1 **Seasonal changes in coat colour and sexual size dimorphism in a subtropical ungulate**

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ABSTRACT

Phenotypes reflect how organisms adapt to their environments. Hong Kong (HK) feral cattle, a crossbreed of *Bos taurus taurus* and *Bos taurus indicus*, present an opportunity to study these adaptations in one of the very few global cattle populations not directly controlled by humans. These cattle are free-ranging since their release from farms in the 1970's. HK has a subtropical climate, characterized by high humidity and temperatures during the wet season, and scarce precipitation during the dry season. We studied seasonal coat colour changes in HK feral cattle, and sexual dimorphism in body size and horn length. We provide the first evidence of seasonal changes in coat colour in cattle, with paler coats being more common in the wet season, while darker coats prevailed in the dry season. These seasonal changes were influenced by temperature, humidity, solar radiation, and body condition. We found that males were larger and had longer horns than females. Our results show a male-biased sex dimorphism in the HK feral cattle. Additionally, our findings suggest that thermoregulation costs drive colouration in these cattle. The phenotypic plasticity we demonstrate in these subtropical feral cattle improves our knowledge of the adaptations of ungulates to their habitat.

Keywords: body size dimorphism; *Bos* taurus; climate; coat colour; free-ranging; Gloger's rule; horn length; thermal melanism;

INTRODUCTION

Animal phenotypes are visible characteristics of individuals that result from the interplay of genotype and environment. In wild populations, in which genetic and ecological information may be scarce, phenotypes provide an overview of the adaptations of organisms to their environment. Phenotypic traits may differ from previous populations as a result of human-generated selection pressures (Stockwell *et al.*, 2003; Allendorf & Hard, 2009) and changes in climatic conditions (Jones *et al.*, 2018; Oli *et al.*, 2023; Otte *et al.*, 2024). A number of phenotype characterization methods have been developed for livestock and companion species (*e.g.* Amin, 2009; Hameed et al., 2022; Ouchene-Khelifi et al., 2018), where individuals can be easily restrained for measurements. However, in populations where restraint is more challenging (*e.g*. large ungulates, wild populations), phenotyping data is often assessed using corpses (Fulgione *et al.*, 2016; Schulz *et al.*, 2024) or using invasive procedures (*e.g.* capture; Canale et al., 2016). Non-invasive methodologies, such as measures on photographs (*i.e.* photogrammetry), are becoming more popular for phenotypic data collection in free-ranging animals (*e.g.* Bro-Jørgensen & Dabelsteen, 2008; Cambreling et al., 2025; Morandi et al., 2022; Prinsloo et al., 2021), providing valuable information about understudied populations.

Coats serve multiple functions, including providing thermal insulation by creating a barrier between the skin and the ambient environment, as well as reflecting solar radiation to reduce heat gain (Stuart-Fox *et al.*, 2017; Beltran *et al.*, 2018; Zimova *et al.*, 2018). Generally, paler coats

reflect more solar radiation compared to darker ones, which is advantageous for animals in tropical environments (Stuart-Fox *et al.*, 2017). Conversely, darker coats provide protection against ultraviolet radiation (UV; Newell et al., 2021). As postulated by Gloger's rule (reviewed by Delhey, 2019), species inhabiting hot and wet environments, such as tropical and subtropical habitats, are expected to have darker coats (Cloudsley-Thompson, 1999; Wacker *et al.*, 2016). This trend has been confirmed in various mammals, notably primates (Kamilar & Bradley, 2011), wild pigs (Newell *et al.*, 2021), rodents (Ge *et al.*, 2021) and more generally in artiodactyls (Stoner, 2003) by comparing populations from temperate habitats to populations in tropical and subtropical habitats.

Phenotypic traits can exhibit plasticity, as demonstrated by the periodic moulting of coats in various endotherm species (Beltran *et al.*, 2018; Zimova *et al.*, 2018). Moulting is influenced by external factors, with photoperiodism (*i.e.* daylight duration) triggering the initiation of the process, while climate conditions, such as temperature and snow cover, affect the speed of moulting (Zimova *et al.*, 2018). Additionally, the timing and duration of moulting are governed by internal factors, including age, sex, body condition, and reproductive status, all modulated by the endocrine system (Beltran *et al.*, 2018; Zimova *et al.*, 2018). Rapid adaptations in coat colouration are often observed in species expanding their distribution (*e.g.* Newell et al., 2021). Predation pressure is a primary driver of coat colouration, as camouflage decreases predation risk through background matching (Atmeh et al., 2018; Caro, 2005). In environments with significant seasonal contrasts, such as temperate and arctic habitats, these seasonal changes in colouration facilitate

adaptations that improve concealment in response to fluctuating vegetation and soil conditions (Zimova *et al.*, 2014, 2018). Typically, endotherm coats are darker in summer and lighter in winter, with variations in colour reflecting the balance of eumelanin (black/brown pigments) and phaeomelanin (yellow/red pigments). Seasonal changes in coat colour are expected when the energetic costs of producing a new coat are lower than the costs associated with suboptimal colouration (Beltran *et al.*, 2018).

Sexual size dimorphism typically results from intrasexual competition and/or intersexual mate choice (Lukas & Clutton-Brock, 2014; Clutton-Brock, 2017; Shuker & Kvarnemo, 2021) and can be expressed in a variety of measurements of body lengths and secondary sexual traits (*e.g.* horns). Although recent meta-analysis revealed that sexual size dimorphism is not as common as previously reported (Tombak *et al.*, 2024), artiodactyl (order Artiodactyla) males tend to be both larger and longer than females (McPherson & Chenoweth, 2012; Cassini, 2020; Tombak *et al.*, 2024). In polygynous ungulates, males are larger than females due to intrasexual competition, as larger body size and longer horns in males result in higher social status and fitness (McElligott *et al.*, 2001; Knierim *et al.*, 2015; Cassini, 2020). Several bovid species are characterized by striking sexual dimorphism, particularly in body size (Cassini, 2020) and horn shape (Capellini & Gosling, 2006.; Caro et al., 2003; Nasoori, 2020), while others have little to no sexual dimorphism (D'Ammando *et al.*, 2022). More extreme sexual dimorphism decreases longevity in male bovids (Bro-Jørgensen, 2012). Horns are secondary sexual characteristics displayed by either one or both sexes in bovids (Davis *et al.*, 2014). Most bovids grow horns continuously by the proliferation of

germinal layer cells (Davis *et al.*, 2014). The horns have a diversity of important biological functions, including defence from predators, fighting weapons, courtship and thermoregulation (Emlen, 2008; Stankowich & Caro, 2009; Davis *et al.*, 2014).

There are 1.5 billion cattle globally, with the vast majority managed on farms (FAO, 2021). It is almost impossible to study cattle phenotypes in populations that are not directly controlled by humans, as there are only a few feral/wild populations. Although it is known that darker cattle display higher signs of heat stress and at lower thresholds than paler coated cattle in agricultural settings (Santos *et al.*, 2017), evidence in wild/feral populations is lacking, and seasonal coat colour changes have not been previously documented in cattle. The feral cattle of Hong Kong (HK) are a genetically distinct mix of *Bos taurus taurus* and *Bos taurus indicus*, with some evidence that they also carry genes from wild Asian bovids (Barbato *et al.*, 2020), similar to other Southeast Asian cattle (Zhang *et al.*, 2007; Gao *et al.*, 2017; Xia *et al.*, 2023; Luo *et al.*, 2025). Originally used as draught animals, these cattle are now regarded as part of the local heritage (SKBW, 2017). HK feral cattle are likely to have adapted to match the local environment and were subjected to low selection pressure for production traits even when they were used on farms (Barbato *et al.*, 2020). They have striking phenotypic diversity, although their appearance has not been formally studied (Barbato *et al.*, 2020).

Despite the striking phenotypic diversity of these animals, little is systematically known about the HK feral cattle phenotypes. We aimed to assess their phenotypes in a non-invasive way,

with a particular focus on body size, horn length and coat colour in respect to sexual dimorphism and seasonality. We expected the HK feral cattle to follow the general assumption of sexual dimorphism in artiodactyls, with males being larger and having longer horns than females. Additionally, we predicted distinct seasonal changes in coat colour between the dry and wet seasons, influenced by solar radiation as observed in other species. In the absence of major predation pressure on this population, we hypothesized that observed seasonal coat colour changes would be driven by thermoregulation needs and that changes in body condition may reflect the costs of moulting.

METHODS

1. Seasonal Coat Colour

1.1 Study sites and animals

For the 317 cattle scored for sexual size dimorphism, we also recorded coat colour. We then selected 12 herds for longitudinal scoring over a period of 13 months, with a total of 253 cattle scored longitudinally. These herds were selected based on their relative ease of access, ensuring reliable follow-up, while also maintaining good representation of the population (*i.e.* herd size, sex ratio, environment type, provisioning, proximity and frequency of interactions with humans). Following initial scoring (*i.e.* August 2022 during body size measurements), we visited each of the 12 selected herds once a month from January 2023 to January 2024 to obtain individual coat colour scores over time. A total of 2,371 coat colour scores were recorded, with each individual scored 1 to 14 times (mean = 9.37 ±SD 4.43).

1.2 Measures

We scored coat colour while maintaining a distance of at least 10 meters to the cattle. Coat colour was scored as a qualitative and subjective measure, controlling for lighting conditions and observer subjectivity influences by using distinct categories of score (Bro-Jørgensen & Dabelsteen, 2008; Caro et al., 2022), using a colour chart adapted from Stoner (2003). Our colour

151 chart consisted of five coat colours: pale, red, grey, dark and black (Fig. 1). All coat colours were
152 estimated by a single observer to reduce subjectivity of scoring, similar to Agosta et al. (2017). To
153 ensure reliability of scores, scores made in August 2022 were also checked by three independent
154 observers, and scores were discussed until all observers reached an agreement. This allowed us
155 to refine the coat colour chart (Fig. 1). We used this colour chart to assess three body parts: fore,
156 middle and hind (D'Ammando et al., 2022; Loehr et al., 2008). Then, we used the mode of those
157 three body part coat colours to obtain each individual's coat colour per month. Individuals for
158 which coat colour in all three body parts differed were not retained for that month; this was the
159 case for eight individual cattle scores. Further description of the eight data points removed is
160 presented in Table S1. Moulting is known to follow patterns across the body which are well
161 described in several species (Zimova *et al.*, 2018), but such prior knowledge was not available for
162 our study animals. Hence, these discrepancies of colour across body part may simply reflect the
163 moulting process but could not be analysed in the present study. To assess coat colour changes,
164 coat colours were replaced by an ordinal scale, with palest coats scored 1 and darkest scored 5
165 (Fig. 1).

166 Each individual received a Body Condition Score (BCS) at the time of coat colour scoring
167 based on a modified visual 9-point scale, with 1 being the thinnest individuals (low body
168 condition), and 9 the fattest (high body condition). This scale was adapted to the HK feral cattle
169 based on beef cattle BCS (D'Occhio *et al.*, 2019; Weik *et al.*, 2021). To control for the subjective
170 nature of body condition scoring, training was conducted to ensure good scorer reliability (for six

weeks from April 1st 2022 to May 5th 2022), with body condition scored once a week by a single observer on cattle in a single herd (n = 60 individuals). BCS scores were expected to be highly correlated from one week to the next, and therefore the scorer trained until BCS from one week to the subsequent reached a significant correlation of more than ρ = 0.8 (based on Spearman's rank correlation) for three consecutive weeks. This same observer scored all BCS used in this study.

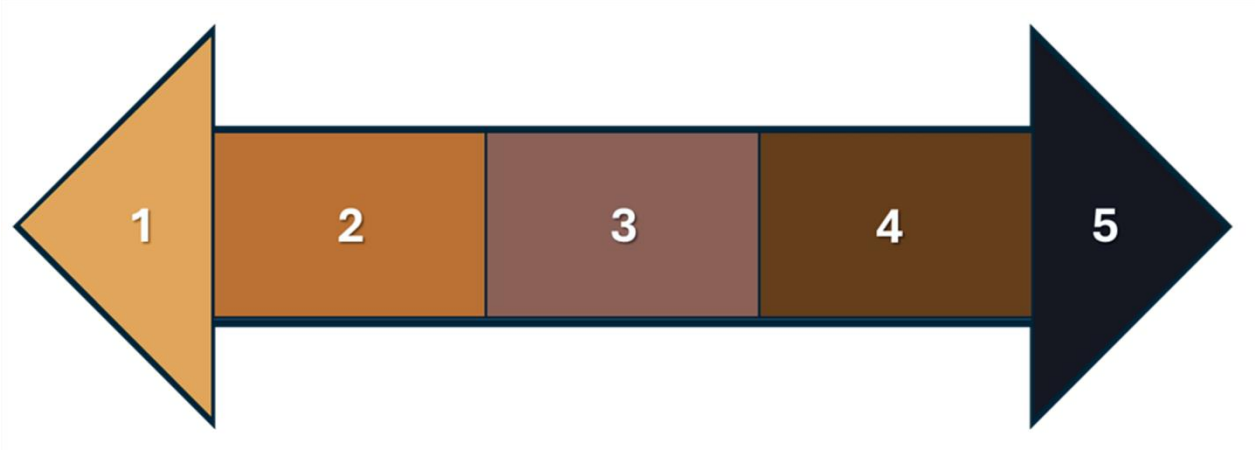

Figure 1: Coat colour scale used to characterize coat colours in Hong Kong feral cattle with 1 corresponding to palest coats, 2 for coats scored as red, 3 for grey, 4 for dark and 5 black (the darkest coat colour). This colour scale is adapted from Stoner (2003).

1.3 Climate Data

We extracted monthly averages for mean daily temperature (in C°), relative humidity (%RH), total rainfall (in mm), total bright sunshine duration (in hours) and mean daily global solar radiation (in megajoule per square meter) from the Hong Kong Observatory database (HKO, 2020). Seasons were defined based on a Principal Component Analysis of climate data from HKO from January 2015 to July 2022, hence independent from our data collection period. Using a Hierarchical Cluster Analysis, we confirmed that HK subtropical weather followed three seasons: dry season (from December to February); the wet season (from May to October); and the intermediate season (March, April and November). Climate during our sampling period is summarized in Table S2.

1.4 Statistical analysis

As our data derived from normality (as tested by Shapiro-Wilk test), we analysed the repeatability of scores between the years with a paired (per individual) Mann-Whitney signed-rank test, comparing scores made in August 2022 with scores in August 2023, and scores made in January 2023 with scores in January 2024. Differences in distribution of coat colours between the sexes were analysed using a χ^2 test and adding months as a layer in the contingency table. Coat colour was transformed into a continuous scale from -4 to 4 to form the variable “coat colour change”; this scale reflects individuals changes in coat colour from one month to the subsequent

202 with negative values for coats getting paler and positive values for coats getting darker while 0
203 indicates no changes in coat colour.

204 The distribution of coat colours in the population was analysed using a General Linear
205 Model for Ordinal Logistic Regression (OLR) using the function “clm” (package “ordinal”). A first
206 OLR compared the distribution of coat colours to the magnitude of coat colour change. Then, a
207 second OLR was used to test the impact of climate variables and BCS from the month of the score
208 and the month before the score. A backwards elimination procedure was conducted, with
209 variables with the highest p-values removed stepwise until only significant variables remained.
210 Multicollinearity of the predictors was checked using the Variation Inflation Factor (VIF) with the
211 function “vif” (package “car”). A Brant test was conducted to ensure that the proportional odds
212 assumption was respected, using the “brant” function (package “brant”), with p-values above
213 0.05 indicating that the assumption holds. Predicted Probabilities (PP) were extracted from the
214 OLR model to facilitate interpretation of the results, using meaningful points on significant
215 predictors (*i.e.* using five integers along the observed predictor natural range).

216 Coat colour change was analysed using an analysis of covariance (hereafter ANCOVA) with
217 the R function “aov” (package “stats), from which significance was obtained using the function
218 “Anova” specifying for type III (package “car”). Coat colour change was used as the dependent
219 variable (outcome). Sex and season were entered as independent variables in the ANCOVA.
220 Climate variables from the month of the measurements and the previous month were added as

221 covariates and eliminated following a backwards elimination procedure. Specifically, covariates
222 with the highest p-values were removed stepwise until only significant covariates remained.
223 ANCOVA assumptions were checked as follows. Homoscedasticity was checked using a Bartlett
224 test, with p-values above 0.05 indicating that the assumption is respected. The homogeneity of
225 regression slopes was obtained by modelling every possible interaction effect between a fixed
226 factor and a covariate. The assumption was respected if no interaction effect had a p-value above
227 0.05. Due to our large sample size, we did not have to conform to normality assumptions based
228 on the central limit theorem (Islam, 2018). Specifically, with a sample of 253 cattle, we can assume
229 a precision of 5-7% (Islam, 2018). Post-hoc tests were conducted for significant independent
230 variables using a Bonferroni correction.

231

232 *2. Sexual Size Dimorphism*

233 *2.1 Study sites and animals*

234 The HK feral cattle population is currently estimated at 900 individuals (Pinkham *et al.*,
235 2022) found in a variety of environments, from urbanized areas to rural country parks, with some
236 herds on geographically isolated islands. Their main predators, the South China tiger (*Panthera*
237 *tigris tigris*) and leopard (*Panthera pardus*), have not been observed in HK since the 1940's, and
238 although cases of predation on calves by Burmese python (*Python bivittatus*) and feral dogs have
239 been reported (Dudgeon & Corlett, 2010), those are uncommon. The Agriculture, Fisheries and

240 Conservation Department (AFCD) of the Government of the Hong Kong Special Administrative
241 Region (HKSAR) provides veterinary care to injured individuals, but routine care is not provided
242 (AFCD, 2018). The AFCD aims to achieve a stable cattle population primarily relying on
243 reproduction control via surgical sterilization (Pinkham *et al.*, 2022).

244 We studied 30 different cattle herds (Fig. 2), scoring one to 43 individuals in each herd
245 (Table S3), with a total of 317 individuals scored (about a third of the population). We visited each
246 location at least once and up to three times. Herds were distributed over 11 different country
247 parks (n=5 to 117 individuals per country park), with country parks defined by the AFCD. We
248 collected data during Hong Kong's wet season, between 27th of July 2022 and 30th of October
249 2022.

250 We excluded calves and only scored adult cattle as recommended for description of breed
251 populations (FAO, 2011). Our exclusion criteria defined calves following two criteria: *i.* absence of
252 apparent horns or horns detached to the skull (horn tips moving separately to jaw movements)
253 and *ii.* similar appearance to same-aged individuals (Fig. S1). We scored all cattle meeting the
254 inclusion criteria (*i.e.*, adult cattle) and gave each a unique identifier; either its tag as provided by
255 the AFCD, or the name of the herd followed by the number of individuals found that day (*e.g.* the
256 4th individual found in Tai O was identified as TO4), unless the animal had been named for other
257 studies.

258

Figure 2: Map of the herds sampled for body size measurements in Hong Kong SAR. The colours represent the number of cattle scored in country parks. Country parks were defined following the Agriculture and Fisheries Conservation Department (AFCD) of Hong Kong SAR. Country Park names have brown labels, while white labels indicate herd names. Dot colour indicates country park membership. Map was created using the QGIS software (version 3.28.2).

2.2 Measures

We scored horn length by visual comparison to ear length along three categories: shorter, similar or longer than ear length. We developed this method to enable scoring horn phenotypes without restraining individuals. We accounted for broken and asymmetrical horns by adding them as a category, resulting in a total of five categories. Horn length was scored for all study animals

(170 females and 147 males). Side view photos were taken of each individual to assess body size measures (Ferreira & Funston, 2010; Berger, 2012; Tarugara *et al.*, 2019).These photos could be taken without restraint, and digital analysis of photographs also decreases intra and inter-observer variability compared to measures made with a tape, particularly for linear measures (Goodenough *et al.*, 2012). We used five measures: wither height, hip height, body length, hip width and chest depth (Tasdemir et al., 2011; Zhang et al., 2018; Table 1; Fig. 3). To ensure reliability of the measures, we used a triangulation method: the scorer took a photo of the cow and a field assistant. The distance to the animal was decreased slowly until equal distance between cow, scorer and field assistant was met, at which point the scorer took the photo. As soon as the photo was obtained, the scorer stepped away from the cow. As this was not possible for all individuals (i.e., not able to safely approach and/or the animal repeatedly moved away), body size measures were not recorded for all cattle, with measurements obtained for 122 females and 100 males. Using the photos, we took measures with Prime Ruler Android application (Grymala, 2022, version 1.7.6). We used the real height of the assistant divided by the height given by the app as a factor to correct the application measures as follows:

$$RR_{cattle} = \mathrm{PR}_{cattle} * \frac{\mathrm{PR}_{assistant}}{\mathrm{RR}_{assisant}}$$

where RR = real measure estimation and PR = Prime Ruler measurements

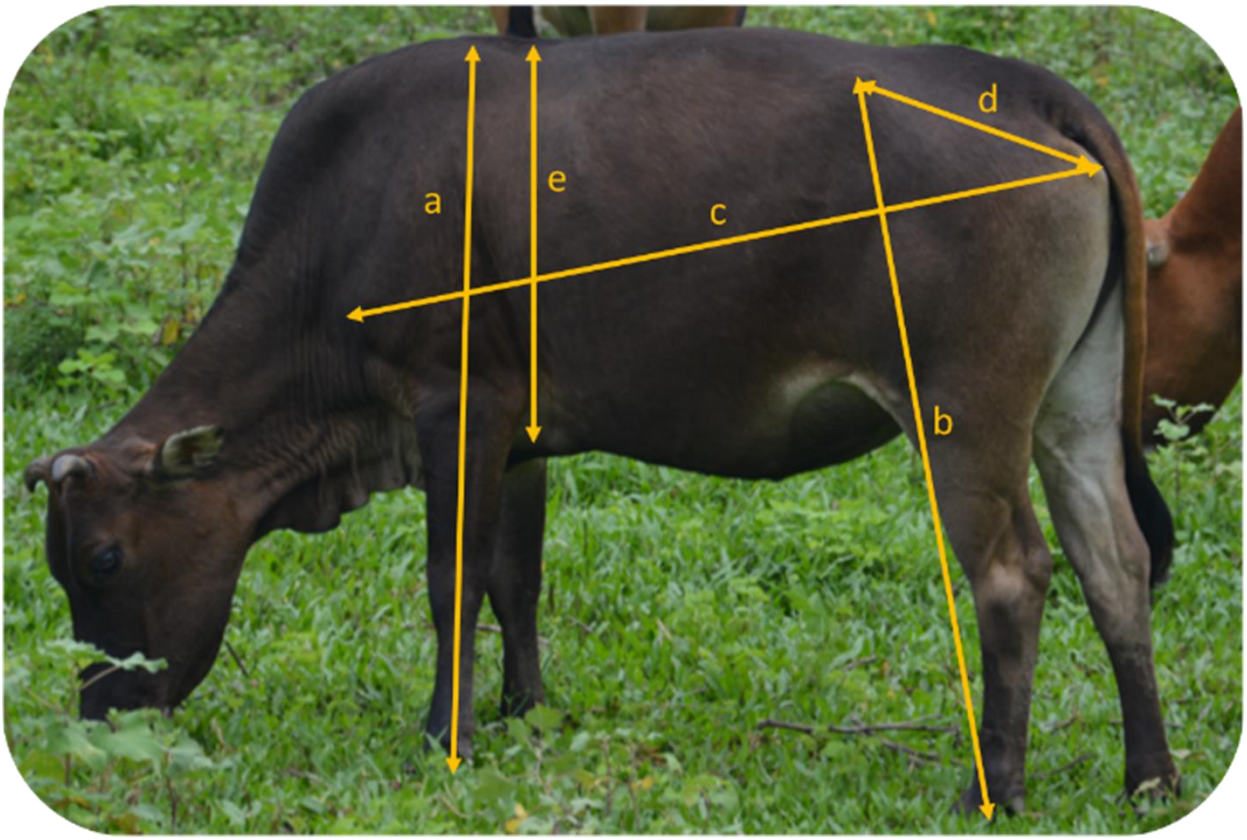

Figure 3: Different measures used to assess body size based on pictures of Hong Kong feral cattle: Wither Height (a), Hip height (b), Body length (c), Hip width (d) and Chest depth (e).

293 Table 1: Body size measures used to describe the Hong Kong feral cattle.

Body Size Measure	Anatomical definition
Wither Height	From wither to hoof of fore limb
Hip height	From tuber coxae to hoof of hind limb
Body length	From shoulder joint to tuber ischii
Hip width	From tuber coxae to tuber ischii
Chest depth	From withers to brachial pit of fore limb

294

295 *2.3 Statistical Analysis*

296 We performed descriptive statistics using JASP software (JASP Team, 2022, Version
297 0.19.0.0), while further tests were performed using R (R Core Team, 2020, version 4.3.3). All
298 scripts and datasets are provided on OSF database.

299 As all measures of body size were highly correlated (based on Spearman's correlation, with
300 all correlations $\rho>0.54$ and $p<0.001$, Table S4), we used a Principal Component Analysis (PCA;
301 function "PCA", package "FactoMineR", Lê et al., 2008) to obtain a summary numerical variable
302 for body size. The first Principal Component (PC1) of the PCA was selected, as it explained 77.81%
303 of the variance, had an eigenvalue of 3.89, and was significantly positively correlated to all five
304 measures of body size ($p<0.0001$). We used a Linear Mixed-effect Model (LMM; function "lmer",
305 package "lme4", Bates et al., 2015) to assess for sexual dimorphism of body size; body size was
306 used as the dependent variable and sex as the independent variable. Location nested within

country park was used as a random factor. The significance was obtained using Satterthwaite's method for single term deletions (“drop1” function, package “stats”).

Sexual dimorphism index (SDI) is a measure developed by Lovich and Gibbons (1992) to quantify the body size difference between the sexes. It was adapted for ruminants (Polák & Frynta, 2009, 2010; Cassini, 2020) as follows: SDI = $\frac{average\ of\ larger\ sex}{average\ of\ smaller\ sex}$. In our analysis, male was the larger sex used in the formula. This measure was calculated to describe sexual dimorphism in all five body measurements. Sexual dimorphism of horn length was assessed using a Pearson's Chi-squared test (function “chisq.test”, package “stats) to compare the distribution of each category of the variable horn length between males and females.

3. Ethical Statement

Our research was reviewed and approved by the Animal Research Ethics Sub-Committee of the authors’ university (Internal Reference: A-0826). We undertook fieldwork in compliance with the Guidelines for the Treatment of Animals in Behavioural Research and Teaching (ASAB/ABS, 2022).

RESULTS

1. Seasonal Coat Colour

Red coats are the most common coat colour in all seasons, while grey coats are the least common (χ^2 = 594.28, p <0.0001; Table 2; Fig. 4). Overall, 31.52% (95%CI = 29.33 – 33.80) of individuals changed coat colour throughout the year, though extreme changes are uncommon. While our methodology would identify individuals that go from black to pale (or pale to black), this was never observed, and extreme changes (-3 and 3) account for less than 1% of individual changes. Coat colours follow seasonal patterns, with no difference between the scores made in August 2022 and 2023 (W = 553.50, p = 0.40) and in January 2023 and 2024 (W = 471.00, p = 0.98), indicating that fluctuation of coat colour follows yearly cycles.

333 Table 2: Coat Colour distribution in the Hong Kong feral cattle in the dry, intermediate and wet

334 season, scored based on a colour chart.

Season	Coat Colour	Counts	Frequency (in %)	95%CI		
Dry	Red	267	38.92	35.34	-	42.62
(686 scores)	Black	167	24.34	21.28	-	27.69
	Dark	133	19.38	16.60	-	22.51
	Pale	91	13.26	10.93	-	16.00
	Grey	28	4.08	2.83	-	5.83
Intermediate	Red	171	35.11	31.00	-	39.45
(487 scores)	Black	110	22.58	19.09	-	26.50
	Dark	90	18.48	15.28	-	22.16
	Pale	81	16.63	13.58	-	20.19
	Grey	35	7.18	5.21	-	9.83
Wet	Red	449	37.92	35.20	-	40.72
(1184 scores)	Black	190	16.04	14.06	-	18.24
	Dark	156	13.17	11.36	-	15.22
	Pale	295	24.91	22.53	-	27.45
	Grey	94	7.93	6.53	-	9.61

335

336 There are significant differences between male and female coat colour distribution (χ^2 =

337 156.20, $p < 0.0001$). Females are in general paler, with red being the most common coat colour in

338 females (44.25%, 95%CI = 41.59 - 46.95), while black coats are the most common in males

339 (30.80%, 95%CI = 28.07 - 33.67). These differences are not consistent throughout the year, with

340 significant sexual differences in coat colour distribution between males and females in all months
341 ($p < 0.05$, Table S5), except in May ($\chi^2 = 8.63$, $p = 0.07$), June ($\chi^2 = 2.96$, $p = 0.56$), September ($\chi^2 =$
342 6.46, $p = 0.16$) and October ($\chi^2 = 8.92$, $p = 0.06$).

343 Individuals with darker (black and dark) coat colours are more likely to change coat colour
344 than cattle with red, grey and pale coats (OLR; OR = 1.80, 95%CI = 1.57 - 2.06, $p < 0.0001$). Coat
345 colour is predicted by the monthly average of the mean daily temperature from the month before
346 the measurement (OLR; OR = -0.06, 95%CI = -0.08 - -0.05, $p < 0.0001$, Table S6) and by the BCS at
347 the time of the measurement (OLR; OR = -0.21, 95%CI = -0.33 - -0.10, $p = 0.0001$, Table S7).
348 Following months of lower temperature (15 °C), the likeliness for cattle to be darker increases
349 (PP; dark = 0.19; black = 0.30), while following higher temperatures (35 °C), the likeliness of cattle
350 being paler increases (PP; pale = 0.32; red = 0.40). Similarly, the likeliness of having a paler coat
351 increases in individuals with higher body condition (BCS 7, PP; pale = 0.28; red = 0.39), while in
352 individuals with lower body condition (BCS 3) the likeliness to be darker increases (PP; dark = 0.17;
353 black = 0.23). The interaction between BCS and the temperature from the previous month could
354 not be computed as it increased VIF/multi-collinearity above 60, making it unsuitable for
355 interpretation.

356 The likeliness for coat colour to change is significantly explained by seasonal variations ($F_{(5,}$
357 $_{1647)} = 5.71$, $p = 0.003$), with coat colours getting paler in the wet season while they get darker in
358 the dry season (Fig. 4). Specifically, cattle are more likely to change colour between the

intermediate and the wet season (Tukey Post-hoc, $t = -3.14$, $p = 0.005$, Table S8). There is no difference between males and females in the magnitude of changes in coat colours ($F_{(5, 1647)} = 0.37$, $p = 0.54$). The impact of seasonal variation in coat colours is driven by the average humidity ($F_{(5, 1647)} = 17.44$, $p<0.001$) and the mean daily global solar radiation ($F_{(5,1647)} = 33.61$, $p<0.001$) in the month of scoring.

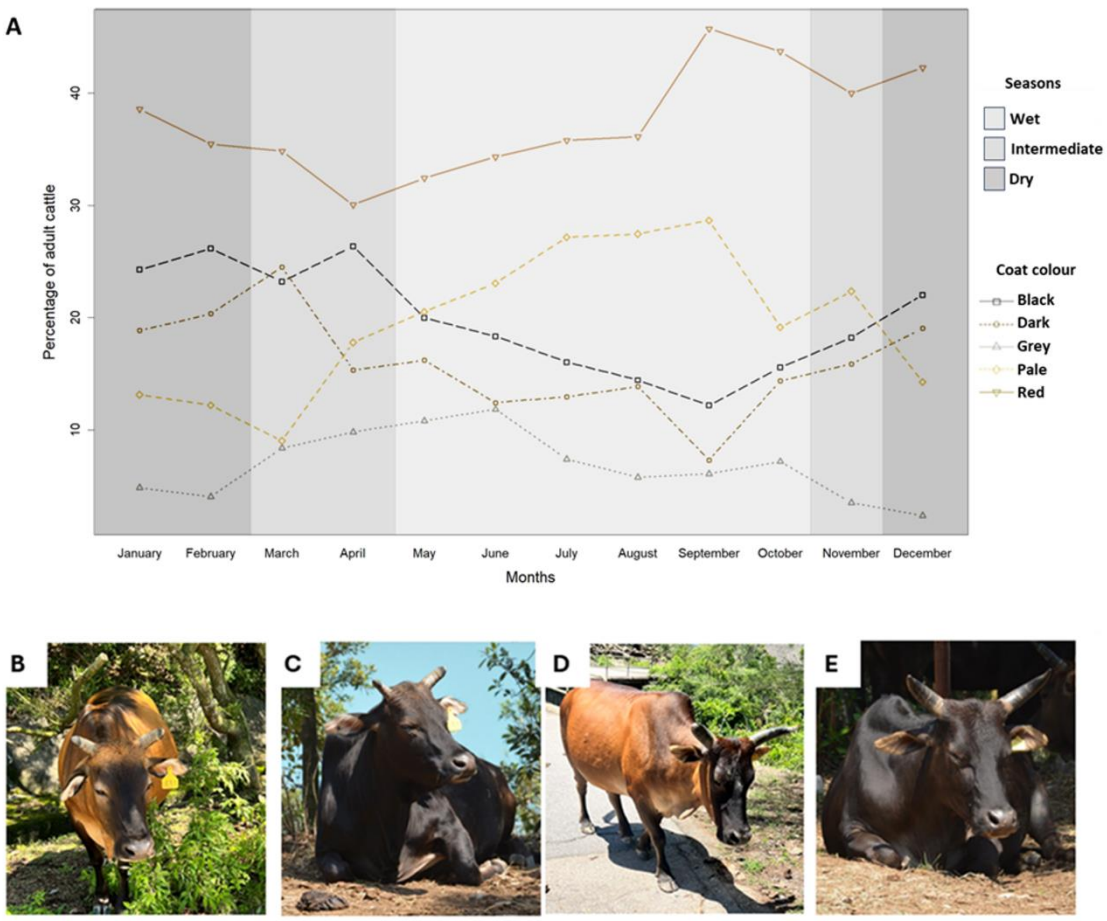

Figure 4: Monthly variation of coat colour of the Hong Kong cattle (A) and examples of coat changes within a same individual: female cattle (tagged 431) in the wet (B) and in the dry (C); and male cattle (tagged 17) in the wet (D) and in the dry (E). Coat colour was scored based on a colour chart.

371 *2. Sexual Size Dimorphism*

372 Males are significantly larger than females (LMM, $p = 0.002$, Fig. 5) in all body size
373 measurements as indicated by the SDI (Table 3). While male and female cattle are dimorphic,
374 their dimorphism is moderate, with a mean SDI of 1.07, ranging from 1.05 for hip height and body
375 length to 1.1 for chest depth.

376

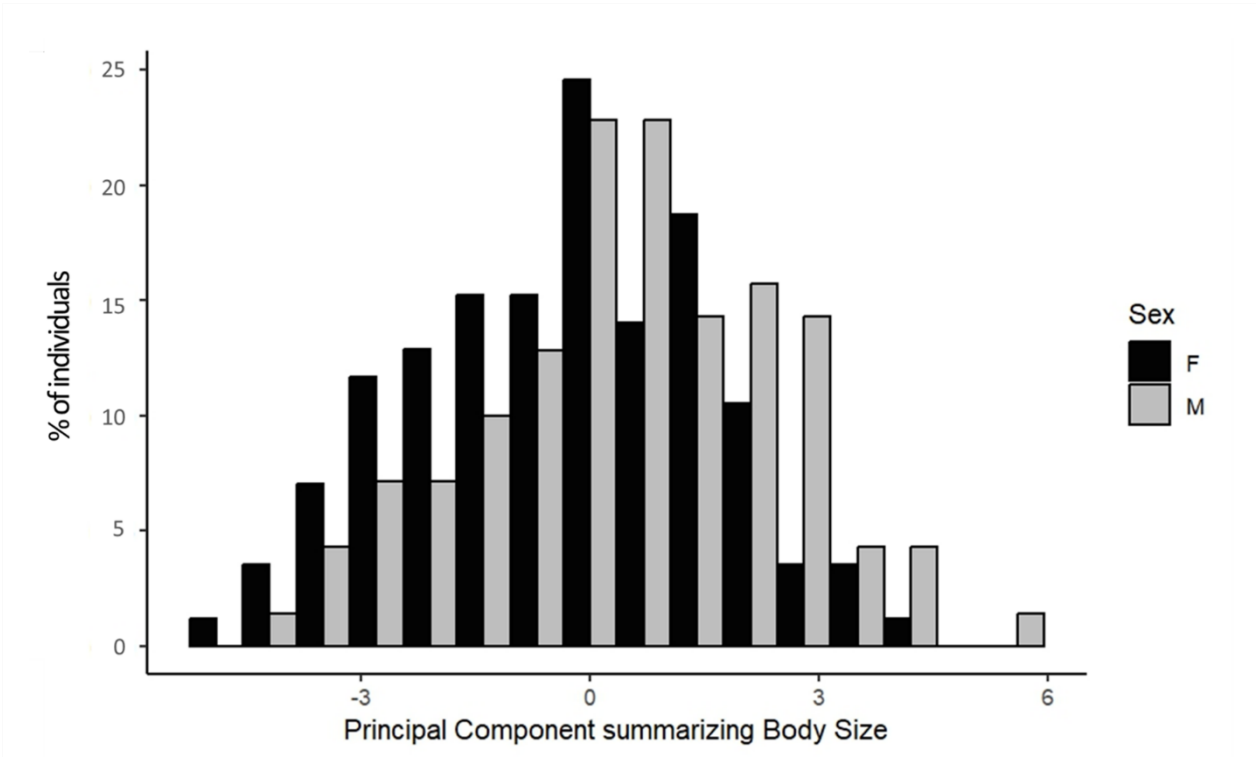

Figure 5: Body size of 100 male (light grey) and 122 female (black) Hong Kong feral cattle. Body size is expressed as a Principal Component (PC, unitless) obtained from a Principal Component Analysis (PCA) summarizing five measures of body size: wither height, hip height, body length, hip width and chest depth.

Table 3: Body size measurements (expressed in centimetres) and Principal Component (PC, unitless) obtained from a Principal Component Analysis (PCA) summarizing the five measures of body size for 100 male and 122 female Hong Kong feral cattle. Sexual Dimorphism Index (SDI) is given for all five body size measurements as the difference between the sexes ($\frac{average\ of\ males}{average\ of\ females}$)

		Mean	Minimum	Maximum	SDI
Wither Height	F	101.65	66.34	146.01	1.08
	M	110.58	67.96	156.21	
Hip height	F	95.20	51.29	144.50	1.05
	M	100.88	30.92	139.08	
Body length	F	112.10	70.42	161.19	1.05
	M	118.48	49.19	174.87	
Hip width	F	30.55	12.67	61.22	1.07
	M	32.97	10.16	52.39	
Chest depth	F	55.54	7.14	91.35	1.1
	M	61.43	14.51	92.40	
PC1	F	-0.33	-5.56	4.75	
	M	0.38	-4.77	6.10	

Males have longer horns than females (χ^2=68.52, p <0.0001; Fig. 6). While short horns are the most common horn type in females (38.24%, 95%CI = 21.26 - 45.72), long horns are the most frequent horn type in males (44.22%, 95%CI = 36.43 - 52.29). Asymmetrical horns are uncommon in both males (2.04%, 95%CI = 0.69 - 5.82) and females (1.76%, 95%CI = 0.60 - 5.05). Females are

more likely than males to have broken horns (22.94%, 95%CI = 17.26 – 29.81, and 11.56%, 95%CI = 7.34 – 17.73, respectively).

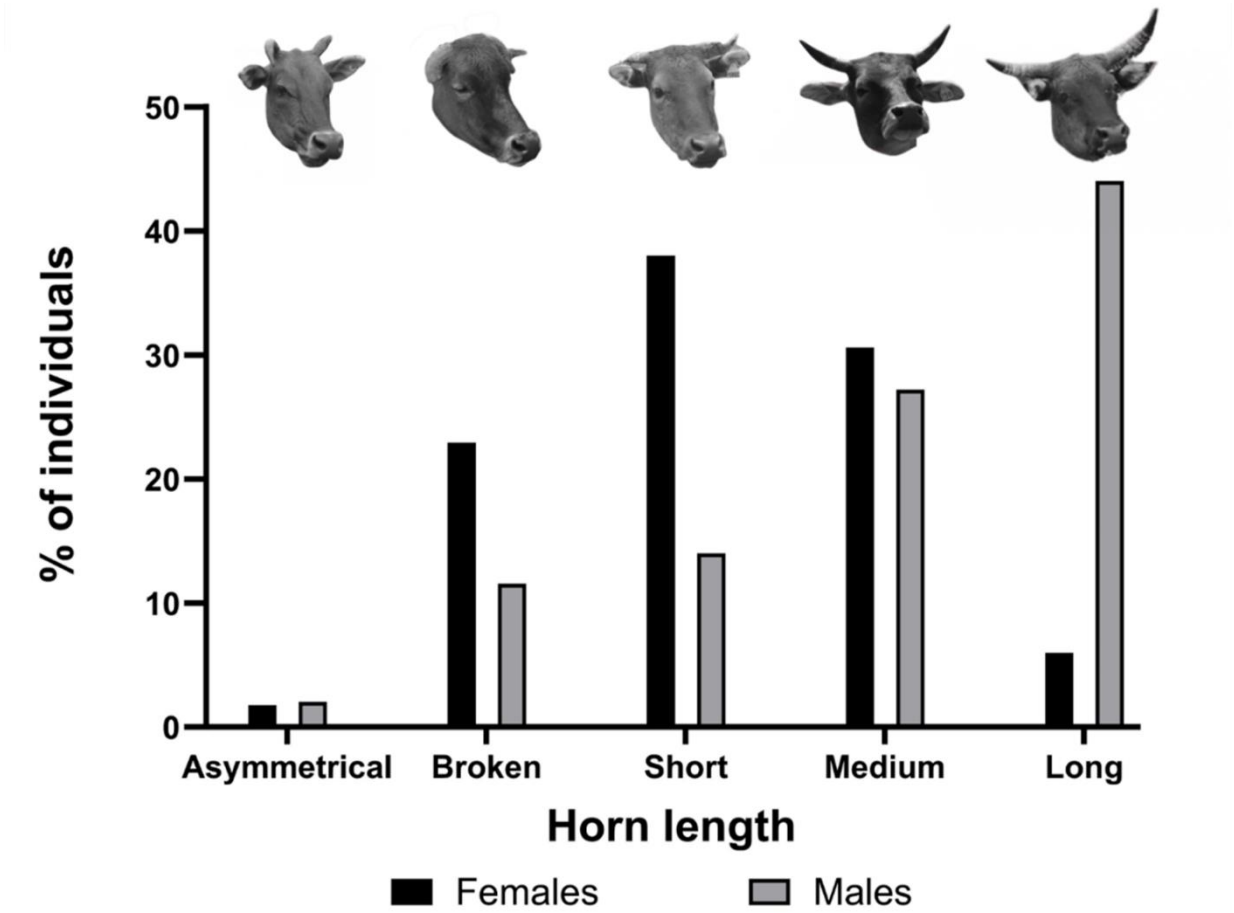

Figure 6: Distribution of horn lengths in 147 males (grey) and 170 females (black) Hong Kong feral cattle. Horn length was measured visually by comparing it to ear length.

DISCUSSION

We provide the first phenotypic analysis of sexual dimorphism in body size and horn length in the Hong Kong (HK) feral cattle and quantify their seasonal coat colour changes. HK feral cattle are sexually dimorphic, with males being darker, larger and having longer horns than females. Additionally, females are more likely to have broken horns than males. We provide the first evidence of seasonal coat colour variation in cattle, with a third of individuals showing coat colour changes every month. Coat colours were predicted by body condition and the temperature from the previous month, while the magnitude of seasonal coat colour change was predicted by humidity and solar radiation. As global temperatures rise and weather patterns shift, many species are predicted to face important imbalances in thermoregulation (*e.g.* North et al., 2023), driving phenotypic expression to adapt to increasingly unpredictable environmental conditions. By understanding the pressures prey populations undergo in the absence of predators and the key role of phenotypic plasticity in their ability to adapt to changing environment, we can improve population dynamics projections.

HK cattle exhibit seasonal changes in coat colour, with more individuals displaying paler coats in the wet season and darker coats in dry season. Thermoregulation appears to be the primary driver of seasonal coat colour changes in HK cattle, influenced by humidity and solar radiation, as seen in other prey species facing high energetic costs from climate factors (Zimova *et al.*, 2014; Kennah *et al.*, 2023). Darker coats are generally better suited to tropical and

419 subtropical environments, aligning with Gloger's rule (Kamilar & Bradley, 2011; Delhey, 2019; Ge
420 *et al.*, 2021). However, the thermal melanism hypothesis predicts that lighter coats can help
421 regulate heat gain and water loss in hot and humid climates (Delhey, 2019; Marcondes *et al.*,
422 2020). For instance, in springbok *(Antidorcas marsupialis),* individuals with paler coats thrive in
423 summer , while those with darker coats are better suited to winter climates (Hetem *et al.*, 2009).
424 Heat stress is a significant welfare concern in farmed cattle, negatively impacting behaviour and
425 physiology, which can compromise long-term health when climatic conditions exceed cattle
426 thermal neutral range (Cook *et al.*, 2007; Becker *et al.*, 2020; North *et al.*, 2023). Darker cattle
427 breeds tend to suffer more from excessive heat loads compared to breeds with paler coats
428 (Mader *et al.*, 2006; Brown-Brandl *et al.*, 2006). Similarly, coat colour variation within breeds leads
429 to individual differences in heat load, with black coated Holstein cattle having higher surface
430 temperature than white cattle (Façanha *et al.*, 2010; Santos *et al.*, 2017). Our findings show that
431 darker individuals have lower body condition, suggesting a higher cost associated with darker
432 coats, in alignment with previous findings in dairy cattle (Anzures-Olvera *et al.*, 2019). Humidity is
433 expected to significantly impact thermoregulation costs in tropical populations (Marcondes *et al.*,
434 2020), which supports our observation that humidity drives the magnitude of seasonal changes
435 in coat colour. Genes related to UV protection and heat tolerance have been identified in other
436 Chinese cattle breeds (Lei *et al.*, 2006; Gao *et al.*, 2017; Xia *et al.*, 2023). Overall, our results
437 support the thermal melanism hypothesis, as we found that temperature, humidity, and solar
438 radiation influence seasonal coat colour changes.

Our findings provide the first evidence of seasonal changes in coat colour in a subtropical cattle population. While coat colour changes in cattle have been previously associated with age (Schmutz, 2012) and with nutritional deficiencies, with for instance copper deficiency being associated with paler coats in farmed cattle (Olkowski & Wojnarowicz, 2018). The association we found between darker coats and lower body condition highlights that it is unlikely to be related to nutritional deficiency and likely associated with seasonal patterns instead. Additionally, repeatability of scores across the years supports the idea of seasonal patterns of coat colour changes in HK cattle. In tropical ungulates, paler coats could be expected in the dry season for camouflage against vegetation, while darker coats in the wet season provide background matching for darker soil and foliage (see for instance Newell et al., 2021). However, our findings do not support these expectations. Coat colour variability is influenced by a trade-off between thermoregulation and predation risk (Beltran *et al.*, 2018; Zimova *et al.*, 2018; Kennah *et al.*, 2023). As HK feral cattle were farmed (and thus likely protected by farmers) when predators were still present in HK, there may have been little to no pressure from predation risk on this population historically. Hence, coat colouration of HK cattle may not serve a function as an anti-predatory response, resulting in it not matching the background colours as would be expected in other free-ranging ruminants with high predation pressure.

We found that darker coats were present in all seasons, although these were more common in males and in the dry season. If darker coats impose higher thermoregulatory costs, their persistence in subtropical environments like HK raises questions. Darker coats correlate with

459 higher androgens levels and reproductive success (Loehr *et al.*, 2008; Bro-Jørgensen &
460 Dabelsteen, 2008; Coulson *et al.*, 2011) as well as enhanced heat dissipation through skin
461 evaporation in Holstein cows (Maia *et al.*, 2005; Santos *et al.*, 2017). Variations in pigmentation
462 relate to behavioural differences (Tucker *et al.*, 2008; Stuart-Fox *et al.*, 2017), with darker
463 mammals often exhibiting greater dominance, fertility, aggression, and sexual activity (Côté &
464 Festa-Bianchet, 2001; Ducrest *et al.*, 2008; Mckinnon & Pierotti, 2010; Roulin, 2014). In giraffes
465 (*Giraffa camelopardalis*), darker males were more likely to live in smaller social groups and to
466 spend more time alone, reflecting different sexual strategies between paler and darker males,
467 with coat colour playing a role as a signal of competitive ability (Castles *et al.*, 2019). Similarly, in
468 eland (*Tragelaphus oryx*), acquiring a higher social status led to darkening of facial colouration,
469 highlighting a social function of phenotypic plasticity in coat colour in ungulates (Bro-Jørgensen
470 & Beeston, 2015). However, contrasting evidence exists with paler male Himalayan tahr
471 (*Hemitragus jemlahicus*) being larger, higher ranked and having a higher reproductive success
472 than their darker conspecifics (Lovari *et al.*, 2009, 2015; Fattorini *et al.*, 2024). Though cattle can
473 discriminate long wavelengths from medium wavelengths (Phillips & Lomas, 2001) suggesting
474 they would be able to discriminate red-based coat colours, further evidence on their ability to
475 discriminate conspecifics based on coat colour and to adjust their behaviour is lacking, but may
476 explain why darker coats persist in this population.

477 While the coat colour of HK cattle is plastic and exhibits seasonal patterns, most individuals
478 show limited variation in colouration. Cattle with extreme coat colours are more likely to moult,

479 which occurs when the cost of producing a different coat is lower than maintaining a suboptimal
480 colouration (Beltran *et al.*, 2018). Consequently, cattle with extreme coats may face higher costs
481 when their pelage becomes maladapted, increasing the likelihood of moulting. Similarly, in
482 springbok, extreme coat colours (black and white) were rare, likely due to variations in
483 thermoregulation costs (Hetem *et al.*, 2009). Extreme colours can yield both significant benefits
484 and higher costs, leading most individuals to exhibit average traits that balance these factors.
485 While paler coats can reduce heat stress, darker individuals often enjoy reproductive and immune
486 advantages (Ducrest *et al.*, 2008; Coulson *et al.*, 2011; Delhey, 2019). Our study addresses a
487 simplified version of Gloger's rule, examining pigmentation as a whole; however, melanin
488 pigments (*i.e.* eumelanin and phaeomelanin) are known to respond differently to climatic
489 conditions (Delhey, 2019; Marcondes *et al.*, 2020). Further investigation into melanism in feral
490 cattle could enhance our understanding of how climate and thermoregulation costs influence the
491 prevalence of coat colours.

492 In artiodactyls, males tend to be both larger and longer than females (Cassini, 2020;
493 Tombak *et al.*, 2024), similar to our findings that HK feral bulls were larger in all body size
494 measures than HK feral cows. Domestication in bovids has led to greater sexual dimorphism with
495 larger males (Polák & Frynta, 2009; McPherson & Chenoweth, 2012). Among cattle, milk breeds
496 are the most sexually dimorphic, while draught breeds are the least dimorphic (Polák & Frynta,
497 2010). Additionally, cattle breeds from the tropics and subtropics are less sexually dimorphic than
498 breeds from temperate zones (Polák & Frynta, 2010), with Sexual Dimorphism Index (SDI) in South

Asian breeds averaging 1.2. Hence, the moderate sexual dimorphism of HK feral cattle (1.07) may result from their South Asian origin and their genetic similarity with other South Asian cattle, along with their history as draught animals. More specifically, SDI in wild bovids averages 1.1 in indicine breeds and Gayal (*Bos frontalis*; Polák & Frynta, 2010). Thus, HK feral cattle not only share genetic relatedness to Asian wild bovids (Barbato *et al.*, 2020), we now show they also share phenotypic similarities through moderate sexual dimorphism.

Male bovids usually have longer horns than their female counterparts (Emlen, 2008; Stankowich & Caro, 2009; McPherson & Chenoweth, 2012), as we found in the HK cattle. Sexual selection has been shown to condition horns in males and females differently (Bro-Jørgensen, 2007; Stankowich & Caro, 2009). Horns are primarily used as weapons in male-male competition (Lundrigan, 1996; Berglund *et al.*, 1996; Emlen, 2008; McCullough *et al.*, 2016), resulting in secondary involvement in mate selection, with females favouring males with longer horns in several bovid species (Berglund *et al.*, 1996; Knierim *et al.*, 2015). Hence, males may benefit from investing resources into growing long horns to improve their reproductive success, while females may favour other functions such as defence against predators, as found in other bovid species (Bro-Jørgensen, 2007). Female HK feral cattle are more likely to have broken horns than males, which may result from differences in behaviour or susceptibility to environmental factors between males and females but is currently unknown.

518 **CONCLUSION**

519 The Hong Kong (HK) feral cattle are free roaming in a subtropical environment. We provide
520 the first assessment of the sexual dimorphism in horn and body size and seasonal changes in coat
521 colour of the HK feral cattle. The sexual dimorphism in HK feral cattle is male-biased, and
522 moderate, comparable to other South Asian and draught breeds. Surprisingly, we found that
523 female HK cattle were more likely than males to have broken horns, but literature about the
524 mechanisms underlying these differences are lacking. Extreme coat colours are less common and
525 more susceptible to seasonal changes, with paler individuals in the wet season and darker ones
526 in the dry season, suggesting plastic phenotypes. The main driver of seasonal coat colour appears
527 to be thermoregulation. As cattle are sensitive to heat stress, understanding the mechanism
528 through which mismatched phenotypes remain (*e.g.* darker individuals with higher
529 thermoregulation costs in the wet season) has consequences for management of ruminants in
530 changing environments. Additionally, with the global shift in climate, understanding the drivers
531 of phenotypic plasticity in subtropical cattle improves our knowledge of adaptation in tropical and
532 subtropical free-ranging populations in increasingly warm and unpredictable habitats.

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790 **SUPPORTING INFORMATION**

791 **Sexual dimorphism and phenotypic plasticity in a feral bovid *Bos taurus* (Artiodactyla:**
792 **Bovidae).**

793

794 *Includes:*

795 **Tables:**

796 Table S1: Description of the eight cattle coat colour scores removed from further analysis due to
797 mode (most frequent value between fore, middle and hind body coat colour) not being
798 obtained.

799 Table S2: Climate variables extracted from the Hong Kong Observatory (HKO) for each month
800 when coat colour scoring was conducted.

801 Table S3: Number of female and male cattle scored in each herd and overall number of
802 individuals where at least one phenotype trait could be scored for each herd and country park.

803 Table S4: Relationships between the five measures of cattle body size (wither height, hip height,
804 body length, hip width and chest depth) used to measure Hong Kong feral cattle body size, as
805 evaluated by Spearman's correlations.

Table S5: Differences of coat colours (scored among 5 categories in a colour chart) between male and female cattle.

Table S6: Coat colour predicted in relation to temperature (in °C) in Hong Kong feral cattle (n = 253) based on Predicted Probabilities (PP) of Ordinal Logistic Regression.

Table S7: Coat colour predicted in relation to Body Condition Score (BCS) in Hong Kong feral cattle (n = 253) based on Predicted Probabilities (PP) of Ordinal Logistic Regression.

Table S8: Coat colour change magnitude between the three seasons in Hong Kong feral cattle (n = 253) based on Tukey Post-hoc test.

Figures:

Figure S1: Calves (A) were defined as both individuals without horns and individuals of similar appearance to same-aged cows. Juveniles (B) have horn tips and distinct coat patterns.