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Animal behaviour

Chameleons communicate with complex colour changes during contests: different body regions convey different information

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Many animals display static coloration (e.g. of feathers or fur) that can serve as a reliable sexual or social signal, but the communication function of rapidly changing colours (as in chameleons and cephalopods) is poorly understood. We used recently developed photographic and mathematical modelling tools to examine how rapid colour changes of veiled chameleons *Chamaeleo calypratus* predict aggressive behaviour during male–male competitions. Males that achieved brighter stripe coloration were more likely to approach their opponent, and those that attained brighter head coloration were more likely to win fights; speed of head colour change was also an important predictor of contest outcome. This correlative study represents the first quantification of rapid colour change using organism-specific visual models and provides evidence that the rate of colour change, in addition to maximum display coloration, can be an important component of communication. Interestingly, the body and head locations of the relevant colour signals map onto the behavioural displays given during specific contest stages, with lateral displays from a distance followed by directed, head-on approaches prior to combat, suggesting that different colour change signals may evolve to communicate different information (motivation and fighting ability, respectively).

1. Introduction

The colour of most animals is relatively fixed (e.g. in dead tissues like exoskeleton, scales, feathers and hair), but some animals are capable of undergoing rapid, physiological colour change which allows them to display different colours and patterns in response to changing environmental contexts (e.g. predators [1], temperature [2] and humidity [3]). A few taxa (predominantly cephalopods, fish and reptiles) also are capable of physiological colour change during intraspecific interactions. Chameleons (Squamata: Chameleonidae) represent an intriguing subject for research on dynamic coloration because, unlike organisms that undergo localized colour change [4] or rely on achromatic pattern alterations [5], they exhibit complex colour changes during social interactions [6]. In fact, selection for conspicuous signals is likely to have driven the evolution of display colours for some chameleons [7]. The complexity of chameleon colour change may permit dynamic signalling opportunities for chameleons, whereby they use diverse chromatic elements on the body to reveal distinct information, either over the course of social interactions or across different behavioural contexts.

To date, most research on physiological colour-change signals has focused on simplified on/off signals [4,5] or mechanistic (e.g. cellular and endocrine) controls [8], with less emphasis on adaptive significance and information content [9]. The relative paucity of investigations undertaken on the signalling role of physiological colour change may be due, in part, to the technological and methodological challenges associated with quantifying such a dynamic trait. However, recent advances in the photographic quantification of colour [10,11] and the visual systems of animals [12] now enable rigorous, non-invasive analyses of colour change,

as it occurs and is perceived by conspecifics during social interactions. Here, we present the first study using these photographic [10,11] and analytical methods [11,13], as well as organism-specific visual models [12,14], to examine how dynamic colour changes of veiled chameleons *Chamaeleo calyptratus* predict behaviours in male–male contests. Though animals engaged in contests have conflicting aims, there is a shared benefit in avoiding unnecessary escalation of such contests. Dynamic signals, for example those provided by multi-component colour changes, may allow contestants to flexibly communicate motivation or ability during contests and could therefore contribute to evolutionarily stable strategies [15].

Male veiled chameleons are well known for intense intra-sexual aggression (see electronic supplementary material, S1), yet agonistic encounters are frequently settled prior to physical contact, putatively through visual signals including rapid, body-wide colour change [6]. Here, we attempt to uncover the components of colour change linked to escalation behaviour (likelihood of approaching an opponent) and contest outcome (likelihood of winning a fight) by evaluating 28 different colour patches (figure 1) from displaying veiled chameleons during staged agonistic encounters. Specifically, we focused on the rate and degree of colour change (calculated using known sensitivities of chameleon photoreceptors [14]), as well as the maximum brightness of each colour patch, during aggressive interactions.

2. Material and methods

In spring 2011, we staged a series of aggressive, dyadic encounters between 10 adult male veiled chameleons in a round-robin tournament format that matched each chameleon against every other chameleon in our study population (see electronic supplementary material, S2). Trials were recorded with two high-definition video cameras that also enabled us to take still photographs of each chameleon. Though chameleons can exhibit a complex suite of behaviours during agonistic encounters (e.g. hissing, tail-curling and rocking), the most salient signals relate to the probability of escalating and winning aggressive encounters [15]. Thus, we monitored both escalation likelihood (whether or not a chameleon moved in a directed fashion toward its opponent) and win/loss outcome (losing chameleons retreated from their opponent at some point during the trial). We then used matrices of approach behaviour and contest outcomes to determine ‘ability’ scores using Bradley–Terry models (see electronic supplementary material, S6). Both chameleons displayed aggressive behaviour and rapid colour change in 17 of our 45 contests.

We collected data on brightness and colour change from 28 different colour patches on each chameleon (encompassing a variety of chameleon body regions and colour types; figure 1) that were photographed every 4 s during display, approach and combat phases of the trials. We first equalized and linearized photographs [11], then used specialized mapping functions to convert RGB (red, green and blue) values from these photographs to relative stimulation values of the different chameleon photoreceptor types (see electronic supplementary material, S3). Photographically derived estimates of chameleon photoreceptor stimulation values obtained from an independent dataset did not differ from spectrophotometrically determined values (see electronic supplementary material, table S2 and figure S2).

Because chameleon display coloration and change has never been quantitatively analysed with respect to intraspecific variation in behaviour, we measured the amount and speed of colour change, as well as maximum display brightness (previously suggested to be an informative component of squamate colour

signals [16]). We measured colour changes as: (i) the perceptual distance travelled (sum of distances between colour measurements taken at different times) and (ii) rate of colour change (perceptual distance/time), both measured using units of just noticeable differences, which capture perceivable changes in colour taking into account species-specific photoreceptor sensitivities [13,17] (see electronic supplementary material, S4). Brightness was quantified by calculating how each colour patch would stimulate chameleon double cones, though only maximum brightness was evaluated in model-averaging and regression analyses.

We used principal components analyses to reduce the number of variables within three body regions (head, stripes and main body; electronic supplementary material, S5 and table S4) and an information theoretic model-averaging approach to evaluate the relative importance (RI; the sum of Akaike weights for all models in which that variable appeared) of colour intensity and change (averaged for each chameleon across trials) in predicting the likelihood of approaching an opponent or winning aggressive interactions (see electronic supplementary material, S6). Lastly, we included predictor variables from the top models in regression analyses to determine the degree to which colour traits explained variation in approach and winning abilities.

3. Results

Approach and fighting abilities were highly correlated ($r = 0.84$, $p = 0.003$), though the colour metrics that best predicted these outcomes were different. Specifically, maximum head (RI = 0.32) and stripe brightness (RI = 0.60) achieved were the best predictors of approach ability during agonistic encounters (figure 2*a*; electronic supplementary material, table S5); in regression analysis, maximum stripe brightness explained 71% of the variation in approach likelihood (figure 2*c*). Chameleons who displayed brighter heads (RI = 0.80) that changed colour faster (RI = 0.31) were more likely to win physical encounters (figure 2*b*; electronic supplementary material, table S6). A regression containing only maximum head brightness explained 83% of the variation in fighting ability (figure 2*d*).

4. Discussion

We found that different aspects of chameleon competition (approach likelihood and contest outcome) were best predicted by separate components of display coloration—maximum stripe brightness and maximum head brightness, respectively. We also found that rate of colour change was an informative component of aggressive displays; chameleons whose head coloration changed faster were more likely to win agonistic encounters. Taken together, these correlational findings represent the first demonstration that multiple components of rapid colour change can be used to signal different aspects of competitive behaviour (e.g. motivation and fighting ability).

Selection may favour separate signal components for motivation and fighting ability [15] because these two aspects of competition can differentially affect contest outcomes; for example, regardless of true ability, animals who fight harder to defend mates or territories can often overcome less-motivated competitors. Separate signals may also be favoured when rival assessment is prolonged and animals progress through a series of escalation and threat behaviours, as occurs for slow-moving chameleons that have the opportunity to sequentially evaluate competitor intent and quality. Interestingly, the physical locations of the key colour-signalling elements of veiled



Figure 1. Colour patches measured during male–male competition between veiled chameleons. (*a,b*) Interindividual variation in location of colour patches can be seen by comparing the location of colour patches in (*a*) to those in (*b*). Because exact locations of colour patches varied among individuals, we focused on similarly located colour patches of equivalent pigmentary and structural makeup. Descriptions of colour patches and relevant principal component loadings are located in the electronic supplementary material, table S4.

chameleons align closely with the behaviours they exhibit during agonistic encounters. Aggressive chameleons display laterally to one another from a distance before approaching, providing their opponents the opportunity to assess body stripe coloration (which best predicted escalation likelihood in our study). Next, as they approach and prepare to engage in head-to-head combat (see electronic supplementary material, S1 and video S1), they have close visual access to head coloration (which best predicted win/loss outcome). Separate plumage patches in lark buntings *Calamospiza melanocorys* also convey different information about approach intensity and physical

aggression [18], but our study is the first to document the use of multiple, behaviourally accentuated colour-change signals to communicate different information.

Costly intraspecific conflict over resources is common throughout the animal kingdom, yet rapid colour change as an agonistic signal is incredibly rare and warrants special examination. One possible explanation for the link between rate of colour change and fighting ability is that expression of bright, rapidly changing colours is causally related to the physiological processes (e.g. hormone status and energetic reserves) associated with fighting ability [4]. An alternative,

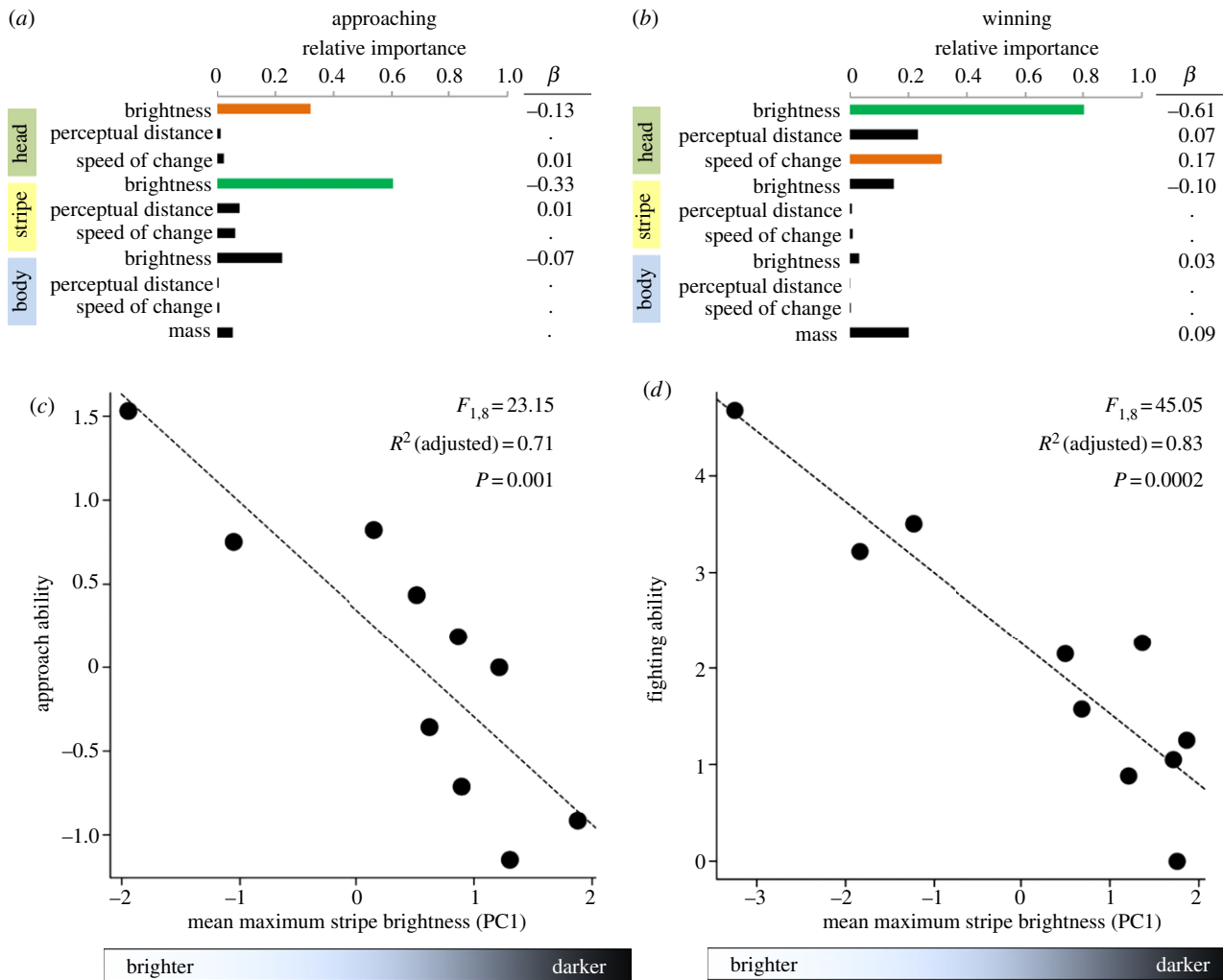


Figure 2. Explanatory variables associated with escalating and winning contests. Multi-model averaging indicates that average maximum stripe brightness (principal component, PC) best explains the likelihood of (a,c) a chameleon approaching his opponent and (b,d) that average maximum head brightness (PC) best explains the likelihood of a chameleon winning a fight. (a,b) Bar length is proportional to RI values of variables predicting (a) likelihood of approaching an opponent or (b) likelihood of winning an aggressive interaction, with green bars indicating RI values greater than 0.60 and orange bars indicating RI values greater than 0.30. Average parameter estimates of regression coefficients (β) were obtained using multi-model-averaging approaches and dots indicate parameter estimates with absolute values less than 0.005. (c) Regression of chameleon stripe brightness and approach ability calculated across trials. Average stripe brightness values represent PC scores, all of which had negative loadings of maximum brightness values (chameleons with brighter bodies had negative PC scores). (d) Regression of head brightness on fighting ability. Colour-metric predictor variables in (a–d) represent principal component scores from multiple colour patches within a region (see electronic supplementary material, table S4). Abilities plotted in (c,d) represent Bradley–Terry ‘ability’ scores.

though not exclusive, explanation suggests that it is more costly for strong individuals facing strong opponents to signal weakness before signalling strength (analogous to brightening slowly) than it is to initially signal strength [15], providing the evolutionary pressure to rapidly signal fighting ability when strong. Regardless of the explanation, documenting the behavioural contexts in which colour change signals occur is an important first step in understanding the function and evolution of this relatively rare signal type and should markedly inform our views on competitive signalling theory. Moreover, future detailed studies of the physiological mechanisms underlying display coloration

will be key for revealing the information communicated by rapidly changing colours.

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SUPPLEMENTARY INFORMATION

1. Study system

We obtained ten, wild-caught male veiled chameleons *Chamaeleo calyptratus* from a feral population in Florida [1]. Veiled chameleons are large, omnivorous, territorial lizards native to the mountainous regions of southwestern Arabia [2,3]. Like many chameleons, male veiled chameleons display intense antagonistic behaviour towards conspecific males [3] and exhibit rapid, body-wide colour changes during intraspecific interactions [4] (*pers. obs*). Upon seeing each other, adult male veiled chameleons typically begin an elaborate display that encompasses both morphological and chromatic transformations. The two males rapidly compress their bodies laterally, dorsoventrally expand their bodies, orient their bodies perpendicular to the direction of their opponents, and curl their tails into a disk-like shape (*cf.* [5]), all to enhance their apparent body size. Additionally, displaying males become noticeably brighter and more colourful to the human eye. At any point during the interaction, either chameleon can cease aggressive behaviours and begin to retreat. If neither chameleon retreats, however, these interactions will escalate to physical combat, including head-butting, lunging, and biting.

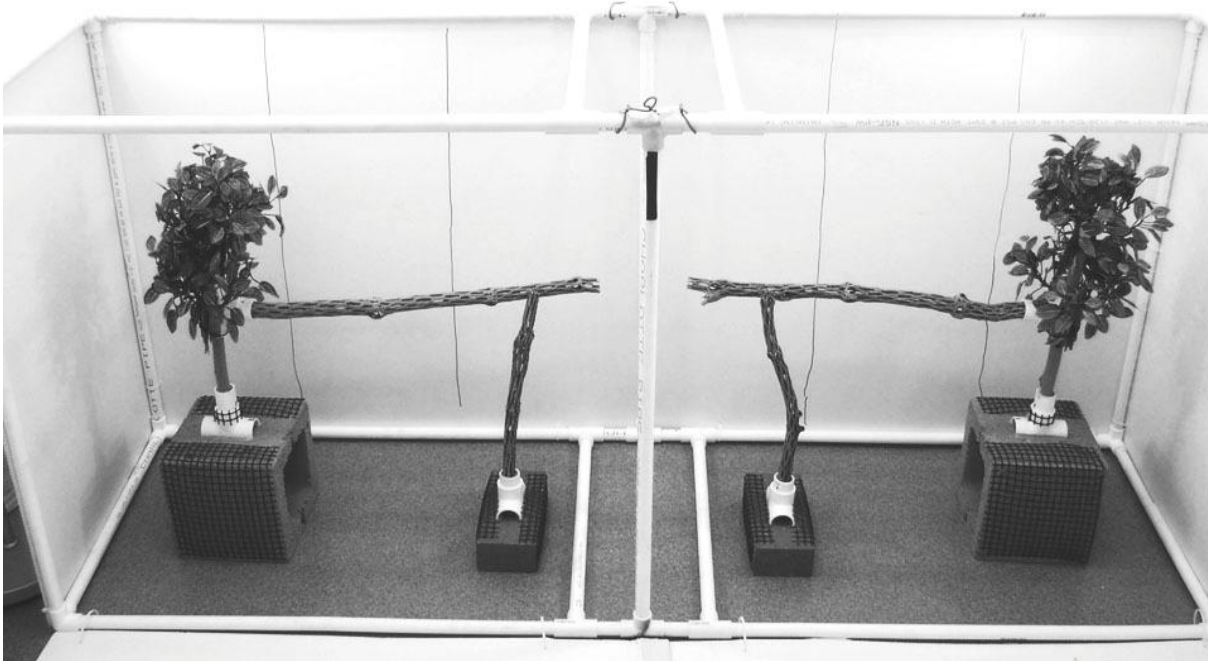
2. Aggression trials

2.1 Trial setup

Over a period of six weeks (15 March - 6 May 2011), we staged dyadic

encounters between 10 adult male veiled chameleons in a tournament format that matched each chameleon against every other. Each chameleon faced no more than one other chameleon per day and never faced a chameleon with which they had any previous experience. Prior to each trial, chameleons were placed separately into cloth bags and set in a heated, darkened box, during which time we obtained the body mass of each individual using a digital balance. After a 10-minute thermal equilibration period, chameleons were sequentially placed on opposite, visually isolated ends of the trial arena (183 x 53 x 81 cm). We then allowed the chameleons to acclimate for five minutes before the central divider was removed and the trial began. Trials were recorded from behind a blind with two Panasonic HDC-TM 700 video cameras (Osaka, Japan), which enabled us to take still photographs while recording video, with one camera focused on each chameleon.

Each half of the trial arena contained a vertical perch (66 cm tall) with plastic foliage to provide cover for chameleons during the acclimation period, a horizontal perch (80 cm long) to allow the chameleons to approach one another, and a second vertical perch (44 cm tall) to allow chameleons to climb up toward or down and away from opponents (Supplementary Figure 1). The order in which chameleons of each dyad were placed into the arena was randomized.



Supplementary Figure 1. Trial arena used to stage agonistic encounters between adult male veiled chameleons *Chamaeleo calytratus*.

2.2 Behaviours monitored

We monitored chameleon behaviour by watching the LCD screens of the video cameras from behind a blind, and trials were terminated once a clear winner was established (see below) or if no interaction occurred within 30 minutes. If, during the trial, there appeared to be a risk of serious injury (biting and twisting, biting at an awkward angle), the trial was terminated and the animals separated to avoid serious physical injury. However, most conflicts were decided prior to physical contact or very quickly thereafter, and, throughout the 45 aggressive trials, such interruption was necessary only once. This single trial did result in broken skin for one individual, but in no other trial did chameleons sustain any other body injury.

3. Using colour photography to measure chameleon colour change

Although most recent studies of animal colouration have relied on

spectrophotometry to objectively quantify colour, there are distinct limitations of this methodology for some applications. Specifically, spectrophotometers can only capture point samples of colour in space and time and, with the exception of some extremely expensive equipment, require the measured sample to come into direct contact with the measurement probe. Fortunately, recent advances in the standardization and quantification of colour obtained from photographs have enabled researchers to undertake detailed studies of animal colouration using digital cameras [6,7]. Using recently developed methods, we: 1) identified a suite of colour patches to measure from each chameleon, 2) standardized photographs [6,7] using a specialized colour standard [8], 3) calculated the receptor sensitivity functions of our digital cameras [7], and 4) used a large set of reflectance data and the known properties of chameleon photoreceptors to create mapping functions to convert RGB camera output

into the relative quantum catch of three chameleon cones [7].

Although veiled chameleons possess four classes of cones, we focused on the relative stimulation of the short-, medium-, and long-wavelength-sensitive cone classes. Despite the fact that logistical constraints prevented us from measuring the UV reflectance of colour patches using colour photography while simultaneously measuring reflectance in the human-visual portion of the light spectrum [7], we feel that this approach was unlikely to generate incomplete or inaccurate data for two reasons. First, full-spectrum spectrophotometry and ultraviolet-filtered photography of veiled chameleon display colouration revealed few regions with significant ultraviolet reflectance (RAL, *unpublished data*). Second, our trials were conducted indoors, under artificial lighting that lacked UV transmittance.

3.1 Colour identification

We analyzed the video recordings of each trial to determine the onset and duration of each colour-changing bout during the course of an interaction. We evaluated pictures taken at approximately 4 s intervals (a rate determined by the processing ability of the cameras) starting from 30 s prior to the onset of colour change (determined by a human observer), through 30 s after the colour-changing bout was determined to be complete. Because it is currently unknown what, if any, aspects of physiological colour change are most informative for chameleons when evaluating one another during agonistic encounters, we measured the colour of 28 different patches (Fig. 1) on each chameleon in each photo throughout the course of each brightening event. We chose these patches because they represented all of the major colour classes exhibited by veiled chameleons (e.g., greens, blues, yellows, oranges, etc.) during

colourful aggressive displays and occurred in body areas accentuated by chameleons during behavioural displays (RAL, *pers obs*). However, the colour and pattern of veiled chameleons varies a great deal, both within and among chameleons. Although the exact location of a particular colour patch varied slightly within a region among individuals (*cf.* Fig. 1a and 1b), we felt that it was more informative from a chromatic-signaling perspective to make comparisons between similarly located colour patches of equivalent pigmentary and structural makeup than to inflexibly focus on a narrowly-defined body location that might contain different colour types among individuals. Within individuals, we focused our analyses on patches defined by the general descriptions outlined in Supplementary Table 4 and measured perceptual changes in these same patches throughout behavioural interactions.

3.2 Photograph standardization (linearization and channel equalization)

A first step in the process of using digital photography to measure colouration is to ensure that the R (red), G (green), and B (blue) channels of the camera response are linearized and equalized. Although there are costly (in both time and money) technical methods to perform these functions [8], we used a simple and highly effective approach to achieve a similar result. Specifically, we used a specialized colour standard (ColourChecker Passport, X-Rite Photo) commonly used in photographic and videographic calibration in conjunction with a software plug-in (PictoColour[®] inCamera[™], PictoColour Software, Burnsville, MN) for Adobe Photoshop. This plug-in creates custom International Colour Consortium (ICC) digital profiles by “evaluating the colour data captured by the camera...and comparing the data to the known colour values of the [standard colour]

charts.” As described by Bergman and Beehner [8], we manually aligned the grid from the inCamera tool to the colour grid of the ColourChecker Passport in a given reference photograph, allowing inCamera to create a custom profile that adjusted pixel values to those of the known colours of the standard. For each reference photograph (containing the ColourChecker Passport, taken at the beginning of each trial day), we created a unique profile that could then be assigned within Photoshop to all other pictures taken under identical conditions (alleviating the need to have a colour standard in every single picture or frame). This method is defined as the “sequential method” by Bergman and Beehner [8] and was found by these authors to provide results that are more accurate than the “adjacent method” (colour standard in the same photograph as the colourful object of interest).

We assessed linearity of our colour responses by using linear regression of the relationship between the different channels (R, G, and B) and the known reflectance values of the six gray standards on the colour standard. This relationship was examined for linearity under varying light conditions, after the inCamera colour corrections were applied. Analyses on two independent data sets using these methods uncovered extremely high R^2 values ($R^2 > 0.98$) for all three channels (M. Amarello unpublished data; R. Ligon unpublished data). RGB equalization ($R = G = B$) was also tested and found to be within the limits described by Bergman and Beehner [8] ($> 95\%$ RGB values within 5% of one another).

3.3 Calculating camera sensitivity functions

Direct measurement of camera sensor sensitivity functions is technically demanding, time consuming, and expensive [6,7]. However, Pike [7] recently described a method that enables individuals to estimate

these sensitivities using a custom Matlab (MathWorks, Natick, MA) function. Users define several key components of sensor sensitivity functions (likely peak and trough locations, for example) before the quadratic programming function identifies the camera sensor sensitivities by comparing the RGB output of known colour standards to the radiance values (reflectance x irradiance) of the same standards. For additional information on the technical aspects of this procedure, see reference 7.

3.4 Mapping functions for converting RGB values to chameleon quantum catch

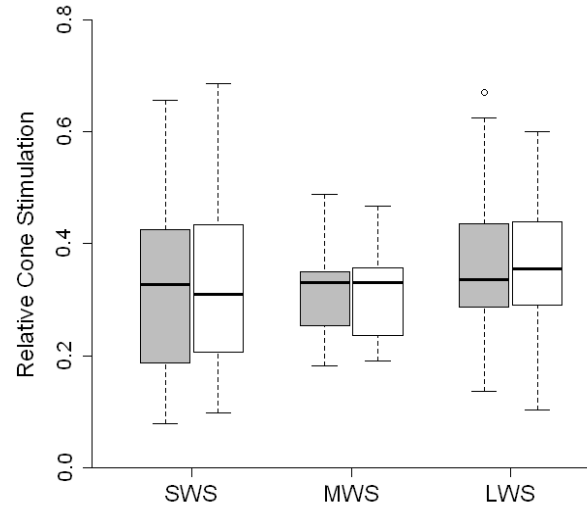
Published data on ocular media and cone sensitivities from several species of chameleons provided the basis of our chameleon-specific visual models [9]. Because the visual pigments found in chameleon photoreceptors possess absorbance characteristic of both rhodopsin and porphyropsin, we constructed cone sensitivity functions using a combination of both pigment types. We originally designed this model to calculate the quantum catch (the number of photons absorbed) of the different cone classes within chameleon eyes using spectral data. To calculate the quantum catch of the different chameleon photoreceptors using the linearized and equalized RGB output of a camera, however, we had to create a mapping function to convert between the two (spectrophotometrically and photographically determined) colour spaces.

The mapping function to obtain the quantum catch of the different chameleon cone types consists of a series of coefficients by which RGB values are multiplied (Supplementary Table 1). To obtain the coefficients necessary to convert between the two colour spaces, we simulated what our camera would see when viewing 1250 Munsell colour chips and what a chameleon would see (one cone type at a time) when

viewing the same 1250 colours. Using matrix algebra within Matlab, we were able to explore the effectiveness of several different equations of the type described by Westland & Ripamonti [10]. The model, included below, that gave us the best fit contained several higher order polynomials. Following the notation of Stevens et al. [6], R, G, and B describe calibrated and linearized pixel values for a given colour, b_i represents the coefficients specific to receptor class i (Supplementary Table 1), and Q_i represents the quantum catch for receptor class i .

$$Q_i = b_{i1}R + b_{i2}G + b_{i3}B + b_{i4}R^2 + b_{i5}G^2 + b_{i6}B^2 + b_{i7}RGB + b_{i8}GB + b_{i9}B^2G^2 + b_{i10}R^3 + b_{i11}G^3 + b_{i12}B^3 \quad (1)$$

After obtaining the mapping coefficients (b_i , Supplementary Table 1) required to convert between photographically determined quantum catch and spectrophotometrically determined quantum catch, we converted RGB values to the relative stimulation of the different photoreceptor types and validated our



Supplementary Figure 2. Comparison of spectrophotometrically (grey boxes) and photographically (white boxes) determined estimates of the relative stimulation of short- (SWS), medium- (MWS), and long-wavelength-sensitive (LWS) cones of a chameleon when viewing an X-Rite™ colour standard. Paired t-tests comparing these methods (Supplementary Table 2) revealed no significant differences between photographically and spectrophotometrically derived estimates.

conversion equation by testing it on an independent data set (Supplementary Figure 2).

Supplementary Table 1. Coefficients for polynomials used to convert between RGB and quantum catch of chameleon photoreceptors.

	b1	b2	b3	b4	b5	b6	b7	b8	b9	b10	b11	b12
LWS	0.427	1.090	-0.500	0.473	-1.514	0.240	-0.766	1.117	0.532	-0.051	0.709	-0.567
MWS	-0.069	1.310	-0.254	0.093	-0.510	0.210	-0.394	0.351	0.296	0.060	0.286	-0.342
SWS	0.027	-0.010	1.004	-0.114	0.146	-0.407	-0.542	-0.276	-0.578	0.148	0.125	1.440

Supplementary Table 2. Outcome of paired t-tests comparing spectrophotometric and photographic estimates of the relative quantum catch of the long- (LWS), medium- (MWS), and short-wavelength-sensitive (SWS) cones of a chameleon, in terms of the mean difference between estimates, the confidence interval for this difference, and whether this difference was significantly different from zero.

Cone Class	Mean Difference	95% CI	t-value	df	p-value
LWS	0.0099	(-0.0053 – 0.0252)	1.346	23	0.192
MWS	-0.0002	(-0.0140 – 0.0137)	-0.023	23	0.982
SWS	-0.0098	(-0.0310 – 0.0115)	-0.952	23	0.351

3.5 Pattern analyses

We used the pattern analysis techniques described by Stoddard and Stevens [11] to quantify chameleon body patterns at different time points during aggressive trials. Briefly, we used a custom Matlab function written by Martin Stevens to analyze the ‘granularity’ of images, which allowed us to determine the relative importance of different marking sizes to the overall chameleon pattern. We chose five body regions from which to extract images for pattern analyses (Supplementary Figure 3) and, in an attempt to standardize our

pattern analyses, limited our analyses to photographs taken when chameleons were perpendicular to the camera.

From each of the five body regions analyzed for pattern, we extracted seven images (by fast Fourier transforming the original image and applying seven isotropic band pass filters [12]) containing information based on different spatial scales. These filters capture pattern element information at different scales, with small filter sizes corresponding to large markings and large filters corresponding to small markings [11]. Evaluating these seven



Supplementary Figure 3. Body regions of veiled chameleons analyzed for pattern elements. We analyzed pattern elements from five square images from the casque (1), first lateral stripe (2), center horizontal stripe between the first and second lateral stripes (3), the first tail band (4), and central body region (5). Figure is in grayscale to illustrate appearance of pictures analyzed for pattern using methods described in main body of the text.

images ('granularity bands' [12]) allowed us to determine the contribution of different pattern element sizes to overall chameleon body pattern.

After filtering images, we measured the overall pattern 'energy' (E) for each granularity band by dividing the number of pixels in the image by the sum of the squared pixel values [13]. The values of E across all granularity bands constitute the 'granularity spectrum' of an image [13], and a number of informative values can be calculated from this spectrum. As in Stoddard and Stevens [11], we focused our subsequent analyses on three pattern properties that capture different components of pattern information. First, we calculated the bandwidth of maximum energy (E_{\max}), which corresponds to the most prevalent pattern element size. Second, as a measure of the relative importance of the highest marking size, we calculated the proportion of energy contained within the predominant marking size relative to the energy across all bandwidths (E_{prop}). Third, we calculated the total energy (E_{tot}) across all bandwidths as a measure of overall pattern contrast [11,13].

In an effort to quantify the extent of pattern-element change over time, we evaluated pattern elements from standardized photographs taken of chameleons taken at the beginning of a given trial, and compared these measurements to those obtained from the same chameleons later in the trial, at the 'moment of determination' (i.e. the time point we identified at which the losing chameleon first began to display submissive behaviours, which typically falls within the 30 s buffer period of the brightening events we evaluated for chromatic changes). In the case of physical interaction, this was when the loser began to retreat or scramble away from the winner. In the case of non-physical interactions, the moment of determination was identified as the time point at which the

loser began to darken or retreat (whichever came first).

To evaluate intra-individual variation in pattern within a given trial, we included images taken from trials conducted at different times and containing different individuals (i.e. trials separate from those conducted and analyzed to uncover the importance of colour change as a signal). However, we restricted our analyses to instances in which we could analyze the pattern of a given chameleon at the beginning of a trial and at the moment of determination. Within-individual comparisons allowed us to use paired t-tests to evaluate differences within individuals over time.

We found that dominant marking filter size (E_{\max}) did not differ within chameleons at different time points (Supplementary Table 3). Additionally there were no differences within chameleons for the proportion of energy contained within the dominant granularity band (E_{prop}) for four out of the five body regions measured (Supplementary Table 3). Lastly, the total energy of the granularity spectrum (E_{tot}), an overall measure of pattern contrast, did not differ statistically over time for three out of the five body regions analyzed (Supplementary Table 3). Because the pattern elements of colour display appear to be largely invariant within individual chameleons, and because our interest was in the changing nature of colour signals, we restricted our analyses to dynamic chromatic variables.

Supplementary Table 3. Outcome of paired t-tests comparing pattern elements within individual chameleons at different time points. Patterns were analyzed from five pictures taken from different chameleon body regions (Supplementary Figure 3) at the beginning of trials and at the moment before conflicts were determined ('moment of determination' defined in Supplementary Information 3.5).

Picture	Pattern Element	Mean Difference	95% CI	t-value	df	p-value
1	E_{\max}	-0.128	(-0.560 — 0.303)	-0.672	9	0.519
	E_{prop}	-0.017	(-0.064 — 0.030)	-0.830	9	0.428
	E_{tot}	-101.894	(-215.44 — 11.65)	-2.030	9	0.073
2	E_{\max}	-0.288	(-0.66 — 0.09)	-1.734	9	0.117
	E_{prop}	-0.013	(-0.08 — 0.06)	-0.414	9	0.689
	E_{tot}	-37.334	(-106.04 — 31.38)	-1.229	9	0.250
3	E_{\max}	-0.304	(-0.68 — 0.07)	-1.887	8	0.096
	E_{prop}	0.0213	(-0.02 — 0.06)	1.208	8	0.262
	E_{tot}	-132.697	(-237.27 — -28.12)	-2.926	8	0.019
4	E_{\max}	0.000	(-0.34 — 0.34)	0.000	5	1.000
	E_{prop}	-0.073	(-0.14 — -0.002)	-2.640	5	0.046
	E_{tot}	-68.00	(-127.87 — -8.12)	-2.919	5	0.033
5	E_{\max}	-0.052	(-0.39 — 0.29)	-0.357	8	0.731
	E_{prop}	-0.002	(-0.04 — 0.03)	-0.132	8	0.898
	E_{tot}	-63.715	(-198.37 — 70.94)	1.091	8	0.307

4. Quantifying brightness and colour change

We quantified the brightness of each colour patch by calculating how that colour patch would stimulate the double cones of chameleons, which are thought to be responsible for achromatic (or brightness) detection [14] and have the same peak sensitivity as the long-wavelength-sensitive cones [9]. After calculating chameleon-specific measures of brightness, we isolated the maximum brightness achieved by a given colour patch during a colour-changing

bout and incorporated these maxima into our principal components analyses (see *Variable selection and data reduction*).

To quantify changes in colour over time, we first calculated perceptual distances between colour measurements taken from a given colour patch at different time points, calculated in units of Just-Noticeable-Differences (JNDs). If three classes of cones are assumed to contribute to colour discrimination, the perceptual distance between two colours is obtained from equation 4 in Vorobyev and Osorio [15]:

$$\Delta S_{VO} = \sqrt{\frac{e^2_S(\Delta f_L - \Delta f_M)^2 + e^2_M(\Delta f_L - \Delta f_S)^2 + e^2_L(\Delta f_S - \Delta f_M)^2}{(e_S e_M)^2 + (e_S e_L)^2 + (e_L e_M)^2}} \quad (2)$$

where e_i refers to the noise in cone type i (L = long wavelength, M = medium wavelength, S = short wavelength sensitive cones), and Δf_i corresponds to the difference in the response of cone class i between the two colours being compared. Receptor noise levels (e_i) vary as a function of the relative densities of the different cone types [15]; however, this information has not been determined for chameleons. Therefore, we used a relatively conservative estimate of equal receptor noise levels ($e = 0.05$) across long- (LWS), medium- (MWS), and short- (SWS) wavelength-sensitive cones for our analyses. Because perceptual distances are influenced by error estimates and we wanted to ensure that the inferences we drew regarding the importance of perceivable colour changes were robust to different noise estimates, we also evaluated all models using biologically informed [9], yet conservative, estimates of relative cone densities of LWS:MWS:SWS set to 6:3:1. Results from these analyses were not qualitatively different than those obtained using equal receptor noise levels of 0.05.

After determining relative discriminabilities, we used the custom R (R Core Development Team) scripts provided by Pike [16] to calculate the Cartesian coordinates of each colour patch across time within the chromaticity space he describes. This chromaticity space preserves the perceptual distance between colours, such that the Euclidean distance between any two colours is exactly equal to their perceptual distances, in JNDs. Because each colour has x and y coordinates within this two-dimensional space, we were then able to calculate changes in Euclidean distances (Δ JND) between colour measurements taken at different times. By dividing Δ JND measurements by the elapsed time between the pictures from which colour values were taken, we were also able to calculate a rate

of colour change within chameleon-specific perceptual space.

5. Variable selection and data reduction

We focused our analyses on three metrics of chameleon colouration: i) the maximum brightness of each body region achieved by a chameleon during a colour changing event, ii) the maximum speed of colour change (JND/sec) of each body region during a colour changing event, and iii) the total perceptual distance (sum of all Δ JNDs) travelled by each body region during a colour changing event. In total, we attempted to collect colour measurements from each of 28 different colour patches for a total of 3,190 photographs (i.e. each picture during colour changing bouts per chameleon per trial). Occasionally, however, some colour patches were not visible. In these cases, we used linear interpolation to determine likely values of missing colours [17,18]. This method represents a conservative approach to obtain measurements of colour movement within chameleon perceptual space because interpolated, straight-line values result in the minimum distance (in terms of JNDs) that a colour can travel through chromaticity space while still changing from one (measured) colour to another (measured) colour. Additionally, because interpolated values minimize distances travelled in chromaticity space, measures of the speed of colour change (Δ JND) will also be minimized using interpolated values.

To reduce the number of variables evaluated in our analyses, we performed separate principal components analyses (PCA) on the three chromatic variables of interest (maximum brightness, maximum JND/sec, total JND distance) for each of three body regions (Supplementary Table 4). Specifically, we analyzed all colour measurements collected from the head region (9 patches), from striped regions of

the body (7 patches), and from non-striped body regions separately (12 patches). This resulted in nine distinct chromatic variables (max brightness, max speed of colour change, and total discriminable colour change from each of the three body regions), which we analyzed using an information theoretic approach [19] (see Supplementary Information 6). Additionally, we included the body mass of each chameleon prior to a given contest in our analyses, though we scaled these values to a mean of 0 and a standard deviation of 1 to facilitate direct comparisons between mass and scaled PC colour scores.

Supplementary Table 4. Colour regions measured during agonistic encounters between adult male veiled chameleons and corresponding factor loadings onto the principal components used in analyses evaluating characters predicting behaviour and contest outcome. Colour identification codes (ID) are used in Figures 1a and 1b.

ID	Colour Patch	Brightness PCs			Maximum Speed PCs			Maximum Distance PCs		
		Head	Body	Stripes	Head	Body	Stripes	Head	Body	Stripes
	<i>Eigenvalues</i>	4.325	5.095	3.524	3.247	4.799	3.517	5.565	7.388	4.875
	<i>Proportion of Variance</i>	0.481	0.425	0.503	0.361	0.400	0.502	0.618	0.616	0.696
<i>PC loadings</i>										
a	Corner of mouth	-0.078			0.376			0.357		
b	Cheek, below corner patch (not orange spot)	-0.389			0.233			0.356		
c	Central casque stripe, top (yellow)	-0.398			0.371			0.335		
d	Central casque stripe, bottom (yellow)	-0.332			0.368			0.328		
e	Posterior casque stripe, top (green)	-0.393			0.146			0.320		
f	Posterior casque stripe, bottom (green)	-0.374			0.354			0.353		
g	Eye, background colour	-0.392			0.196			0.314		
h	Eye, stripe colour	-0.211			0.442			0.351		
i	Front-most throat cone	-0.285			0.387			0.279		
j	Behind 1st stripe, dorsal, light		-0.346			0.269			0.306	
k	Behind 2nd stripe, dorsal, light		-0.338			0.263			0.305	
l	Behind 1st stripe, dorsal, dark colour		-0.153			0.345			0.279	
m	Behind 2nd stripe, dorsal, dark colour		-0.168			0.375			0.322	
n	Center of top lateral stripe in front of 1st yellow stripe		-0.345			0.278			0.287	
o	Center of top lateral stripe in front of 2nd yellow stripe		-0.303			0.179			0.292	
p	Below top lateral stripe, between yellow stripes, light		-0.331			0.305			0.318	
q	Below top lateral stripe, between yellow stripes, dark		-0.158			0.154			0.242	
r	Belly below 2nd yellow stripe, light		-0.325			0.260			0.300	
s	Belly below 2nd yellow stripe, dark		-0.112			0.276			0.222	
t	Non-yellow tail band, posterior to closest yellow band		-0.372			0.318			0.281	
u	Rear belly (blue equivalent)		-0.335			0.357			0.291	
v	Front full stripe, yellow, center			-0.402			0.348			0.400
w	Mid full stripe, yellow, center			-0.317			0.266			0.363
x	Dots in front stripe, central			-0.443			0.265			0.389
y	Dots in mid stripe, central			-0.428			0.45			0.390
z	Orange surrounding 1st yellow stripe, dorsal			-0.417			0.447			0.377
§	Orange surrounding middle yellow stripe, dorsal			-0.315			0.47			0.361
∅	Yellow tail band closest to body			-0.292			0.339			0.364

6. Model averaging

Our primary interest was to determine the colourimetric variable(s) that best explained the approach likelihoods and contest outcomes of aggressive interactions between adult male veiled chameleons. Colour variables related to the likelihood of approaching an opponent may be related to the underlying motivation of a given chameleon to engage in a fight, while colour traits linked to contest outcome may reveal a male's competitive ability and resource holding potential. Alternatively, colour signals that predict contest outcome could also be related to motivation, given that motivation has been shown to influence success in competitive interactions [20].

For both approaching and winning, we first identified individual 'ability' scores using Bradley-Terry (BT) analysis [21,22] which can be used to identify underlying 'ability' parameters (representing the likelihood of one individual beating another) from a matrix of contest outcomes. We restricted our BT analyses to a subset of trials ($n = 17$ out of the original 45 trials) in which both chameleons exhibited some degree of brightening colour display and for which there were no missing colour values. On average, each chameleon was represented in over three of these trials ($\bar{x} = 3.4$, range 1-5). After identifying approach ability and fighting ability using BT models, we used Akaike's information criterion (AIC) within an information-theoretic (IT) framework [19] to evaluate a set of generalized linear models to determine the colourimetric and body mass variables (averaged across trials) that best explained the likelihood of approaching and the likelihood of winning aggressive encounters.

Although an all-subset approach, wherein researchers evaluate every possible combination of explanatory variables, is commonly used in behavioural ecology when explicit predictions cannot be made

regarding the relative strengths of models containing different combinations of explanatory variables [23], we followed the recommendations of Grueber et al. [24] and evaluated only a specific, biologically plausible, subset of the total number of possible models when analysing 10 predictor variables (i.e. 9 colour variables + body mass). Specifically, we began by evaluating the predictive ability of models that included each of our 10 explanatory variables individually (individual predictor models). Next, we considered models that included all colour variables for a given body region (body region models) and models that included a given colour variable for all body regions (colorimetric models). Next, we evaluated the effect of adding body mass to the body region and colorimetric models. At this point, we assessed models that contained the strongest single predictor variable (assessed by AICc score) and one additional relevant (i.e. same colour variable/different region, same body region/different colour variable) parameter. Lastly, we evaluated the effect of including mass in the top model as well as coupling body mass with the individual variables in the top model (if it contained more than one colour variable).

Multiple models may be well-supported within the framework of IT, but it is still possible to evaluate the relative importance of specific variables in explaining the dependent variable [19,25]. In instances when IT-AIC analyses do not clearly identify a single best model (Akaike weight < 0.9), evaluation of multiple well-supported hypotheses is typically required [19]. Model averaging is a technique that allows researchers to incorporate parameter estimates from multiple models, which provides weighted estimates according to the support of the model. Specifically, the regression coefficient estimate is obtained for each model in which a given variable is

present and multiplied by the Akaike weight of that model (w_i), then summed. This formula can be represented as:

$$\sum_{i=1}^R w_i \hat{\beta}_i \quad (3)$$

where $\hat{\beta}_i$ is the estimate for the predictor in a given model i , and w_i is the Akaike weight of that model. Variables that are represented infrequently or only show up in poorly supported models will exhibit negligible parameter estimates, while variables that turn up repeatedly in strongly supported models will have appreciably larger parameter estimates and contribute more to predictive models. In addition to model-averaged parameter estimates, we also calculated the relative importance (RI) for each predictor variable as the sum of Akaike weights for all models in which that variable appeared. Because Akaike weights from a given model set sum to 1, RI values can range from 0 to 1. An RI value near 0 indicates that the variable is infrequently represented or present only in poorly-supported (low w_i) models, while a high RI value indicates that the variable is present in many, highly-supported (large w_i) models.

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Supplementary Table 5. 95% confidence set of best-ranked linear models (the 10 models whose cumulative Akaike weight, $\text{cum } w_i \approx 0.95$) used to determine the variables that best explain whether a male veiled chameleon will *approach* another male chameleon during an agonistic encounter.

Model	Log L	k	AIC _c	Δ AIC _c	w_i
STRIPESMaxB.PC1	-6.84	1	20.17	0.00	0.229
HEADMaxB.PC1	-6.87	1	20.24	0.07	0.222
BODYMaxB.PC1	-7.39	1	21.28	1.11	0.132
STRIPESMaxB.PC1 + HEADMaxB.PC1	-6.17	2	22.04	1.87	0.090
STRIPESMaxB.PC1 + BODYMaxB.PC1	-6.33	2	22.37	2.20	0.076
STRIPESMaxB.PC1 + STRIPESMaxD.PC1	-6.47	2	22.65	2.48	0.066
STRIPESMaxB.PC1 + STRIPESMaxSpeed.PC1	-6.77	2	23.25	3.08	0.049
STRIPESMaxB.PC1 + ScaledMass	-6.83	2	23.38	3.21	0.046
STRIPESMaxB.PC1 + HEADMaxB.PC1	-6.17	3	24.33	4.16	0.029
HEADMaxSpeed.PC1	-9.73	1	25.97	5.80	0.013

Model variables where 'MaxB' represents maximum brightness, 'MaxD' represents maximum perceptual distance travelled, and 'MaxSpeed' represents maximum speed of chameleon-perceivable colour change. Body regions (Head, Stripes, Body) refer to those summarized in Table S4. Model statistics include Log-Likelihood function (Log L), number of estimated parameters (k), selection criterion (AIC_c), distances from best model (Δ AIC_c), and Akaike weights (w_i). Akaike weights (w_i) can be considered the probability of a given model i , given the variables evaluated and the data analyzed (Burnham et al. 2011).

Supplementary Table 6. 95% confidence set of best-ranked linear models (the 11 models whose cumulative Akaike weight, $\text{cum } w_i \approx 0.95$) used to determine the variables that best explain whether a male veiled chameleon will *win* an agonistic encounter with another male chameleon.

Model	Log L	k	AIC _c	Δ AIC _c	w_i
HEADMaxB.PC1	-9.20	1	24.89	0.00	0.215
HEADMaxB.PC1 + HEADMaxD.PC1	-7.78	2	25.26	0.37	0.179
HEADMaxB.PC1 + HEADMaxSpeed.PC1	-8.09	2	25.89	1.00	0.130
HEADMaxB.PC1 + STRIPESMaxB.PC1	-8.65	2	27.02	2.13	0.074
HEADMaxB.PC1 + BODYMaxB.PC1	-8.70	2	27.12	2.23	0.070
HEADMaxSpeed.PC1 + ScaledMass	-8.71	2	27.12	2.23	0.070
HEADMaxB.PC1 + ScaledMass	-8.90	2	27.51	2.62	0.058
HEADMaxB.PC1 + HEADMaxSpeed.PC1 + ScaledMass	-6.83	3	27.65	2.76	0.054
STRIPESMaxB.PC1	-10.78	1	28.05	3.16	0.044
HEADMaxB.PC1 + HEADMaxD.PC1 +	-7.10	3	28.19	3.30	0.041
HEADMaxB.PC1 + BODYMaxB.PC1	-7.65	3	29.30	4.41	0.023

Model variables and model statistics as described in Table S5.