizard ID (N = 21) and trial ID (N = 29). Colour is measured as contrast relative to an achromatic black (2%) background. Colour change is measured as the contrast between the lizard's colour at the end of the interaction and its baseline colour. RIV values of 1.00 (in bold) indicate predictors that were found in all models within the subset of top models. Effect sizes with 95% Cls that do not overlap zero can be considered statistically significant and are indicated in bold.

### Table 5 Male colour and colour change for males that did and did not attempt copulation in male-female interactions

Body region, contrast	Colour mean ± SE		Colour change mean ± SE		
	Attempted copulation	No attempted copulation	Attempted copulation	No attempted copulation	
Beard, dL Dark back, dI	$48.12 \pm 3.18$ 58 59 + 1 96	$52.17 \pm 3.24$ 57 72 + 0.94	$-10.04 \pm 4.09$ 1.86 + 1.06	$0.17 \pm 5.40$ 2 91 + 1 82	
Light back, dS	3.10 ± 0.27	$3.22 \pm 0.27$	$-1.45 \pm 0.67$	$-1.31 \pm 0.76$	

dL = luminance contrast; dS = chromatic contrast. N = 22 trials. Colour is measured as contrast relative to an achromatic black (2%) background. Colour change is measured as the contrast between the lizard's colour at the end of the interaction and its baseline colour.

Cadena, Endler, Kearney, et al., 2016; Smith, Cadena, Endler, Porter, et al., 2016) and functions for both crypsis and thermoregulation in the wild (Smith, Cadena, Endler, Kearney, et al., 2016). It also varies geographically in relation to substrate colour and is locally adapted to enhance background matching (Cadena, Smith, et al., 2017). By contrast, beard coloration is similar between populations and does not show significant colour change in response to temperature (Smith, Cadena, Endler, Porter, et al., 2016). Instead, beard colour change is largely restricted to social interactions. If dorsal coloration changes more than beard coloration in response to other cues such as temperature, beard coloration may convey more reliable information during social interactions.

Darkening is a common feature of social signals, although it can communicate different information including dominance (Moyer, 1976; Zucker, 1989) or submission (Hoglund, Balm, & Winberg, 2000; Ligon, 2014; O'Connor, Metcalfe, & Taylor, 1999; Plavicki, Yang, & Wilczynski, 2004). In male green anoles, Anolis carolinensis, a patch behind the eye (eyespot) rapidly darkens during social interactions. The speed and extent of darkening reliably signals social dominance (Korzan, Overli, & Summers, 2006; Korzan, Summers, Ronan, & Summers, 2000; Korzan, Summers, & Summers, 2002; Larson & Summers, 2001; Summers et al., 2005; Summers & Greenberg, 1994). One potential advantage of darkening specific body regions is that it often produces high contrast with neighbouring colour patches, giving the overall impression of more intensely saturated colours, which may in turn enhance signal efficacy. Thus, even though dorsal coloration did not predict context outcome, males with darker beards are likely to appear more intensely coloured overall. Mechanistically, darkening of the beard involves dispersion of melanosomes through the dendrites of melanophores (melanin-containing pigment cells) towards the skin surface (Bagnara & Matsumoto, 2006; Bagnara, Taylor, & Hadley, 1968; Cooper & Greenberg, 1992). However the metabolic cost of this colour change remains unclear (Caro,

## Stoddard, & Stuart-Fox, 2017; Galván & Alonso-Alvarez, 2017; Ligon & McCartney, 2016).

Bearded dragons changed colour in both male-male and male-female interactions with the beard darkening in both contexts. However, neither colour nor colour change predicted the probability of a male successfully mounting a female. Instead, the only strong predictor of attempted copulation was the duration of chasing or the frequency of biting, which were highly correlated with each other. This is unsurprising given that males chase the female and bite her neck in a mating grip during attempted mounts. Although males courted females with head bobs in which they displayed their beard, females had limited ability to escape persistent male chases in experimental enclosures. In natural situations, males may display to females for longer periods or at greater distances, where females may evaluate males by visual cues including colour. However, the extent to which female bearded dragons exercise mate choice is unknown. Our results contrast with the Indian rock agama in which male colour change was greater in male-female than male-male experimental interactions (Batabyal & Thaker, 2017). However, that study did not evaluate effects of colour change on contest outcome or copulation attempts.

The behavioural repertoire and frequency of behaviours of male bearded dragons differed during male-male and male-female Males never fled or arm-waved interactions. during male-female interactions. Arm waving is a widespread behaviour in Australian lizards but appears to convey different information in different species. For example, arm waves are primarily performed by nonreproductive females in Lake Eyre dragons, Ctenophorus maculosus (Jessop, Chan, & Stuart-Fox, 2009), whereas arm waving is typically an aggressive signal in male Jacky dragons, Amphibolurus muricatus (Peters, Clifford, & Evans, 2002; Peters & Ord, 2003). In bearded dragons, arm waving was almost exclusively performed by losers in male-male interactions, suggesting that it indicates submission. Males puffed out their beards and headbobbed in both male-male and male-female interactions, although head bobbing was most frequent in the latter. By contrast, circling was a clear display of aggression and was almost exclusively displayed in male-male interactions. During circling, males extend their beards, flatten themselves horizontally and circle round each other displaying their flattened flanks, presumably to exaggerate body size. Similar behaviours to accentuate body size are a common feature of animal contests (Cooper & Greenberg, 1992; Hoffman & Blouin, 2000; Seehausen, Mayhew, & Alphen, 1999). Despite the complex behavioural repertoire of bearded dragons, colour change tended to be simple, involving only darkening of the beard and intensifying dorsal coloration in some individuals (although this was inconsistent and did not predict outcomes of interactions). Furthermore, male coloration was generally uncorrelated with behaviour, although males that fled their opponent more in male-male interactions tended to have lighter dorsal coloration and males that bit females in male-female interactions tended to have lighter beards. Since we took colour measurements after interactions, the paling could be due to losing. This contrasts with veiled chameleons, Chamaeleo calyptratus, in which males show complex colour change on the head and body that correspond with behavioural displays during specific contest stages (Ligon & McGraw, 2013).

Unsurprisingly, the strongest predictor of contest outcome in our experiments was residency. Defence of a territory, or residency, is a strong predictor of contest outcome across a wide range of taxa including crabs (Hoefler, 2002; Jennions & Backwell, 1996), lizards (Olsson & Shine, 2000; Sacchi et al., 2009; Umbers, Osborne, & Keogh, 2012), fish (Johnsson & Forser, 2002), birds (Krebs, 1982; Strong, Sherman, & Riehl, 2018) and territorial butterflies (Bergman, Olofsson, & Wiklund, 2010: Kemp & Wiklund, 2001). Residents are typically motivated to defend their territory from intruders due to the investment in territory establishment, value of the resource and cost of establishing a new territory should they lose (Kemp & Wiklund, 2004; Maher & Lott, 2000). Because residency strongly affects outcome, it could override subtle effects of other factors, such as body condition and colour change. We detected an effect of beard darkening on contest outcome despite the strong effect of residency, indicating that male beard colour is an important visual signal in bearded dragon contests.

Overall, our results show that dynamic colour change plays an important role in the social interactions of bearded dragons, but this role differs depending on the social context. Specifically, colour and colour change predicted dominance in contests but not the probability of male copulation attempts. Colour change occurs during courtship and females may evaluate male coloration and behaviour at longer distances; however, the primary determinant of copulation attempts at close distance was male biting behaviour. Furthermore, although both the beard and back can change colour during social interactions, only the beard changed consistently and reliably predicted contest outcome. This suggests that beard colour is a more reliable indicator of dominance than dorsal colour, which changes in response to other cues such as temperature and background colour. Thus, even for species capable of rapid colour change, selection for competing functions of colour results in variation in the role of colour and colour change on different body regions to meet different requirements.

#### **Author Contributions**

Conception and design of the experiment: A.L.D., V.C., J.A.E.; D.S-F.; collection and processing of the data: A.L.D., V.C; analysis and interpretation of the data: A.L.D.; K.J.R.; D.S-F.; drafting or revising the article for intellectual content: D.S-F, A.L.D., K.J.R., J.A.E., V.C. All authors approved the final version.

#### **Data Availability**

The raw data are available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.fxpnvx0q3.

#### **Declaration of Interest**

None.

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#### **Supplementary Material**

Supplementary material associated with this article can be found online at https://doi.org/10.1016/j.anbehav.2020.10.014.

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#### Appendix

 Table A1

 Correlations between all behaviour and colour variables for male-male interactions

	SVL	Condition_residuals	dL_Beard	dL_DB	dS_LB	HB_freqmins	Tpuff_durmins	Circling_durmins	Chase_durmins	Flee_freqmins
SVL										
Condition_residuals	0.036									
dL_Beard	0.008	-0.135								
dL_DB	-0.265	-0.172	0.119							
dS_LB	0.164	0.142	0.074	0.194						
HB_freqmins	-0.014	-0.005	0.041	-0.128	-0.023					
Tpuff_durmins	0.055	0.037	-0.006	0.019	0.129	0.541***				
Circling_durmins	-0.092	-0.158	-0.121	0.150	0.039	0.339**	0.521***			
Chase_durmins	-0.026	0.222	0.021	0.078	0.159	0.570***	0.431***	0.212		
Flee_freqmins	-0.005	-0.154	0.016	0.309*	0.235	-0.377**	-0.343*	0.009	-0.245	
Bite_freqmins	-0.171	0.018	0.013	0.159	0.044	0.454***	0.391**	0.562***	-0.617***	-0.073

Spearman correlation coefficients for morphological, colour and behavioural variables for contestants (N = 54) in male-male interactions. SVL = snout-vent length, dS = chromatic contrast, dL = luminance contrast, DB = dark back, LB = light back, HB = head bob, Tpuff = throat puff, \_freqmins = frequency per min, durmins = duration (s) per min. Colour is measured as contrast relative to an achromatic black (2%) background. \* $P \le 0.05$ ; \*\*  $P \le 0.01$ ; \*\*\* $P \le 0.001$ .

#### Table A2

Correlations between all behaviour and colour variables for male-female interactions

	Res_SVL	Res_condition_ residual	dL_Beard	dL_DB	dL_LB	Res_HB_freqmins	Res_Tpuff_durmins	Res_Chase_durmins	Res_Flee_freqmins
Res_SVL									
Res_condition_residual	-0.024								
dL_Beard	0.495*	0.299							
dL_DB	-0.196	-0.102	-0.645**						
dL_LB	0.096	0.152	0.266	-0.014					
Res_HB_freqmins	0.034	0.145	-0.201	0.046	-0.137				
Res_Tpuff_durmins	-0.330	0.457*	-0.124	0.136	0.009	0.083			
Res_Chase_durmins	0.094	0.078	-0.361	0.480*	-0.052	0.565**	0.167		
Res_Flee_freqmins	-0.087	0.052	0.000	-0.224	0.258	-0.247	-0.217	-0.217	
Res_Bite_freqmins	-0.146	0.054	-0.487*	0.489*	-0.070	0.662***	0.253	0.803***	-0.232

Spearman correlation coefficients for morphological, colour and behavioural variables for males (N = 22) in male–female interactions. Res = resident, SVL = snout–vent length, dS = chromatic contrast, dL = luminance contrast, DB = dark back, LB = light back, HB = head bob, Tpuff = throat puff, \_freqmins = frequency per min, durmins = duration (s) per min. Colour is measured as contrast relative to an achromatic black (2%) background. \* $P \le 0.05$ ; \*\* $P \le 0.01$ ; \*\*\* $P \le 0.01$ .

#### Table A3

Correlations between colour and colour change for winning males

	Colour	Colour change
dL beard	0.2657	0.5105
dL dark back	0.4126	0.6364*
dS light back	0.6084*	0.4336

Spearman correlation coefficients for colour and colour change of body regions for males that won during male – male interactions and their colour following male – female interactions. N = 12 males. dS = chromatic contrast, dL = luminance contrast. Colour is measured as contrast relative to an achromatic black (2%) background. \*  $P \le 0.05$ .

#### Table A4

Correlations between colour and colour change for losing males

	Colour	Colour change
dL beard	0.169	0.578*
dL dark back	0.266	0.604*
dS light back	0.807***	0.820***
dS light back	0.6084*	0.4336

Spearman correlation coefficients for colour and colour change of body regions for males that lost during male – male interactions and their colour following male – female interactions. N = 14 males. dS = chromatic contrast, dL = luminance contrast. Colour is measured as contrast relative to an achromatic black (2%) background.

\*  $P \le 0.05$ ; \*\*\*  $P \le 0.001$ .