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ORIGINAL PAPER

Facultative brightness-change in an invasive gecko entering a novel background environment

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Abstract Background matching is a common form of crypsis in animals, resulting from selective pressures imposed by visual systems of predators and/or prey. Therefore, it could be expected that novel backgrounds would pose a barrier to the establishment of invasive species, due to a lack of crypsis. Behavioural flexibility in crypsis—through facultative crypsis and/or choice of matching backgrounds—has been suggested as a trait that may facilitate invasiveness. We assessed background-matching and facultative brightness-change in an Australian population of the invasive Asian House Gecko (*Hemidactylus frenatus*). This species is currently expanding from urban environments into surrounding tropical woodland, and demonstrates great variability in colour and pattern among individuals. We quantified wild background-matching in terms of both colour and brightness. We then experimentally tested whether geckos facultatively change brightness in the direction expected for a given background. *Hemidactylus frenatus* consistently brightness-matched across the backgrounds on which they were found, more than would be expected by chance. Experiments showed that *H. frenatus* rapidly changed in their dorsal brightness, in the direction expected given their background, suggesting that brightness-matching observed in wild geckos is due to facultative brightness-change. Successful invasion may benefit from facultative crypsis; however, it remains to be demonstrated how facultative brightness-change in *H. frenatus* is linked to predation and invasion success. We outline how recognition of facultative colour-pattern change in invasive species may be important for early detection and management actions.

Keywords Background matching · Crypsis · Colour change · *Hemidactylus frenatus* · House gecko · Invasive traits · Reptile

Introduction

Background-matching is a common form of camouflage in animals, seen in both prey and predators alike, with individuals sharing characteristics of colour, brightness, or pattern with their surroundings (Cott 1940; Martins et al. 2008; Foley et al 2020; Briolat et al. 2021a, b). While the benefits for predators are difficult to quantify, experiments focusing on prey species have established that deviation from

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a general background-matching colour-pattern often results in increased predation (Farallo and Forstner 2012; Walton and Stevens 2018). Furthermore, populations experimentally or naturally released from predation become more conspicuously coloured (Endler 1980; Bliard et al. 2020). The required accuracy of a prey species' background-matching depends on the visual system of the predator(s) in question (Endler 1990; Théry et al. 2005; Stevens 2007; Merilaita and Dimitrova 2014), with prey colouration expected to be constrained by key factors of predators' vision (Endler and Mielke 2005), such as colour perception, spectral sensitivity, contrast sensitivity, and visual acuity—the level of detail visible from different viewing distances (Martin 2017; van den Berg et al. 2019).

Matching across heterogenous backgrounds presents challenges for many species. Commonly, variable colouration, either through continuous pigment variation or the presence of discrete colour-pattern polymorphisms within a population, allows for background-matching across microhabitats or habitat elements (Endler 1984; Hoekstra and Nachman 2003; Hughes et al 2019). This strategy can be aided by variant-specific background-choice, where individuals choose backgrounds that maximise their crypsis (e.g., Choi and Jang 2014; Marshall et al. 2016; Salisbury and Peters 2019). Yet there is a further strategy—colour-pattern plasticity ('colour-change'), which can be rapid or long-term. Unlike static colour variation, colour-change allows individuals to maintain crypsis in variable habitats (Akkaynak et al. 2017), track seasonal environmental changes (Zimova et al. 2018), transition from conspicuous signalling colours to cryptic colouration (Batabyal and Thaker 2017), and/or optimise camouflage under a specific predator's visual system (Stuart-Fox et al. 2008). Such situational colour-pattern change, adjusted to suit different backgrounds or predators, has been termed 'facultative crypsis' (Stuart-Fox et al. 2006).

Research on background-matching tends to focus on diurnal species, or nocturnal species exposed during daytime rest (Webster et al. 2008; Allen et al. 2020). Yet species active at night can also benefit from background-matching (Fulgione et al. 2019; Parejo et al. 2023; Negro et al. 2025). The degree and type of background-matching required at night is expected to be different from those required during daytime settings. For instance, many nocturnal predators rely on non-visual cues for prey detection (Gracheva et al. 2010; Carr and Christensen-Dalsgaard, 2015; Allen et al. 2020), and those that do use vision face inherent trade-offs; for example, diminished colour discrimination under low light conditions is common across many taxa (Kelber and Roth 2006; Martin 2017; Warrant and Somanathan 2022). Consequently, achromatic (e.g., brightness) rather than chromatic (colour) background-matching may be more important at night (van der Kooi and Kelber 2022). Moreover, nocturnal background-matching may be complicated by the presence of artificial light at night. Although such artificial light can enhance predator perception and discrimination (Briolat et al. 2021a; Moyse et al. 2023; Horn et al. 2023), it also introduces additional heterogeneity in substrate brightness across a habitat. Under these conditions, facultative crypsis may enable some species to remain effectively cryptic in both illuminated and unlit microhabitats (Zaidan and Wiebusch 2007).

Plastic traits such as facultative crypsis are of interest in studying adaptation in invasive species because these traits may facilitate the invasion of novel environments. A species capable of facultative crypsis has a greater chance of being cryptic on novel backgrounds (Stevens and Ruxton 2019), and hence this trait could enhance an invasive species' establishment chances and range expansion due to reduced predation pressure in the important initial stages of establishment and population growth (Sakai et al. 2001; Zenger et al. 2003). However, this hypothesis has not been explicitly tested. Two main questions need to be addressed: do invasive species display facultative crypsis, especially to novel backgrounds, and does this facilitate invasiveness?

The genus *Hemidactylus* (Gekkonidae) includes several globally invasive species ('House Geckos'; Weterings and Vetter 2018), with the Asian House Gecko (*H. frenatus*) considered to be the most invasive (Hoskin 2011). A nocturnal human-commensal originating in southern Asia, *H. frenatus* travel great distances on shipping containers, vehicles, and building materials (Hoskin 2011; Chapple et al. 2013). Now present throughout the global tropics, *H. frenatus* has been implicated in the decline of island gecko species through competition, including the extinction of native *Nactus* geckos on the Mascarene islands (Cole et al. 2005). Despite this, *H. frenatus*'s apparent restriction to urban environments on larger landmasses, like Australia, has generated little concern about potential negative impacts (but see Hoskin 2011). However, recent surveys have shown *H. frenatus* in north-eastern Australia existing in high-density populations at least 2 km into natural bushland habitat (Barnett et al. 2017). This area is home to a high diversity of native gecko species, many with small distributions, and some that are ecologically similar to *H. frenatus* (e.g., *Gehyra*, *Oedura*, and *Amalosia* species; Hoskin 2011). Consequently, there is an incentive to understand any traits assisting invasiveness and competitive ability in the Asian House Gecko.

In this study, we tested for the presence of facultative background-matching in the Asian House Gecko to assess whether behaviourally-flexible crypsis (specifically 'facultative crypsis') may assist invasiveness (Stevens and Ruxton 2019). Expansion from urban environments to natural environments involves many differences, but some of the most substantial are the difference in the colour and structure of available backgrounds (Barnett et al. 2017; Fulgione et al. 2019). Understanding background-matching in variable natural settings would enable better assessment of *H. frenatus*'*s* invasion potential into natural habitats in Australia, and potentially provide information for their management. We examined the possibility of facultative background-matching in two ways. First, we assessed the extent of background-matching in the wild in this species, via colour and brightness levels. We predicted that geckos would be more matched to their background than expected by chance. Second, we conducted experimental trials to determine whether *H. frenatus* is capable of short-term facultative brightness-matching, predicting that changes in dorsal brightness over two hours would be in the expected direction to more closely match their current background.

Materials and methods

Field sampling and photographic data collection

Data collection for the two components of this study was simultaneous, with many individuals used for both aspects where possible. A total of 228 *Hemidactylus frenatus* were located through opportunistic nocturnal spotlighting (6:30 pm to 10:00 pm) on the James Cook University, Townsville (Bebegu Yumba) campus, from 6 May to 18 June 2021. The campus sits at the urban–bushland interface and consists of approximately equal areas of built environment and woodland environment (see Supplementary Fig. S1.1). To ensure adequate sampling in both habitats, and that geckos were not captured more than once, the campus area was broken up into a grid of 100 m^2 squares, each of which was only sampled once. Photographs formed the basis of all raw data. Images were taken in RAW (.CR2) format, approximately 65 cm from the subject, with a Canon EOS 60D and Canon EF-S 60 mm macro lens. Aperture was set at f/18, and ISO speed at 100. A mounted flash unit (Canon Macro Twin Lite) was used for illumination, with flash strength manually set to an output of 1/4. Colour and exposure standardisation was facilitated by an X-Rite ColorChecker Mini, placed beside the gecko in every image.

Observing the extent of wild background-matching

To investigate whether *H. frenatus* engage in background matching behaviour, we took photographs of each gecko and the background it was first observed on. Because geckos moved upon being spotlit, each individual was captured and returned to the point of first observation. Geckos were then held in place for the photograph by gently pressing on a back leg with a finger. Their background was denoted as either 'natural' or 'human-made', allowing for the comparison of behaviour on natural surfaces (e.g., tree trunks, wood, rocks, and leaf-litter) versus artificial surfaces (e.g., concrete, paint, plastic, plaster, and metal). We photographed 96 individuals first seen on natural surfaces, and 81 individuals first seen on human-made surfaces, for a total of 177 individuals. Among geckos on natural substrates, tree trunks were the most common background (n = 69), followed by rocks (n = 15), wood (n = 6), and leaf litter (n = 6). For geckos on human-made substrates, geckos were mainly on walls; either painted/plastered walls (n = 33) or concrete walls (n = 24). Fewer geckos were found on metal backgrounds (n = 10) and non-wall concrete backgrounds (n = 10). Finally, two geckos were found on fire hydrants, one on a rubbish bin, and one on a plastic parking sign (see Supplementary Fig. S1.2 for visualisation).

Within each image, the gecko's dorsal area and an equivalent area of its background were designated using ImageJ's polygon selection tool (Schneider et al. 2012). This resulted in a 'dorsum-background pair' of selections for each individual, containing the relevant information for analysis. Dorsal area was defined as the region between the front of the gecko's forelegs and back of its hindlegs, excluding the legs themselves and any folds of ventral skin. The shape created from the dorsum selection was placed next to the gecko in order to sample an equivalent portion of background (see Supplementary Fig. S1.2 for visual representations of this process). Each dorsum-background pair was assessed for the degree of background-matching in terms of colour, and of brightness.

Assessment of background colour-matching

Colour-matching between each gecko and its background was explored by calculating a colour dissimilarity index (CDI). This metric was adapted from the colour overlap index (COI) created by Francini and Samia (2015), which describes percentage overlap in colour between two selections, itself based on an adapted version of the Renkonen similarity index (Renkonen 1938, in Francini and Samia 2015). Overlap in colour is determined through both the colours present within selections (binned into RGB colour classes), and the relative frequency of those colours (for visualisation, see Fig. S1.3). Specifically, COI describes the sum of the lowest relative frequencies among colour classes shared by the animal and substrate. Here, we used an inverse version (CDI = 1 − COI) so that all metrics were of dissimilarity rather than similarity (e.g., higher values represent larger differences), thereby facilitating ease of comparison between colour and brightness metrics. Only visible colours were investigated; while some areas of the belly and throat of *H. frenatus* reflect in the UV spectrum, there is no such reflectance on the dorsum (J. Endler, MH, & CJH, unpub. data).

Before image processing, RAW files were colour-corrected by applying Digital Camera Profiles (DCP) generated using the ColourChecker Camera Calibration software (Version 2.0; X-Rite, 2019). Exposure was further standardised using Adobe CameraRaw's exposure slider, so that the RGB values of the grey standards in each image were as, or very close to, the following: 244 (white), 158 (neutral 6.5), and 45 (black). Each processed image was converted to a TIFF and loaded into ImageJ (Schneider et al. 2012). Colour Inspector 3D (ImageJ plugin; Bathel 2006) was used to record the frequency of colours within each dorsum-background pair. Colours were partitioned into RGB colour classes using the plugin's default colour interval of 30 colour cells (Francini and Samia, 2015; see Supplementary Fig. S1.3 for more detail). The dissimilarity index for each pair was subsequently calculated in R (R Core Team 2021).

Distribution of CDI scores, and the possible effects of substrate type (natural vs. human-made) were visualised using histograms. To test whether the geckos were better colour-matched (lower median CDI) than expected by chance, one-way permutation tests were conducted in R to compare the median CDI of the observed samples against a null distribution. Two tests were conducted: one for geckos on natural backgrounds, and the other for those on human-made backgrounds. The null distribution was created by generating a dataset of all possible gecko-background CDIs (for natural substrate geckos N = 9216, for human-made N = 6561). We achieved this by pairing every sampled gecko (for natural substrate geckos N = 96, for human-made N = 81) with every sampled substrate, including its own. Then, 96 (natural substrate) or 81 (human-made substrates) CDIs were randomly drawn from this dataset and the median calculated. This was repeated for 10,000 replicates, thereby creating a null distribution of 10,000 median CDIs.

Assessment of background brightness-matching

We assessed whether background-matching in *H. frenatus* involves brightness-matching by comparing the mean brightness of each dorsum-background pair. Greyscale value (GSV) was used as a proxy for brightness, which assigned each selection a relative brightness level on a scale from 0 GSV (pure black) to 255 GSV (pure white). The MicaToolbox (Troscianko and Stevens 2015) and Quantitative Colour Pattern Analysis framework plugins for ImageJ (QCPA; van den Berg et al. 2019) were used to convert each RAW image into a multispectral image. Again, the white, neutral 6.5, and black standards on the colour-checker were used to standardise exposure, with reflectance values of 91.57%, 38.40%, and 3.22% respectively (van den Berg et al. 2019). After selection of the dorsum-background pair within ImageJ, each image was transformed into a 24-bit RGB presentation image.

We obtained mean RGB values of the dorsum and background via the region-of-interest measurement tool, and calculated GSV using the averaging equation (R + G + B)/3.

Absolute difference in GSV between dorsum-background, and the possible effects of substrate type, were visualised using histograms. As before, two one-way permutation tests were used to test the likelihood of active brightness-matching. Observed median difference in brightness between 96 geckos on natural substrates, and 81 geckos on human-made substrates, was compared against null distributions created in the same manner as described above. To further understand the relationship between gecko and background brightness, mean brightness of each individual was regressed against the mean brightness of its background. This regression was fitted with a linear model that tested for a significant effect or interaction involving substrate type.

Experimentally testing for short-term facultative brightness-change

We experimentally tested for the presence of facultative short-term brightness-change in *H. frenatus* by placing 164 individuals (N = 50 originally from natural substrates, N = 114 from human-made) in enclosures with differing backgrounds and photographing them at three time points over two hours (0 min, 15 min, 2 h). These timepoints were chosen to obtain the initial colouration of the gecko (0 min photo), test for very rapid brightness-change (15 min), and less rapid, but still short-term brightness-change (2 h). After capture, each gecko was immediately photographed on an A4 sheet of card covered in plain white printing paper (0 min photo). Then the gecko was randomly assigned to one of five printed paper backgrounds: black, dark grey, medium grey, light grey, and white. Lidded plastic containers were lined with printed paper along all sides, excluding on the transparent lid, to create the enclosures (Supplementary Fig. S1.4). To prevent the spread of pathogens, paper backgrounds were replaced and the tubs cleaned with ethanol after each use.

Once a gecko was introduced to the enclosure, the enclosure was placed gently on the ground as close as possible to that individual's point of capture. Geckos thus performed any background-matching under the lighting conditions in which they were first found. Placing the gecko quickly into the container and not transporting back to a lab avoided stress and associated impacts on behaviour in the experiment. Lighting conditions for each gecko varied from near darkness to fairly bright artificial light. Each gecko was left undisturbed for 15 min, after which it was briefly removed from the tub and placed back on the white card for a second image (15 min photo). After being returned to the treatment enclosure, geckos were left for a further 1 h and 45 min before a third and final image was taken (2 h photo). Geckos were then released at their point of capture. To quantify likely error in brightness measurements between these repeated photographs, we took several test images of an *H. frenatus* preserved specimen (i.e., incapable of brightness-change) on white card with exaggerated inconsistencies in camera angle and lighting. We determined that error across images was likely ± 5 GSV or below (for full description, see Supplementary Material S3).

For each individual, a dorsal brightness measure was generated at each of the three timepoints, using the methods described above for tests of wild brightness-matching. Between-group comparisons of mean dorsal brightness were investigated using three one-way ANOVAs, one for each time point. To look at within-group changes in mean dorsal brightness over the time points, we used paired t-tests, with P values adjusted for multiple tests using the P.ADJUST function in R, with METHOD = FDR (false discovery rate). Overall changes in GSV from 0 min to 2 h for each treatment, including the slopes of individual geckos through time, were visualised using paired violin plots. Analyses were performed in R (R Core Team 2021), and visualised with the GGPLOT2 (Wickham 2016) and GGPUBR (Kassambara 2023) packages.

Results

Observing the extent of wild background-matching

Assessment of background colour-matching

The magnitude of colour dissimilarity between geckos and their backgrounds formed a broad and bimodal distribution (Supplementary Fig. S2.1a), spanning from 10 to 100% dissimilarity in colour, with a median CDI score of 68.2%. Substrate type drove this bimodality (Fig. 1a, b), with geckos on natural substrates more similar in colour to their backgrounds (median CDI of 47.1%) than geckos on human-made substrates (median CDI of 95.3%). Exceptions to these trends included geckos photographed on concrete mixed with pebbles, a human-made but naturalistic substrate that drove unusually low CDIs of below 50%. Conversely, some geckos on natural backgrounds had very high (70–100%) dissimilarity scores, mainly individuals on pale *Eucalyptus platyphylla* trunks, a tree species common within the study area.

Geckos found on natural substrates were more similar in colour to their backgrounds than expected by chance (median observed CDI < median permuted CDI: one-way permutation test, $P < 0.001$; Fig. 1a inset). Conversely, geckos sampled on human-made substrates were not more similar to their backgrounds than expected by chance (median observed CDI < median permuted CDI: one-way permutation test, $P = 0.110$; Fig. 1b inset).

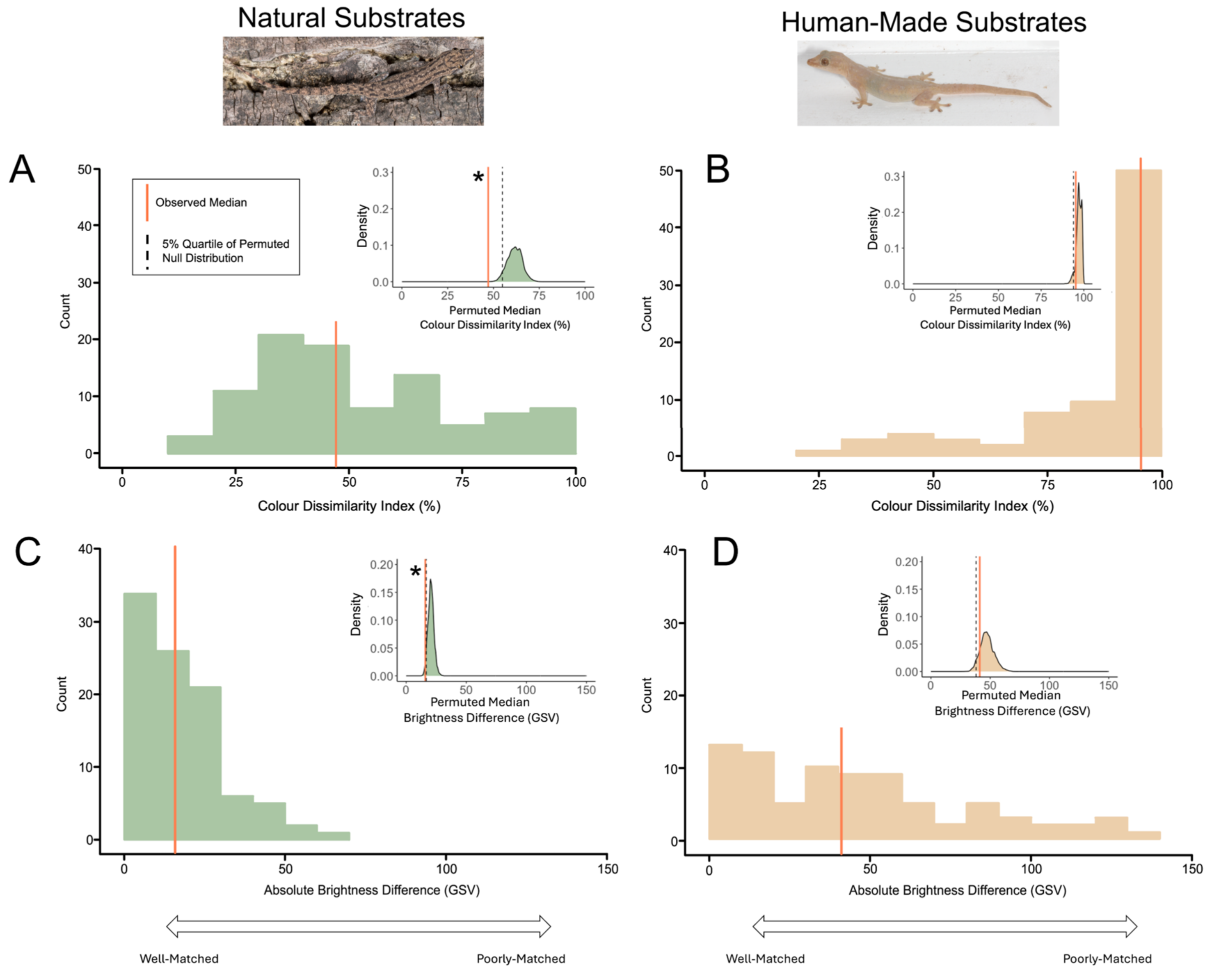

Fig. 1 **A** Distribution of observed colour dissimilarity index (CDI) scores showing percentage dissimilarity in colour between a gecko and its background for geckos on natural substrates (n = 95), with a median score of 47.1%. Inset shows observed median tested against a null distribution of 10,000 median scores, where each sample contained 95 CDIs randomly generated from all possible dorsum-background pairs in the original dataset. **B** As **A** but for geckos on human-made substrates (n = 81), with an observed median CDI of 95.3%. **C**. Distribution of observed dorsum-background brightness differences for geckos on natural substrates, with inset showing observed median of 15.9 GSV, tested against a null distribution as in **A**. **D** As **C** but for geckos on human-made substrates, with an observed median of 41.2 GSV. Observed medians that were significantly lower than permuted medians are marked by an asterisk

Assessment of background brightness-matching

Our sampled absolute brightness differences (henceforth referred to as 'brightness differences') between each gecko's dorsum and its background formed a positively skewed distribution. Most individuals had a dorsal brightness within 0–40 GSV points of their background, although there was also a long 'tail' of individuals with larger differences in brightness (up to 140 GSV) (Supplementary Fig. S2.1b). The median brightness difference for a dorsum-background pair was 21.1 GSV. When split by substrate type, most geckos on natural substrates had brightness differences below 30 GSV, with a median difference of 15.9 GSV. In contrast, individuals on human-made substrates constituted all the pairings with extreme differences (over 70 GSV), and a high median brightness difference of 41.2 GSV (Fig. 1c, d).

Geckos observed on natural substrates were more similar in brightness to their backgrounds than when randomly assigned to backgrounds of their same substrate type (observed brightness difference < median permuted brightness difference: one-way permutation test, $P = 0.021$; Fig. 1c inset). While the magnitude of this improvement was fairly small, it highlights the more restricted brightness variation in the sampled natural substrates; the medians of the random distribution only varied from ~13 to 31 GSV. The human-made environment varied more, reflected in a mean brightness difference spanning from ~27 to 71 GSV. In this wide-variation environment, geckos were not significantly more similar in their brightness to their backgrounds than geckos randomly assigned to human-made backgrounds (one-way permutation test, $P = 0.140$; Fig. 1d inset), although the observed median brightness difference for these pairs was lower than that of the permuted distribution.

Using linear regression modelling, we found a positive relationship between gecko dorsum and background brightness (adjusted $R^2 = 0.66$; Fig. 2a). The slope of this relationship was significantly different for geckos on a natural substrate versus geckos on a human-made substrate (mean dorsum GSV × mean background GSV interaction term: $t = -4.52$, $df = 172$, $P < 0.001$). Even when the data was restricted to points where background brightness was within the range of both substrate types (i.e., < 163 GSV), the above interaction remained significant (mean dorsum GSV × mean background GSV interaction term: $t = -2.93$, $df = 149$, $P = 0.004$; Fig. 2b).

Geckos on natural backgrounds were more closely matched to their background than those on human-made backgrounds (Fig. 2a), as determined by the slope of each relationship: natural slope

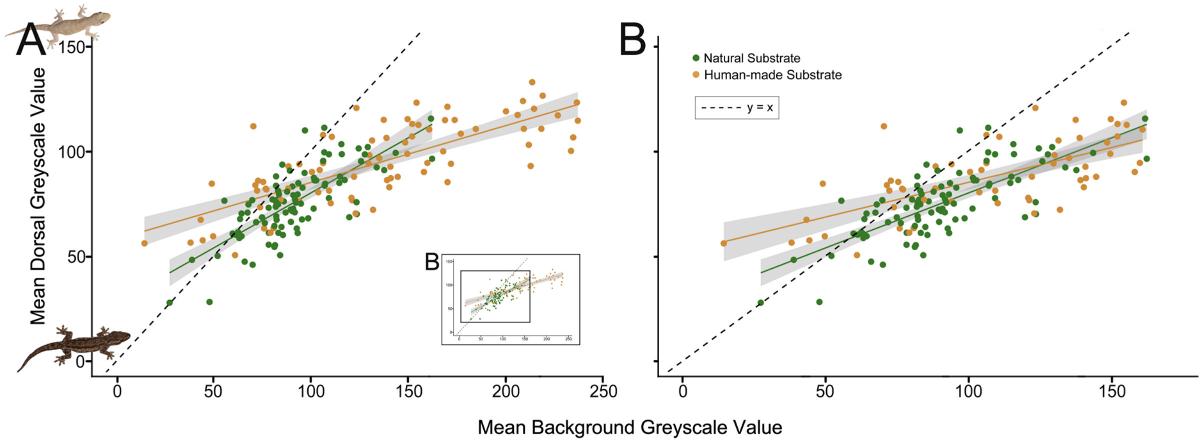

Fig. 2 **A** A linear regression of 176 geckos' mean dorsal brightness against their mean background brightness, including the effect of substrate type and its interaction, shows that the dorsum brightness is positively associated with background brightness (Adjusted $R^2 = 0.663$). Background type (natural/human-made) significantly modifies the slope of this relationship. The inset visualises the subset of samples used to compare the two slopes only where both substrates have overlapping data. The dashed line indicates the expected slope if $y = x$, or if every gecko was the same mean brightness as its substrate. Grey shading indicates a 95% confidence interval. **B** This interaction persists even when data is restricted to the overlapping subset

$=0.52$, $P < 0.001$; human-made slope $=0.33$, $P = <0.001$, although both slopes were less than $y = x$ (the dashed 1:1 line shown in Fig. 2). The interaction in the above model appears to be driven by geckos on dark human-made backgrounds being lighter than those on dark natural backgrounds (seen to the left of the x-axis on Fig. 2b). Additionally, there was a limit to dorsal brightness in *Hemidactylus frenatus*, leading to excessively large brightness differences between dorsum-background pairs when backgrounds exceeded ~120 GSV. A Cook's Distance test suggested there were no significant outliers in the linear model, both at an overall level, and when the results were separated by substrate.

Experimentally testing for short-term facultative brightness-change

Geckos were observed changing their dorsal brightness throughout the 2-h duration of our experimental trials. These changes in brightness (GSV) were generally in the direction expected if geckos were attempting to better match their backgrounds (Fig. 3a). At the beginning of the trial (0 min), treatment groups did not significantly differ from one another (one-way ANOVA: $F_{4,158} = 0.68$, $P_{adj} = 0.641$; Fig. 3a). Although geckos varied in their initial dorsal brightness (Fig. 3a), random assignment of individuals to each treatment background yielded similar mean brightness across treatments. There were, however,

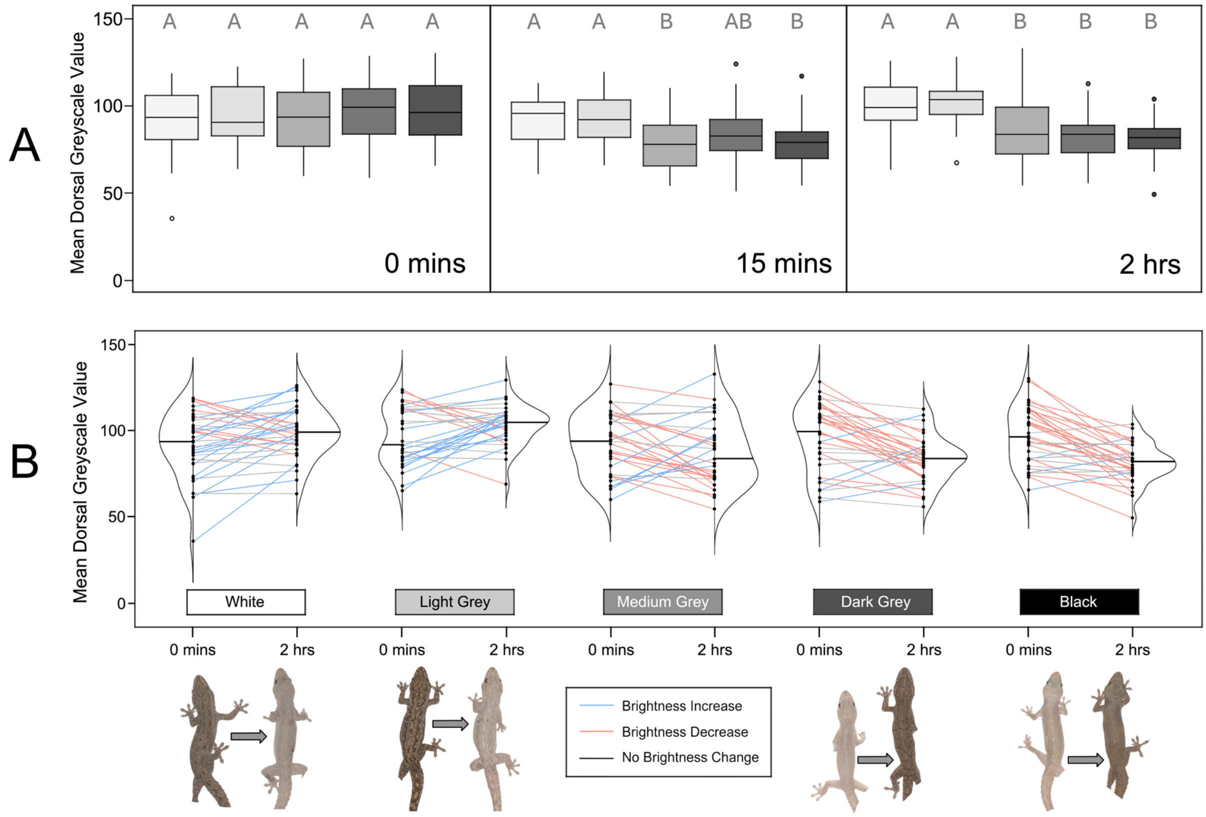

Fig. 3 **A** There was no difference in mean dorsal brightness between background treatments at the start of the experiment, but light and dark background groups drew apart over the two hours of the experiment. Different letters indicate significant differences between groups at each timepoint; groupings for 15 min and two hours were taken from Tukey Post Hoc analysis of ANOVAs (see Table 1). **B**. Paired boxplots for each treatment showing individual geckos' brightness change slopes from 0 min to 2 h. Results of paired t-tests on each treatment group may be seen above in Table 2. Changes of less than 5 GSV between timepoints were taken to indicate no change in brightness. Images show extreme changes in individual brightness for four of the treatments (after colour/exposure correction) visualising the ability of *Hemidactylus frenatus* to rapidly change dorsal brightness over two hours

differences between the treatments after fifteen minutes (one-way ANOVA: $F_{4,158} = 6.69$, $P_{adj} = 0.002$) and two hours (one-way ANOVA: $F_{4,158} = 13.85$, $P_{adj} = 0.002$). Tukey's Post Hoc analysis of the groups after fifteen minutes showed that geckos on the black treatment were already significantly darker than those on light grey or white (Fig. 3a, Table 1). At two hours, geckos on the three darkest treatments were all significantly darker than those kept on light grey or white (Fig. 3a, Table 1). No significant difference was found between the three darker treatments, and between the two lighter treatments, at either 15 min or 2 h (Table 1).

After just 15 min on the treatment backgrounds, average dorsal brightness of geckos on the medium grey, dark grey and black treatments was significantly darker than at 0 min. Conversely, the average dorsal brightness of geckos on white and light grey were no different between the 0- and 15-min timepoints (Table S2.1). After 2 h, geckos in all treatments, excluding medium and light grey, showed a significant change from their initial mean dorsal brightness (Fig. 3b, Table 2). Geckos on white generally became lighter, while geckos on dark grey and black tended to become darker. Geckos on light grey visually became lighter, and the result was significant prior to adjusting for multiple tests (FDR) but was marginally non-significant after this adjustment (Table 2). In these four groups, geckos that adjusted in the opposite direction than expected were often those who were already similar to that background; e.g., light geckos placed on white or light grey, and dark geckos on dark grey or black. There was variation in individual responses throughout the treatments, and a number of individuals showed no discernible brightness-change (Fig. 3b; a change of within ±5 GSV; see Supplementary Material S3). Unlike those on the other treatments, geckos placed on medium grey showed no trend in the direction of brightness differences between 0 min and 2 h. Although the individuals in the group exhibited changes in brightness, they were not consistent with any general trend (Fig. 3b).

Table 2 Statistical differences within treatment groups over time

Treatment group	*t*	df	*P*	*P* adjusted
White	− 2.61	33	**0.014**	**0.023**
Light grey	− 2.12	30	**0.042**	0.053
Medium grey	1.38	30	0.178	0.178
Dark grey	4.44	32	**< 0.001**	**0.003**
Black	5.74	33	**< 0.001**	**0.003**

Results of paired t-tests conducted on the treatment groups, comparing the initial group dorsal brightness mean against their mean after 2 h. An adjusted *P* value is used to account for the multiple tests, using the False Discovery Rate method. Significant results are highlighted in bold

Discussion

Hemidactylus frenatus use facultative colour and brightness-matching

We found that the Asian House Gecko (*Hemidactylus frenatus*) likely uses an 'active' background matching strategy for its dorsal colouration, with active matching of brightness, and some evidence towards matching of colour. On natural substrates such as trees, leaf litter, and rocks, Asian House Geckos were significantly more similar in colour and brightness to their own background than other backgrounds inhabited

Table 1 Statistical differences between treatment groups at 15 min and 2 h

	White	Light grey	Medium grey	Dark grey	Black
White		1.000	**0.002**	0.117	**0.004**
Light grey	0.922		**0.004**	0.142	**0.005**
Medium grey	**0.011**	**< 0.001**		0.658	1.000
Dark grey	**< 0.001**	**< 0.001**	0.783		0.765
Black	**< 0.001**	**< 0.001**	0.461	0.986	

Pairwise *P* values showing the treatment groups found to be significantly different from each other by Tukey's Post Hoc analysis of ANOVAs at the 15 min and 2 h timepoints. Values above the diagonal indicate significant groupings at 15 min, while values below the diagonal indicate significant groupings after geckos were on the treatments for 2 h. Note that while the same groups mostly remain significant during both time periods, the magnitude of difference increases at 2 h. Significant results are highlighted in bold by geckos in the same population over the same time period. A similar trend of brightness-matching was seen for those geckos on human-made substrates, although this matching was seemingly restricted by an upper limit on dorsal brightness. Experimental manipulation of background brightness found that Asian House Geckos can rapidly (within 15 min) adjust their dorsal brightness to be more like that of their background, revealing that active brightness matching is implemented through facultative brightness-change.

Drivers and limitations of background-matching

Colour-matching

Asian House Geckos on natural substrates had moderate CDI scores because their neutral grey, brown, or yellowish colouration was broadly similar to surfaces such as tree bark and leaf-litter. This likely reflects a 'generalist' background matching strategy (Allen et al. 2020; Briolat et al. 2021a, b; Murali et al. 2021). However, for geckos on natural substrates, dorsum-background pairs (i.e., gecko dorsum and adjacent background) were also more similar than expected by chance, suggesting additional active colour-matching. This could be driven either through background choice or facultative colour-change. Individuals on human-made substrates were dissimilar to their backgrounds, and not significantly more similar than expected by chance, implying either weaker selective pressure for background-matching or limits to colour-change ability.

While Asian House Geckos are potential prey for a variety of predators that span mammals, reptiles, and birds, it is likely that birds are the main predators within our study area. Examples include nocturnal and crepuscular birds such as the Bush Stone-curlews, Tawny Frogmouths, and various owls, in addition to some mostly diurnal birds such as Australian Magpies, Blue-winged Kookaburras, and Pacific Baza (C. Hoskin, pers. obs.). While generally nocturnal, *H. frenatus* may be visible in sub-optimal retreat sites or be diurnally active to opportunistically bask and feed (e.g., Nordberg 2019; author obs.). Birds generally have excellent colour discrimination (Jones et al. 2007; Stuart-Fox et al. 2006), but this ability is diminished for birds in low light levels, likely due to a trade-off with visual acuity (Bowmaker and Martin 1978; Martin 2017). Colour-matching may be under stronger selection in the natural environment because retreat sites are less numerous, or lower quality, than in urban environments (Barnett et al. 2017; Kim et al. 2019), exposing geckos to diurnal predators.

Withdrawal to retreat sites may serve as a critical anti-predator strategy in urban environments, especially under artificial night lighting. *Hemidactylus frenatus* frequently congregate around these light sources to feed on attracted insects (Zozaya et al. 2015); however, such conditions may enhance predator colour discrimination (Martin 2017; Moyse et al. 2023; Horn et al. 2023). Furthermore, in urban settings, colour-matching may prove ineffective, as geckos often cannot replicate the extreme lightness/darkness or saturation of colour in urban substrates (Caro 2021; Fig. S2.2). Consequently, geckos may rely more heavily on alternative strategies such as proximity and escape to retreat sites (Muller et al. 2020; Caro 2021) or caudal autotomy (Clause and Capaldi 2006). Future research should focus on identifying key visual predators in these systems and developing refined models of predator vision under diurnal, nocturnal and artificial lighting conditions.

Brightness-matching

Brightness-matching appears to be an important factor in the colouration of Asian House Geckos. We observed brightness-matching consistently across a wide range of backgrounds, as well as geckos adjusting their dorsal colouration over two hours to better match a provided background. An increasing mismatch between dorsal and background brightness as backgrounds grew lighter appears to show biological limits to lightening. This upper limit is clearly shown in our study, where gecko dorsum brightness remains at about 120 GSV, even as background brightness climbs to nearly 250 GSV (white wall backgrounds; right side of axis, Fig. 2a). Dorsal brightness in *H. frenatus* is likely bounded by dermal melanophore numbers and constriction ability (Svensson and Sköld 2011; Fulgione et al. 2014), as well as the colour of organs under the skin, which become more apparent as a gecko lightens and becomes slightly transparent. Brightness discrimination is considered uniformly poor in birds (Ghim and Hodos 2006; Martin 2017). As such, approximate brightness-matching may be sufficient to enhance predator avoidance, although this hypothesis requires testing through predator vision modelling under diurnal, nocturnal and artificial light conditions. Alternatively, geckos on high brightness backgrounds may employ alternate anti-predator strategies, as expected for geckos unable to colour-match (Caro 2021).

While brightness-matching was consistently seen across the sampled substrates, we found an interaction between substrate type and brightness difference, with geckos on dark human-made substrates lighter than those from natural substrates of the same brightness. This may stem from human-made substrates being more likely to be well-lit at night, increasing their perceived brightness, or similarly, because many dark plastics and metals (the darkest human-made substrates sampled here) are highly reflective, again increasing perceived brightness. The urban environment can also be highly heterogenous, with very light and very dark substrates close together (Edelaar et al. 2019). We observed that human-made substrates inhabited by geckos varied far more in brightness (14–237 GSV; Fig. S2.2) than the natural substrates geckos were also found on (27–162 GSV; Fig. S2.2). As individuals traverse surfaces that vary on a fine scale, they may be more likely to be mismatched, even given their relatively rapid ability to change brightness. For example, the outlier visible in the centre left of Fig. 2a, b represents a medium-light gecko initially found on a black metal fence immediately adjacent to a medium-light concrete wall.

Facultative brightness-matching

We tested whether brightness matching is implemented in *H. frenatus* through facultative change. In our study, geckos generally changed their brightness to better match a given background. Over two hours, the mean dorsal brightness of geckos placed on white or light grey backgrounds increased, while the mean brightness of those placed on dark grey or black backgrounds decreased. After two hours, the mean dorsal brightness of the two lightest backgrounds was significantly different from that of the two darkest backgrounds. Curiously, geckos placed on the medium grey treatment saw no significant change over two hours. Individuals within the group did change substantially in brightness, but without the consistency seen in the other groups. Poorer matching on intermediate backgrounds, in comparison to very light or dark backgrounds, has also been noted in previous studies of other gecko species (Zaidan and Wiebusch 2007; Vroonen et al. 2012). This effect, along with similar variation in the other treatment groups, may stem from individual-specific stress responses (discussed below) and differences in perceived background brightness under varying field lighting conditions.

While dorsal brightness-change may have signalling and thermoregulatory functions in diurnal reptiles (Vroonen et al. 2012; Allen et al. 2020), it is implicated as a background-matching tool in many geckos, particularly nocturnal arboreal species like *Hemidactylus* (Zaidan and Wiebusch 2007; Vroonen et al. 2012; Das et al. 2014; Fulgione et al. 2019). Notably, dorsal darkening can occur incredibly rapidly—in a matter of seconds—in response to stimuli such as bird calls (Ito et al. 2013) and is often linked to physiological stress responses (e.g., the release of glucocorticoids or adrenalin; Hadley and Goldman 1969; Kindermann et al. 2013; Lewis et al. 2017). Anecdotally, we often observed rapid dorsal darkening in geckos after they were photographed at the 0-min timepoint. This handling-induced darkening may explain why geckos on the three darkest background treatments (medium grey, dark grey and black) were already significantly darker at 15 min compared to 0 min. Conversely, the ability of geckos to match the two lightest treatments (light grey and white)—which were not significantly different between 0 and 15 min—may have been compromised by initial darkening. Although we observed brightness-matching over two hours, undisturbed *H. frenatus* may be able lighten themselves more rapidly. It is unclear whether lightening and darkening incur different energetic costs, but both actions involve hormonal control of pigment within dermal melanophores, which either aggregate (to produce a lighter appearance) or disperse (to produce a darker appearance; Vroonen et al. 2012; Ligon and McCartney 2016).

We have demonstrated facultative brightness-change ability in one population of this invasive gecko, but several aspects of this system remain unresolved. Firstly, the relationship between predation and brightness-matching should be explicitly tested. Employing gecko models of various colours and brightness levels could help assess the benefits of brightness-matching both at night and during the day. Camera observation of the models would also facilitate the identification of key visual predators of *H. frenatus*, whose visual systems can then be incorporated into more specific models of crypsis efficacy (including that of colour). Secondly, further investigation into crypsis as an invasive trait could be advanced by comparing brightness-change ability between different populations (e.g., city centre vs. bushland), or between invasive and non-invasive species. For *H. frenatus*, this might involve comparisons with non-invasive sister species within *Hemidactylus* and, in Australian populations, comparisons with ecologically and morphologically similar native *Gehyra* geckos could also prove informative.

Finally, it is still unknown how *H. frenatus* perceive their backgrounds and adjust their brightness or colour. Recent studies have highlighted many intriguing aspects of crypsis in lizards, including the use of light-sensitive opsins—rather than eyes—to assess background brightness (Fulgione et al. 2014). Reptiles may also undergo long-term colour-change to better match frequently encountered backgrounds, through structural modifications of dermal chromatophore units over time (Pellitteri-Rosa et al. 2020). Moreover, the extent to which *H. frenatus* actively selects matching backgrounds is unclear. Here, we demonstrated that geckos are capable of relatively rapid changes in dorsal brightness; however, *H. frenatus* may also choose substrates on which they can better match colour, brightness, and/or pattern. Such adaptive background choice has been documented in several reptile species (e.g., Marshall et al. 2016; Salisbury and Peters 2019; Kravchuk and Watson 2020).

Management implications

Invasive species are one of the greatest threats to biodiversity globally, and increased knowledge on traits that contribute to invasiveness may increase the ability to better predict invasions, detect them earlier, and control them more effectively if they become established. Behavioural flexibility in camouflage, comprising active background choice and/or facultative crypsis, might facilitate invasiveness in a species (Zaidan and Wiebusch 2007; Stevens and Ruxton 2019). Like most 'invasive traits', facultative crypsis may not guarantee invasiveness (Gibson et al. 2011) but it may be an under-appreciated component in the success of some invasions.

Hemidactylus frenatus has reached urban areas throughout the tropics and across Australia due to its close association with humans (Hoskin 2011; Zozaya et al. 2015; Weterings and Vetter 2018), resilient eggs that survive harsh conditions and transport (Hoskin 2011), and a tolerance for high densities of conspecifics (Cisterne et al. 2019). Yet the main issue with this species—where it truly becomes an invasive threat to biodiversity—is when it transitions into natural habitats, potentially affecting native gecko species through competition (Cole et al. 2005; Hoskin 2011; Barnett et al. 2017). The ability to rapidly switch from a light, plain appearance to a dark one (or vice versa) may allow *H. frenatus* to be highly cryptic immediately upon entering the natural environment, reducing predation pressure and supporting persistence in the key initial stages of invasion and enhancing spread thereafter. Asian House Geckos have generally been seen as very pale geckos on white walls but the results herein suggest background-matching and colour-pattern change abilities should be considered carefully when assessing the invasive potential of a species.

On a more practical level, facultative colour-pattern change also complicates detection and management of some invasive species. There is substantial variation in appearance of individual *H. frenatus*, at least in part driven by the ability to adjust dorsal brightness (Fig. 4a.). While *H. frenatus* is a familiar species to many Australians, this familiarity is for a very pale gecko inhabiting a wall or ceiling, rather than the dark or patterned individuals found in natural habitats. Such variation increases the chances that populations in natural habitats are misidentified as similar native species, such as *Gehyra* species (Fig. 4b), and are hence overlooked. To catch invasions in their early stages, managers and the public need to be aware of this variation, particularly as public engagement with invasive species detection and control continues to grow (Crall et al. 2011; Andow et al. 2016; Morais and Reichard 2018; Johnson et al. 2020; Werenkraut et al. 2020).

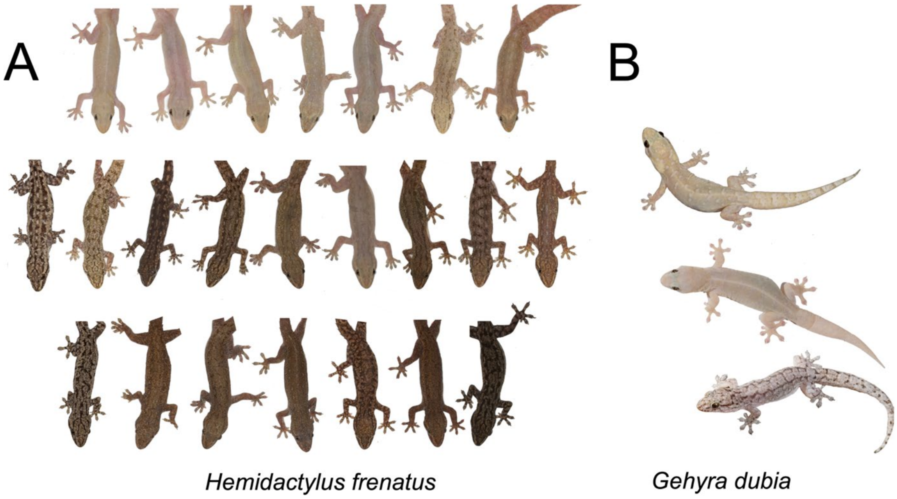

Fig. 4 **A** Example variation in brightness and colour-pattern of the invasive house gecko *Hemidactylus frenatus*, observed over the course of this study. **B** The sympatric native Australian house gecko *Gehyra dubia*, which is frequently confused with *H. frenatus*, especially when both inhabit urban spaces. (Photos by Stephen Zozaya)

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Author contributions All authors contributed to study conception, experimental design, and statistical analysis design. NEL carried out data collection and data analysis, with input from MH and CJH. NEL wrote the first draft of the manuscript, and all authors provided feedback on, and approved, the final draft.

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Data availability Photographic data and code for this study can be made available upon request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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