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

Tania A. Perroux[1*], Alan G. McElligott[2,3], George M. W. Hodgson[2,3], Kate J. Flay[1*]

[1.] Department of Veterinary Clinical Sciences, Jockey Club College of Veterinary Medicine and Life Sciences, City University of Hong Kong, Hong Kong SAR, China

[2.] Department of Infectious Diseases and Public Health, Jockey Club College of Veterinary Medicine and Life Sciences, City University of Hong Kong, Hong Kong SAR, China

[3.] Centre for Animal Health and Welfare, Jockey Club College of Veterinary Medicine and Life Sciences, City University of Hong Kong, Hong Kong SAR, China

***Corresponding authors:**

Tania A. Perroux (tperroux2-c@my.cityu.edu.hk) and Kate J. Flay (kateflay@cityu.edu.hk)

City University of Hong Kong, Kowloon, Hong Kong, Hong Kong SAR, China

TAP ORCID: 0000-0001-5164-2490

AGM ORCID: 0000-0001-5770-4568

GMWH ORCID: 0000-0002-2531-6058

KJF ORCID: 0000-0003-3770-3765

Acknowledgements

The authors are grateful to the “Sai Kung Bovid Watch”, “Hong Kong Bovid Conservation Association” and the AFCD cattle management team that provided valuable information on the cattle. We are thankful to Yeuk Wan Sharon Lam, Wing Sum Wong, Wang Hin Wong and Claire Giraudet for their valuable contribution to fieldwork and data collection. We are also grateful to Yifu Wang for providing the files for the maps of Hong Kong. We also thank Dieter Lukas and André Vieira Rodrigues for their helpful comments on previous versions of this manuscript.

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 sexual dimorphism in body size and horn length, and seasonal coat colour changes in HK feral cattle. We found that males were larger and had longer horns than females. 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. 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.

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

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.

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).

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

86 Delhey, 2019), species inhabiting hot and wet environments, such as tropical and subtropical
87 habitats, are expected to have darker coats (Cloudsley-Thompson, 1999; Wacker *et al.*, 2016).
88 This trend has been confirmed in various mammals, notably primates (Kamilar & Bradley, 2011),
89 wild pigs (Newell *et al.*, 2021), rodents (Ge *et al.*, 2021) and more generally in artiodactyls (Stoner,
90 2003) by comparing populations from temperate habitats to populations in tropical and
91 subtropical habitats.

92 Phenotypic traits can exhibit plasticity, as demonstrated by the periodic moulting of coats
93 in various endotherm species (Beltran *et al.*, 2018; Zimova *et al.*, 2018). Moulting is influenced by
94 external factors, with photoperiodism (*i.e.* daylight duration) triggering the initiation of the
95 process, while climate conditions, such as temperature and snow cover, affect the speed of
96 moulting (Zimova *et al.*, 2018). Additionally, the timing and duration of moulting are governed by
97 internal factors, including age, sex, body condition, and reproductive status, all modulated by the
98 endocrine system (Beltran *et al.*, 2018; Zimova *et al.*, 2018). Rapid adaptations in coat colouration
99 are often observed in species expanding their distribution (*e.g.* Newell et al., 2021). Predation
100 pressure is a primary driver of coat colouration, as camouflage decreases predation risk through
101 background matching (Atmeh et al., 2018; Caro, 2005). In environments with significant seasonal
102 contrasts, such as temperate and arctic habitats, these seasonal changes in colouration facilitate
103 adaptations that improve concealment in response to fluctuating vegetation and soil conditions
104 (Zimova *et al.*, 2014, 2018). Typically, endotherm coats are darker in summer and lighter in winter,
105 with variations in colour reflecting the balance of eumelanin (black/brown pigments) and

106 phaeomelanin (yellow/red pigments). Seasonal changes in coat colour are expected when the
107 energetic costs of producing a new coat are lower than the costs associated with suboptimal
108 colouration (Beltran *et al.*, 2018).

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

123 Despite the striking phenotypic diversity of these animals, little is systematically known
124 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. Sexual Size Dimorphism

1.1 Study sites and animals

The HK feral cattle population is currently estimated at 900 individuals (Pinkham *et al.*, 2022) found in a variety of environments, from urbanized areas to rural country parks, with some herds on geographically isolated islands. Their main predators, the South China tiger (*Panthera tigris tigris*) and leopard (*Panthera pardus*), have not been observed in HK since the 1940's, and although cases of predation on calves by Burmese python (*Python bivittatus*) and feral dogs have been reported (Dudgeon & Corlett, 2010), those are uncommon. The Agriculture, Fisheries and Conservation Department (AFCD) of the Government of the Hong Kong Special Administrative Region (HKSAR) provides veterinary care to injured individuals, but routine care is not provided (AFCD, 2018). The AFCD aims to achieve a stable cattle population primarily relying on reproduction control via surgical sterilization (Pinkham *et al.*, 2022).

We studied 30 different cattle herds (Fig. 1), scoring one to 43 individuals in each herd (Table S1), with a total of 317 individuals scored (about a third of the population). We visited each location at least once and up to three times. Herds were distributed over 11 different country parks (n=5 to 117 individuals per country park), with country parks defined by the AFCD. We collected data during Hong Kong's wet season, between 27th of July 2022 and 30th of October 2022.

Figure 1: 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).

We excluded calves and only scored adult cattle as recommended for description of breed populations (FAO, 2011). Our exclusion criteria defined calves following two criteria: *i.* absence of apparent horns or horns detached to the skull (horn tips moving separately to jaw movements) and *ii.* similar appearance to same-aged individuals (Fig. S1). We scored all cattle meeting the inclusion criteria (*i.e.*, adult cattle) and gave each a unique identifier; either its tag as provided by

the AFCD, or the name of the herd followed by the number of individuals found that day (*e.g.* the 4th individual found in Tai O was identified as TO4), unless the animal had been named for other studies.

1.2 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. 2). 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

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

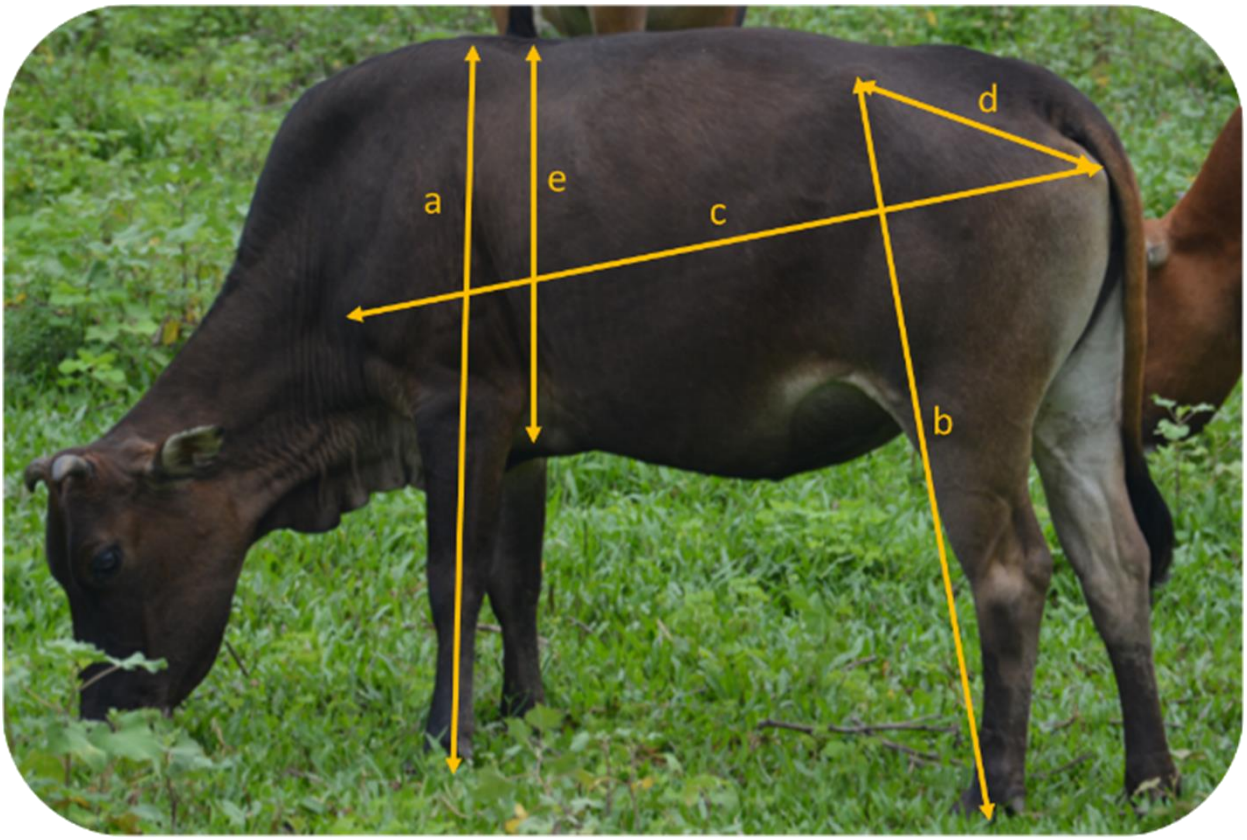

Figure 2: Different measures used to assess body size based on pictures of Hong Kong feral cattle: Wither Height (a), Hip height (b), Body length (c), Hip width (d) and Chest depth (e).

1.3 Statistical Analysis

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

As all measures of body size were highly correlated (based on Spearman's correlation, with all correlations $\rho>0.54$ and $p<0.001$, Table S2), we used a Principal Component Analysis (PCA; function "PCA", package "FactoMineR", Lê et al., 2008) to obtain a summary numerical variable for body size. The first Principal Component (PC1) of the PCA was selected, as it explained 77.81% of the variance, had an eigenvalue of 3.89, and was significantly positively correlated to all five measures of body size ($p<0.0001$). We used a Linear Mixed-effect Model (LMM; function "lmer", package "lme4", Bates et al., 2015) to assess for sexual dimorphism of body size; body size was 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.

2. Seasonal Coat Colour

2.1 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).

2.2 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 chart consisted of five coat colours: pale, red, grey, dark and black (Fig. 3). All coat colours were

238 estimated by a single observer to reduce subjectivity of scoring, similar to Agosta et al. (2017). To
239 ensure reliability of scores, scores made in August 2022 were also checked by three independent
240 observers, and scores were discussed until all observers reached an agreement. This allowed us
241 to refine the coat colour chart (Fig. 3). We used this colour chart to assess three body parts: fore,
242 middle and hind (D'Ammando et al., 2022; Loehr et al., 2008). Then, we used the mode of those
243 three body part coat colours to obtain each individual's coat colour per month. Individuals for
244 which coat colour in all three body parts differed were not retained for that month; this was the
245 case for eight individual cattle scores. Further description of the eight data points removed is
246 presented in Table S3. Moulting is known to follow patterns across the body which are well
247 described in several species (Zimova *et al.*, 2018), but such prior knowledge was not available for
248 our study animals. Hence, these discrepancies of colour across body part may simply reflect the
249 moulting process but could not be analysed in the present study. To assess coat colour changes,
250 coat colours were replaced by an ordinal scale, with palest coats scored 1 and darkest scored 5
251 (Fig. 3).

252

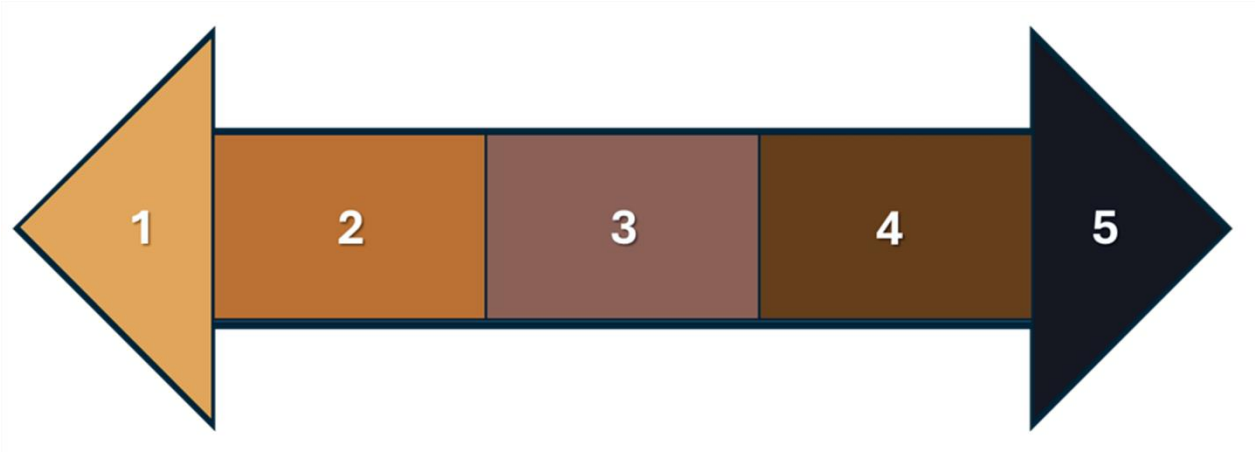

Figure 3: Coat colour scale used to characterize coat colours in Hong Kong feral cattle with 1 corresponding to palest coats, 2 for coats scored as red, 3 for grey, 4 for dark and 5 black (the darkest coat colour). This colour scale is adapted from Stoner (2003).

Each individual received a Body Condition Score (BCS) at the time of coat colour scoring based on a modified visual 9-point scale, with 1 being the thinnest individuals (low body condition), and 9 the fattest (high body condition). This scale was adapted to the HK feral cattle based on beef cattle BCS (D'Occhio *et al.*, 2019; Weik *et al.*, 2021). To control for the subjective 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 $\rho = 0.8$ (based on Spearman's

267 rank correlation) for three consecutive weeks. This same observer scored all BCS used in this
268 study.

269

270 *2.3 Climate Data*

271 We extracted monthly averages for mean daily temperature (in C°), relative humidity
272 (%RH), total rainfall (in mm), total bright sunshine duration (in hours) and mean daily global solar
273 radiation (in megajoule per square meter) from the Hong Kong Observatory database (HKO,
274 2020). Seasons were defined based on a Principal Component Analysis of climate data from HKO
275 from January 2015 to July 2022, hence independent from our data collection period. Using a
276 Hierarchical Cluster Analysis, we confirmed that HK subtropical weather followed three seasons:
277 dry season (from December to February); the wet season (from May to October); and the
278 intermediate season (March, April and November). Climate during our sampling period is
279 summarized in Table S4.

280

281 *2.4 Statistical analysis*

282 As our data derived from normality (as tested by Shapiro-Wilk test), we analysed the
283 repeatability of scores between the years with a paired (per individual) Mann-Whitney signed-
284 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 with negative values for coats getting paler and positive values for coats getting darker while 0 indicates no changes in coat colour.

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

Coat colour change was analysed using an analysis of covariance (hereafter ANCOVA) with the R function “aov” (package “stats), from which significance was obtained using the function “Anova” specifying for type III (package “car”). Coat colour change was used as the dependent variable (outcome). Sex and season were entered as independent variables in the ANCOVA. Climate variables from the month of the measurements and the previous month were added as covariates and eliminated following a backwards elimination procedure. Specifically, covariates with the highest p-values were removed stepwise until only significant covariates remained. ANCOVA assumptions were checked as follows. Homoscedasticity was checked using a Bartlett test, with p-values above 0.05 indicating that the assumption is respected. The homogeneity of regression slopes was obtained by modelling every possible interaction effect between a fixed factor and a covariate. The assumption was respected if no interaction effect had a p-value above 0.05. Due to our large sample size, we did not have to conform to normality assumptions based on the central limit theorem (Islam, 2018). Specifically, with a sample of 253 cattle, we can assume a precision of 5-7% (Islam, 2018). Post-hoc tests were conducted for significant independent variables using a Bonferroni correction.

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

322 with the Guidelines for the Treatment of Animals in Behavioural Research and Teaching

323 (ASAB/ABS, 2022).

RESULTS

1. Sexual Size Dimorphism

Males are significantly larger than females (LMM, $p = 0.002$, Fig. 4) in all body size measurements as indicated by the SDI (Table 2). While male and female cattle are dimorphic, their dimorphism is moderate, with a mean SDI of 1.07, ranging from 1.05 for hip height and body length to 1.1 for chest depth.

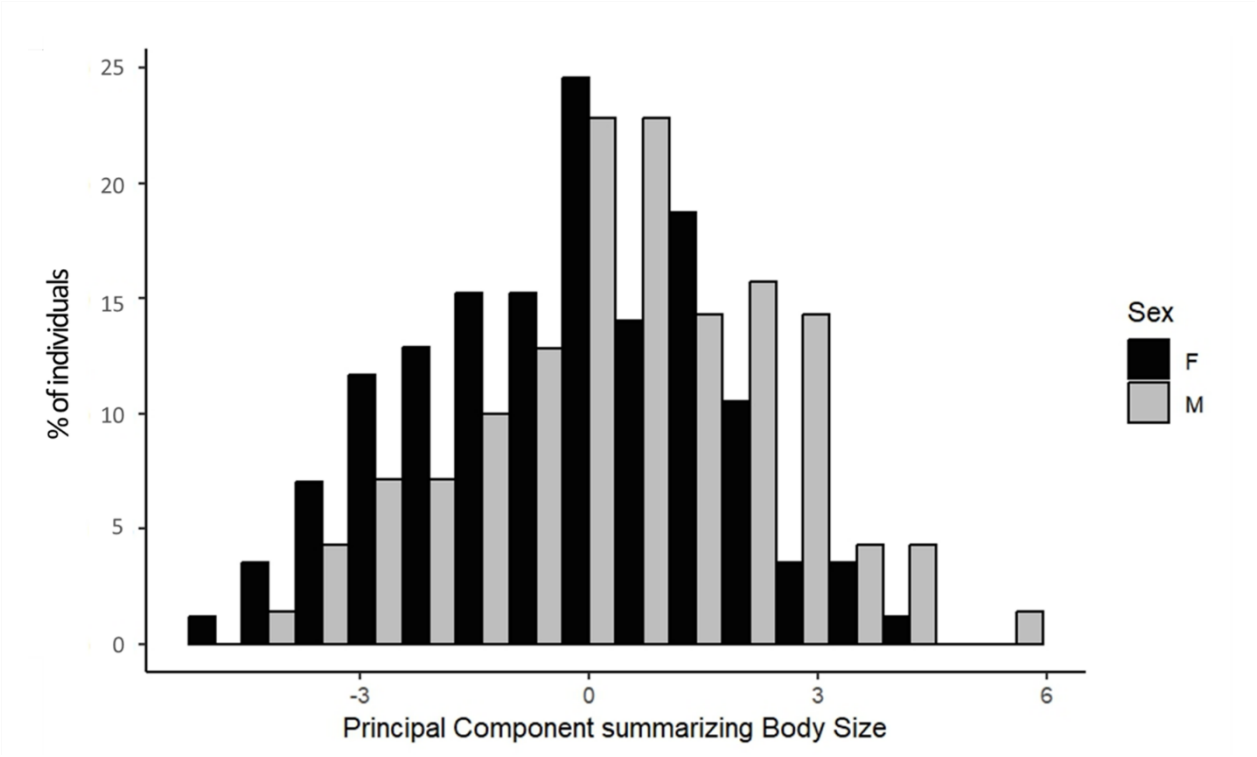

Figure 4: Body size of 100 male (light grey) and 122 female (black) Hong Kong feral cattle. Body size is expressed as a Principal Component (PC, unitless) obtained from a Principal Component Analysis (PCA) summarizing five measures of body size: wither height, hip height, body length, hip width and chest depth.

Males have longer horns than females (χ^2=68.52, p <0.0001; Fig. 5). 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).

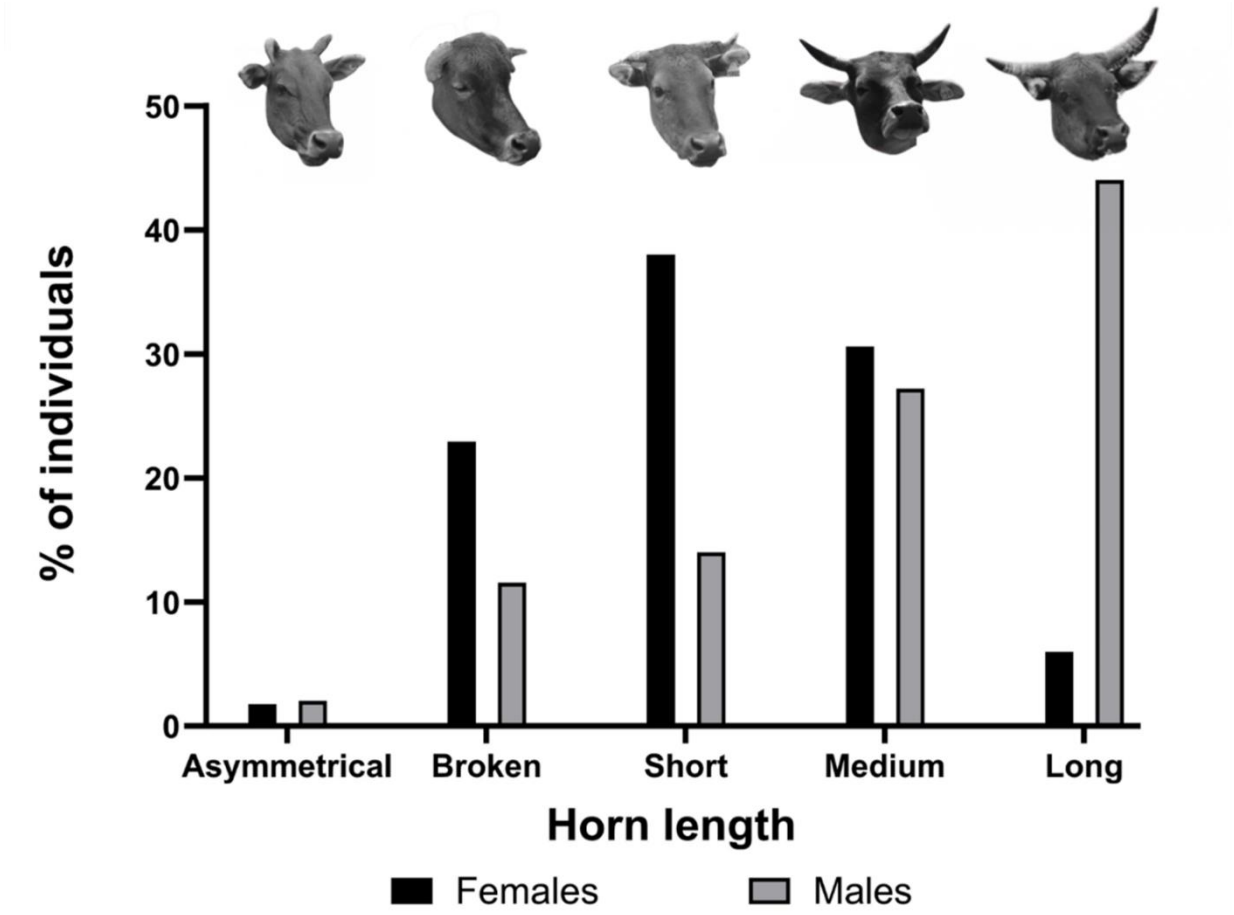

Figure 5: Distribution of horn lengths in 147 males (grey) and 170 females (black) Hong Kong feral cattle. Horn length was measured visually by comparing it to ear length.

Table 2: 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	

2. 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 3; Figure 6). 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.

364 Table 3: Coat Colour distribution in the Hong Kong feral cattle in the dry, intermediate and wet

365 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

366

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

368 156.20, $p < 0.0001$). Females are in general paler, with red being the most common coat colour in

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

370 (30.80%, 95%CI = 28.07 - 33.67). These differences are not consistent throughout the year, with

371 significant sexual differences in coat colour distribution between males and females in all months
372 ($p < 0.05$, Table S5), except in May ($\chi^2 = 8.63$, $p = 0.07$), June ($\chi^2 = 2.96$, $p = 0.56$), September ($\chi^2 =$
373 6.46, $p = 0.16$) and October ($\chi^2 = 8.92$, $p = 0.06$).

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

387 The likeliness for coat colour to change is significantly explained by seasonal variations ($F_{(5,}$
388 $_{1647)} = 5.71$, $p = 0.003$), with coat colours getting paler in the wet season while they get darker in
389 the dry season (Fig. 6). 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 6: 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.

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.

In artiodactyls, males tend to be both larger and longer than females (Cassini, 2020; Tombak *et al.*, 2024), similar to our findings that HK feral bulls were larger in all body size measures than HK feral cows. Domestication in bovids has led to greater sexual dimorphism with larger males (Polák & Frynta, 2009; McPherson & Chenoweth, 2012). Among cattle, milk breeds are the most sexually dimorphic, while draught breeds are the least dimorphic (Polák & Frynta,

2010). Additionally, cattle breeds from the tropics and subtropics are less sexually dimorphic than 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.

440 HK cattle exhibit seasonal changes in coat colour, with more individuals displaying paler
441 coats in the wet season and darker coats in dry season. Thermoregulation appears to be the
442 primary driver of seasonal coat colour changes in HK cattle, influenced by humidity and solar
443 radiation, as seen in other prey species facing high energetic costs from climate factors (Zimova
444 *et al.*, 2014; Kennah *et al.*, 2023). Darker coats are generally better suited to tropical and
445 subtropical environments, aligning with Gloger's rule (Kamilar & Bradley, 2011; Delhey, 2019; Ge
446 *et al.*, 2021). However, the thermal melanism hypothesis predicts that lighter coats can help
447 regulate heat gain and water loss in hot and humid climates (Delhey, 2019; Marcondes *et al.*,
448 2020). For instance, in springbok *(Antidorcas marsupialis),* individuals with paler coats thrive in
449 summer , while those with darker coats are better suited to winter climates (Hetem *et al.*, 2009).
450 Heat stress is a significant welfare concern in farmed cattle, negatively impacting behaviour and
451 physiology, which can compromise long-term health when climatic conditions exceed cattle
452 thermal neutral range (Cook *et al.*, 2007; Becker *et al.*, 2020; North *et al.*, 2023). Darker cattle
453 breeds tend to suffer more from excessive heat loads compared to breeds with paler coats
454 (Mader *et al.*, 2006; Brown-Brandl *et al.*, 2006). Similarly, coat colour variation within breeds leads
455 to individual differences in heat load, with black coated Holstein cattle having higher surface
456 temperature than white cattle (Façanha *et al.*, 2010; Santos *et al.*, 2017). Our findings show that
457 darker individuals have lower body condition, suggesting a higher cost associated with darker
458 coats, in alignment with previous findings in dairy cattle (Anzures-Olvera *et al.*, 2019). Humidity is
459 expected to significantly impact thermoregulation costs in tropical populations (Marcondes *et al.*,

460 2020), which supports our observation that humidity drives the magnitude of seasonal changes
461 in coat colour. Genes related to UV protection and heat tolerance have been identified in other
462 Chinese cattle breeds (Lei *et al.*, 2006; Gao *et al.*, 2017; Xia *et al.*, 2023). Overall, our results
463 support the thermal melanism hypothesis, as we found that temperature, humidity, and solar
464 radiation influence seasonal coat colour changes.

465 Our findings provide the first evidence of seasonal changes in coat colour in a subtropical
466 cattle population. While coat colour changes in cattle have been previously associated with age
467 (Schmutz, 2012) and with nutritional deficiencies, with for instance copper deficiency being
468 associated with paler coats in farmed cattle (Olkowski & Wojnarowicz, 2018). The association we
469 found between darker coats and lower body condition highlights that it is unlikely to be related
470 to nutritional deficiency and likely associated with seasonal patterns instead. Additionally,
471 repeatability of scores across the years supports the idea of seasonal patterns of coat colour
472 changes in HK cattle. In tropical ungulates, paler coats could be expected in the dry season for
473 camouflage against vegetation, while darker coats in the wet season provide background
474 matching for darker soil and foliage (see for instance Newell et al., 2021). However, our findings
475 do not support these expectations. Coat colour variability is influenced by a trade-off between
476 thermoregulation and predation risk (Beltran *et al.*, 2018; Zimova *et al.*, 2018; Kennah *et al.*,
477 2023). As HK feral cattle were farmed (and thus likely protected by farmers) when predators were
478 still present in HK, there may have been little to no pressure from predation risk on this population
479 historically. Hence, coat colouration of HK cattle may not serve a function as an anti-predatory

480 response, resulting in it not matching the background colours as would be expected in other free-
481 ranging ruminants with high predation pressure.

482 We found that darker coats were present in all seasons, although these were more
483 common in males and in the dry season. If darker coats impose higher thermoregulatory costs,
484 their persistence in subtropical environments like HK raises questions. Darker coats correlate with
485 higher androgens levels and reproductive success (Loehr *et al.*, 2008; Bro-Jørgensen &
486 Dabelsteen, 2008; Coulson *et al.*, 2011) as well as enhanced heat dissipation through skin
487 evaporation in Holstein cows (Maia *et al.*, 2005; Santos *et al.*, 2017). Variations in pigmentation
488 relate to behavioural differences (Tucker *et al.*, 2008; Stuart-Fox *et al.*, 2017), with darker
489 mammals often exhibiting greater dominance, fertility, aggression, and sexual activity (Côté &
490 Festa-Bianchet, 2001; Ducrest *et al.*, 2008; Mckinnon & Pierotti, 2010; Roulin, 2014). In giraffes
491 (*Giraffa camelopardalis*), darker males were more likely to live in smaller social groups and to
492 spend more time alone, reflecting different sexual strategies between paler and darker males,
493 with coat colour playing a role as a signal of competitive ability (Castles *et al.*, 2019). Similarly, in
494 eland (*Tragelaphus oryx*), acquiring a higher social status led to darkening of facial colouration,
495 highlighting a social function of phenotypic plasticity in coat colour in ungulates (Bro-Jørgensen
496 & Beeston, 2015). However, contrasting evidence exists with paler male Himalayan tahr
497 (*Hemitragus jemlahicus*) being larger, higher ranked and having a higher reproductive success
498 than their darker conspecifics (Lovari *et al.*, 2009, 2015; Fattorini *et al.*, 2024). Though cattle can
499 discriminate long wavelengths from medium wavelengths (Phillips & Lomas, 2001) suggesting

they would be able to discriminate red-based coat colours, further evidence on their ability to discriminate conspecifics based on coat colour and to adjust their behaviour is lacking, but may explain why darker coats persist in this population.

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

CONCLUSION

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

536 **REFERENCES**

537 AFCD. 2018. Stray Cattle and Buffalo Management Plan. *Agriculture, Fisheries and Conservation*
538 *Department*.

539 Allendorf FW, Hard JJ. 2009. Human-induced evolution caused by unnatural selection through
540 harvest of wild animals. *Proceedings of the National Academy of Sciences, USA* 106: 9987–9994.

541 Amin M. 2009. Intervention of genetic flow of the foreign cattle toward diversity of phenotype
542 expressions of local cattle in the district of Banyuwangi. *Biodiversitas Journal of Biological*
543 *Diversity* 11.

544 Anzures-Olvera F, Véliz FG, De Santiago A, García JE, Mellado J, Macías-Cruz U, Avendaño-Reyes
545 L, Mellado M. 2019. The impact of hair coat color on physiological variables, reproductive
546 performance and milk yield of Holstein cows in a hot environment. *Journal of Thermal Biology*
547 81: 82–88.

548 ASAB Ethical Committee, ABS Animal Care committee. 2022. Guidelines for the treatment of
549 animals in behavioural research and teaching. *Animal Behaviour* 183: I–XI.

550 Atmeh K, Andruszkiewicz A, Zub K. 2018. Climate change is affecting mortality of weasels due to
551 camouflage mismatch. *Scientific Reports* 8: 7648.

552 Barbato M, Reichel MP, Passamonti M, Low WY, Colli L, Tearle R, Williams JL, Ajmone Marsan P.
553 2020. A genetically unique Chinese cattle population shows evidence of common ancestry with
554 wild species when analysed with a reduced ascertainment bias SNP panel. *PLOS ONE* 15:
555 e0231162.

556 Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4.
557 *Journal of Statistical Software* 67.

558 Becker CA, Collier RJ, Stone AE. 2020. Invited review: Physiological and behavioral effects of
559 heat stress in dairy cows. *Journal of Dairy Science* 103: 6751–6770.

560 Beltran RS, Burns JM, Breed GA. 2018. Convergence of biannual moulting strategies across birds
561 and mammals. *Proceedings of the Royal Society B: Biological Sciences* 285: 20180318.

562 Berger J. 2012. Estimation of body-size traits by photogrammetry in large mammals to inform
563 conservation. *Conservation Biology* 26: 769–777.

Berglund A, Bisazza A, Pilastro A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* 58: 385–399.

Bro-Jørgensen J. 2007. The intensity of sexual selection predicts weapon size in male bovids. *Evolution* 61: 1316–1326.

Bro-Jørgensen J. 2012. Longevity in bovids is promoted by sociality, but reduced by sexual selection. *PLoS ONE* 7: e45769.

Bro-Jørgensen J, Beeston J. 2015. Multimodal signalling in an antelope: fluctuating facemasks and knee-clicks reveal the social status of eland bulls. *Animal Behaviour* 102: 231–239.

Bro-Jørgensen J, Dabelsteen T. 2008. Knee-clicks and visual traits indicate fighting ability in eland antelopes: multiple messages and back-up signals. *BMC Biology* 6: 47.

Brown-Brandl TM, Nienaber JA, Eigenberg RA, Mader TL, Morrow JL, Dailey JW. 2006. Comparison of heat tolerance of feedlot heifers of different breeds. *Livestock Science* 105: 19–26.

Cambreling S, Gaillard JM, Lemaître JF, Smith AF, David A, Ciuti S. 2025. Antler size decreases with increasing age: evidence of reproductive senescence in male Fallow Deer (*Dama dama*) (B McMillan, Ed.). *Journal of Mammalogy*: gyae154.

Canale CI, Ozgul A, Allainé D, Cohas A. 2016. Differential plasticity of size and mass to environmental change in a hibernating mammal. *Global Change Biology* 22: 3286–3303.

Capellini I, Gosling LM. 2006. Evolution of fighting structures in the hartebeest. *Evolutionary Ecology Research* 8: 997–1011.

Caro T. 2005. The Adaptive Significance of Coloration in Mammals. *BioScience* 55: 125.

Caro T, Brockelsbury K, Ferrari A, Koneru M, Ono K, Rowe ZW, Touche E, Walker H, Stankowich T. 2022. On the evolution of distinctive natal coat coloration in primates. *American Journal of Biological Anthropology* 177: 530–539.

Caro TM, Graham CM, Stoner CJ, Flores MM. 2003. Correlates of horn and antler shape in bovids and cervids. *Behavioral Ecology and Sociobiology* 55: 32–41.

Cassini MH. 2020. Sexual size dimorphism and sexual selection in artiodactyls. *Behavioral Ecology* 31: 792–797.

Castles MP, Brand R, Carter AJ, Maron M, Carter KD, Goldizen AW. 2019. Relationships between male giraffes' colour, age and sociability. *Animal Behaviour* 157: 13–25.

Cloudsley-Thompson JL. 1999. Multiple factors in the evolution of animal coloration. *Naturwissenschaften* 86: 123–132.

Clutton-Brock T. 2017. Reproductive competition and sexual selection. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372: 20160310.

Cook NB, Mentink RL, Bennett TB, Burgi K. 2007. The effect of heat stress and lameness on time budgets of lactating dairy cows. *Journal of Dairy Science* 90: 1674–1682.

Côté SD, Festa-Bianchet M. 2001. Life-history correlates of horn asymmetry in mountain goats. *Journal of Mammalogy* 82: 389–400.

Coulson T, MacNulty DR, Stahler DR, vonHoldt B, Wayne RK, Smith DW. 2011. Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. *Science* 334: 1275–1278.

D'Ammando G, Franks DW, Bro-Jørgensen J. 2022. Living in mixed-sex groups limits sexual selection as a driver of pelage dimorphism in bovids. *Behavioral Ecology* 33: 541–548.

Davis EB, Brakora KA, Stilson KT. 2014. Evolution, development and functional role of horns in cattle. In: Melletti M, Burton J, eds. *Ecology, Evolution and Behaviour of Wild Cattle*. Cambridge University Press, 72–82.

Delhey K. 2019. A review of Gloger's rule, an ecogeographical rule of colour: definitions, interpretations and evidence. *Biological Reviews* 94: 1294–1316.

D'Occhio MJ, Baruselli PS, Campanile G. 2019. Influence of nutrition, body condition, and metabolic status on reproduction in female beef cattle: A review. *Theriogenology* 125: 277–284.

Ducrest A, Keller L, Roulin A. 2008. Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology & Evolution* 23: 502–510.

Dudgeon D, Corlett R. 2010. *Hills and streams: an ecology of Hong Kong*. Hong Kong: Hong Kong University Press.

Emlen DJ. 2008. The Evolution of Animal Weapons. *Annual Review of Ecology, Evolution, and Systematics* 39: 387–413.

Façanha DAE, Silva RGD, Maia ASC, Guilhermino MM, Vasconcelos AMD. 2010. Anual variation of morphologic traits and hair coat surface temperature of Holstein cows in semi-arid environment. *Revista Brasileira de Zootecnia* 39: 837–844.

Fattorini N, Tizzani P, Dematteis A, Lovari S. 2024. Do honest signals or piercing weapons determine rank in a polygynous ungulate? *Biological Journal of the Linnean Society* 142: 417–423.

Ferreira S, Funston PJ. 2010. Age assignment to individual African lions. *South African Journal of Wildlife Research* 40: 1–9.

Food and Agriculture Organization of the United Nations. 2021. FAOSTAT. *Food and Agriculture Organization of the United Nations*.

Food And Organizations of the United Nations. 2011. *Phenotypic characterization of animal genetic resources*. FAO.

Fulgione D, Rippa D, Buglione M, Trapanese M, Petrelli S, Maselli V. 2016. Unexpected but welcome. Artificially selected traits may increase fitness in wild boar. *Evolutionary Applications* 9: 769–776.

Gao Y, Gautier M, Ding X, Zhang H, Wang Y, Wang X, Faruque MO, Li J, Ye S, Gou X, Han J, Lenstra JA, Zhang Y. 2017. Species composition and environmental adaptation of indigenous Chinese cattle. *Scientific Reports* 7: 16196.

Ge D, Feijó A, Abramov AV, Wen Z, Liu Z, Cheng J, Xia L, Lu L, Yang Q. 2021. Molecular phylogeny and morphological diversity of the *Niviventer fulvescens* species complex with emphasis on species from China. *Zoological Journal of the Linnean Society* 191: 528–547.

Goodenough AE, Smith AL, Stubbs H, Williams R, Hart AG. 2012. Observer variability in measuring animal biometrics and fluctuating asymmetry when using digital analysis of photographs. *Annales Zoologici Fennici*. BioOne, 81–92.

Grymala | Mobile Apps Development. 2022. Prime Ruler.

Hameed A, Schlecht E, Tariq M, Buerkert A, Scheper C, König S, Roessler R. 2022. Phenotypic and genetic diversity of domestic yak (*Bos grunniens*) in high-altitude rangelands of Gilgit-Baltistan, Pakistan. *Journal of Animal Breeding and Genetics*: jbg.12730.

Hetem RS, De Witt BA, Fick LG, Fuller A, Kerley GIH, Meyer LCR, Mitchell D, Maloney SK. 2009. Body temperature, thermoregulatory behaviour and pelt characteristics of three colour morphs

of springbok (*Antidorcas marsupialis*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 152: 379–388.

Hong Kong Observatory. 2020. Climate of Hong Kong. *Hong Kong Observatory*.

Islam MR. 2018. Sample Size and Its Role in Central Limit Theorem (CLT). *International Journal of Physics and Mathematics* 1: 37–47.

JASP Team. 2022. JASP.

Jones MR, Mills LS, Alves PC, Callahan CM, Alves JM, Lafferty DJR, Jiggins FM, Jensen JD, Melo-Ferreira J, Good JM. 2018. Adaptive introgression underlies polymorphic seasonal camouflage in snowshoe hares. *Science* 360: 1355–1358.

Kamilar JM, Bradley BJ. 2011. Interspecific variation in primate coat colour supports Gloger's rule: Primate coloration supports Gloger's rule. *Journal of Biogeography* 38: 2270–2277.

Kennah JL, Peers MJL, Vander Wal E, Majchrzak YN, Menzies AK, Studd EK, Boonstra R, Humphries MM, Jung TS, Kenney AJ, Krebs CJ, Boutin S. 2023. Coat color mismatch improves survival of a keystone boreal herbivore: Energetic advantages exceed lost camouflage. *Ecology* 104: e3882.

Knierim U, Irrgang N, Roth BA. 2015. To be or not to be horned—Consequences in cattle. *Livestock Science* 179: 29–37.

Lê S, Josse J, Husson F. 2008. FactoMineR : An *R* Package for Multivariate Analysis. *Journal of Statistical Software* 25.

Legislative Council Panel on Food Safety and Environmental Hygiene. 2017. *Feral Cattle Care and Welfare Issues in Sai Kung*.

Lei CZ, Chen H, Zhang HC, Cai X, Liu RY, Luo LY, Wang CF, Zhang W, Ge QL, Zhang RF, Lan XY, Sun WB. 2006. Origin and phylogeographical structure of Chinese cattle. *Animal Genetics* 37: 579–582.

Loehr J, Carey J, Ylönen H, Suhonen J. 2008. Coat darkness is associated with social dominance and mating behaviour in a mountain sheep hybrid lineage. *Animal Behaviour* 76: 1545–1553.

Lovari S, Fattorini N, Boesi R, Bocci A. 2015. Male ruff colour as a rank signal in a monomorphic-horned mammal: behavioural correlates. *The Science of Nature* 102: 39.

Lovari S, Pellizzi B, Boesi R, Fusani L. 2009. Mating dominance amongst male Himalayan tahr: Blonds do better. *Behavioural Processes* 81: 20–25.

Lovich JE, Gibbons JW. 1992. A review of techniques for quantifying sexual size dimorphism. *Growth Development and Aging* 56: 269–269.

Lukas D, Clutton-Brock T. 2014. Costs of mating competition limit male lifetime breeding success in polygynous mammals. *Proceedings of the Royal Society B: Biological Sciences* 281: 20140418.

Lundrigan B. 1996. Morphology of horns and fighting behavior in the family Bovidae. *Journal of Mammalogy* 77: 462–475.

Mader TL, Davis MS, Brown-Brandl T. 2006. Environmental factors influencing heat stress in feedlot cattle. *Journal of Animal Science* 84: 712–719.

Maia ASC, Gomes Da Silva R, Bertipaglia ECA. 2005. Environmental and genetic variation of the effective radiative properties of the coat of Holstein cows under tropical conditions. *Livestock Production Science* 92: 307–315.

Marcondes RS, Stryjewski KF, Brumfield RT. 2020. Testing the simple and complex versions of Gloger's rule in the Variable Antshrike (*Thamnophilus caerulescens*, Thamnophilidae). *The Auk* 137: ukaa026.

McCullough EL, Miller CW, Emlen DJ. 2016. Why sexually selected weapons are not ornaments. *Trends in Ecology & Evolution* 31: 742–751.

McElligott AG, Gammell MP, Harty HC, Paini DR, Murphy DT, Walsh JT, Hayden TJ. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behavioral Ecology and Sociobiology* 49: 266–272.

Mckinnon JS, Pierotti MER. 2010. Colour polymorphism and correlated characters: genetic mechanisms and evolution: Genetics of colour and correlated traits. *Molecular Ecology* 19: 5101–5125.

McPherson FJ, Chenoweth PJ. 2012. Mammalian sexual dimorphism. *Animal Reproduction Science* 131: 109–122.

Morandi K, Lindholm AK, Lee DE, Bond ML. 2022. Phenotypic matching by spot pattern potentially mediates female giraffe social associations. *Journal of Zoology* 318: 147–157.

Nasoori A. 2020. Formation, structure, and function of extra-skeletal bones in mammals. *Biological Reviews* 95: 986–1019.

Newell C, Walker H, Caro T. 2021. Pig pigmentation: testing Gloger's rule. *Journal of Mammalogy* 102: 1525–1535.

North MA, Franke JA, Ouweneel B, Trisos CH. 2023. Global risk of heat stress to cattle from climate change. *Environmental Research Letters* 18: 094027.

Oli MK, Kenney AJ, Boonstra R, Boutin S, Murray DL, Peers MJL, Gilbert BS, Jung TS, Chaudhary V, Hines JE, Krebs CJ. 2023. Does coat colour influence survival? A test in a cyclic population of snowshoe hares. *Proceedings of the Royal Society B: Biological Sciences* 290: 20221421.

Olkowski A, Wojnarowicz C. 2018. Problems associated with excess of sulfur in drinking water sources: livestock producers' perspective. *Industry News*.

Otte PJ, Cromsigt JPGM, Smit C, Hofmeester TR. 2024. Snow cover-related camouflage mismatch increases detection by predators. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 341: 327–337.

Ouchene-Khelifi NA, Ouchene N, Da Silva A, Lafri M. 2018. Multivariate characterization of phenotypic traits of Arabia, the main Algerian goat breed. *Livest. Res. Rural Dev* 30.

Phillips CJC, Lomas CA. 2001. The perception of color by cattle and its influence on behavior. *Journal of Dairy Science* 84: 807–813.

Pinkham R, Koon KK, To J, Chan J, Vial F, Gomm M, Eckery DC, Massei G. 2022. Long-term effect of a GnRH-based immunocontraceptive on feral cattle in Hong Kong. *PLOS ONE* 17: e0272604.

Polák J, Frynta D. 2009. Sexual size dimorphism in domestic goats, sheep, and their wild relatives: sexual size dimorphism. *Biological Journal of the Linnean Society* 98: 872–883.

Polák J, Frynta D. 2010. Patterns of sexual size dimorphism in cattle breeds support Rensch's rule. *Evolutionary Ecology* 24: 1255–1266.

Prinsloo ND, Postma M, De Bruyn PJN. 2021. How unique is unique? Quantifying geometric differences in stripe patterns of Cape mountain zebra, *Equus zebra zebra* (Perissodactyla: Equidae). *Zoological Journal of the Linnean Society* 191: 612–625.

R Core Team. 2020. R: A Language and Environment for Statistical Computing.

Roulin A. 2014. Melanin-based colour polymorphism responding to climate change. *Global Change Biology* 20: 3344–3350.

Santos SGCG, Saraiva EP, Pimenta Filho EC, Gonzaga Neto S, Fonsêca VFC, Pinheiro ADC, Almeida MEV, De Amorim MLCM. 2017. The use of simple physiological and environmental measures to estimate the latent heat transfer in crossbred Holstein cows. *International Journal of Biometeorology* 61: 217–225.

Schmutz SM. 2012. Genetics of Coat Color in Cattle. In: Womack JE, ed. *Bovine Genomics*. Wiley, 20–33.

Schulz AK, Kaufmann LV, Reveyaz N, Ritter C, Hildebrandt T, Brecht M. 2024. Elephants develop wrinkles through both form and function. *Royal Society Open Science* 11: 240851.

Shuker DM, Kvarnemo C. 2021. The definition of sexual selection. *Behavioral Ecology* 32: 781–794.

Stankowich T, Caro T. 2009. Evolution of weaponry in female bovids. *Proceedings of the Royal Society B: Biological Sciences* 276: 4329–4334.

Stockwell CA, Hendry AP, Kinnison MT. 2003. Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution* 18: 94–101.

Stoner CJ. 2003. Ecological and behavioral correlates of coloration in artiodactyls: systematic analyses of conventional hypotheses. *Behavioral Ecology* 14: 823–840.

Stuart-Fox D, Newton E, Clusella-Trullas S. 2017. Thermal consequences of colour and near-infrared reflectance. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372: 20160345.

Tarugara A, Clegg BW, Gandiwa E, Muposhi VK, Wenham CM. 2019. Measuring body dimensions of leopards (*Panthera pardus*) from camera trap photographs. *PeerJ* 7: e7630.

Tasdemir S, Urkmez A, Inal S. 2011. Determination of body measurements on the Holstein cows using digital image analysis and estimation of live weight with regression analysis. *Computers and Electronics in Agriculture* 76: 189–197.

Tombak KJ, Hex SBSW, Rubenstein DI. 2024. New estimates indicate that males are not larger than females in most mammal species. *Nature Communications* 15: 1872.

Tucker CB, Rogers AR, Schütz KE. 2008. Effect of solar radiation on dairy cattle behaviour, use of shade and body temperature in a pasture-based system. *Applied Animal Behaviour Science* 109: 141–154.

Wacker CB, McAllan BM, Körtner G, Geiser F. 2016. The functional requirements of mammalian hair: a compromise between crypsis and thermoregulation? *The Science of Nature* 103: 53.

Weik F, Archer JA, Morris ST, Garrick DJ, Miller SP, Boyd AM, Cullen NG, Hickson RE. 2021. Live weight and body condition score of mixed-aged beef breeding cows on commercial hill country farms in New Zealand. *New Zealand Journal of Agricultural Research*: 1–16.

Xia X, Qu K, Wang Y, Sinding MHS, Wang F, Hanif Q, Ahmed Z, Lenstra JA, Han J, Lei C, Chen N. 2023. Global dispersal and adaptive evolution of domestic cattle: a genomic perspective. *Stress Biology* 3: 8.

Zhang GX, Wang ZG, Chen WS, Wu CX, Han X, Chang H, Zan LS, Li RL, Wang JH, Song WT, Xu GF, Yang HJ, Luo YF. 2007. Genetic diversity and population structure of indigenous yellow cattle breeds of China using 30 microsatellite markers. *Animal Genetics* 38: 550–559.

Zhang ALN, Wu BP, Jiang CXH, Xuan DCZ, Ma EYH, Zhang FYA. 2018. Development and validation of a visual image analysis for monitoring the body size of sheep. *Journal of Applied Animal Research* 46: 1004–1015.

Zimova M, Hackländer K, Good JM, Melo-Ferreira J, Alves PC, Mills LS. 2018. Function and underlying mechanisms of seasonal colour moulting in mammals and birds: what keeps them changing in a warming world? *Biological Reviews* 93: 1478–1498.

Zimova M, Mills LS, Lukacs PM, Mitchell MS. 2014. Snowshoe hares display limited phenotypic plasticity to mismatch in seasonal camouflage. *Proceedings of the Royal Society B: Biological Sciences* 281: 20140029.

SUPPORTING INFORMATION

Sexual dimorphism and phenotypic plasticity in a feral free-ranging bovid *Bos taurus* (Artiodactyla: Bovidae).

Includes:

Tables:

Table S1: Number of female and male cattle scored in each herd and overall number of individuals where at least one phenotype traits could be scored for each herd and country park.

Table S2: Relations between the five measures of cattle body size (wither height, hip height, body length, hip width and chest depth) used to measure Hong Kong feral cattle body size, as evaluated by Spearman's correlations.

Table S3: Description of the eight coat colour scores removed from further analysis due to mode (most frequent value between fore, middle and hind body coat colour) not being obtained.

Table S4: Climate variables extracted from the Hong Kong Observatory (HKO) for each month when coat colour scoring was conducted.

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.