1 **Evolution of the ungulate dewlap:**

2 **Thermoregulation rather than sexual selection or predator deterrence?**

3

4 Jakob Bro-Jørgensen

5

6 Mammalian Behaviour & Evolution Group, Department of Evolution, Ecology & Behaviour,

7 Institute of Integrative Biology, University of Liverpool, Leahurst Campus, Neston CH64

8 7TE, United Kingdom

9 T: +44 (0)151 794 6009. F: +44 (0)151 794 6107. E: bro@liv.ac.uk

10   ABSTRACT

11   **Background:** Dewlaps are iconic features of several ungulate species and, although a role in

12   signalling has been postulated, their function remains largely unexplored. We recently failed to find

13   any age-independent link between dewlap size and social status in the common eland (*Tragelaphus*

14   *oryx*), pointing to the possibility that sexual selection may not be the primary cause of dewlap

15   evolution in ungulates. Here I use a two-pronged approach to test hypotheses on the function of

16   ungulate dewlaps: an interspecific comparative analysis of bovids and deer, and an intraspecific study

17   of eland antelopes in the wild.

18   **Results:** Across species, the presence of dewlaps in males was not found to be associated with sexual

19   size dimorphism, a commonly used measure of the intensity of sexual selection. The presence of

20   dewlaps was, however, linked to very large male body size (>400kg), which agrees with a

21   thermoregulatory function as lower surface/volume-ratio counteracts heat dissipation in large-bodied

22   species. In eland antelopes, large dewlap size was associated with higher, rather than lower, incidence

23   of claw-marks (independently of age), a result which speaks against the dewlap as a predator deterrent

24   and rather indicates a predation cost of the structure.

25   **Conclusion:** The findings suggest that, although an additional function in communication should not

26   be ruled out, the dewlap of ungulates may contrast with that of lizards and birds in thermoregulation

27   being a primary function.

28

29   **Keywords:** Natural selection; Signal evolution; Ornaments; Male competition; Female Mate Choice;

30   Bovidae; Cervidae; Mammalia.

31   BACKGROUND

32   Extravagant ornament-like male morphologies that are sexually dimorphic are often assumed to have

33   evolved by sexual selection to signal individual quality, either owing to female mate choice, male-

34   male combat or both [1,2]. However, often other explanations are possible and the importance of

35   examining alternative hypotheses has recently been stressed [3]. Dewlaps, i.e. loose skin flaps

36   hanging from the neck, are a case in point. These striking yet enigmatic structures are found in various

37   vertebrate taxa, notably iguanid and agamid lizards, birds and ungulates. To date, studies of dewlap

38   evolution and function have focused almost entirely on lizards and, to a lesser extent, birds. In lizards,

39   a function of the often colourful dewlap in intraspecific communication is indicated by the fact that

40   the dewlap is moveable and dewlap extensions constitute part of male territorial displays, with the

41   display rate increasing during both intra- and intersexual encounters [4,5]. However, recent studies

42   suggest that rather than directly reflecting male competitive ability, a selective advantage of the

43   dewlap may arise from drawing attention to head-bob and push-up displays [3]. In birds, dewlaps –

44   often referred to as wattles – are present as a diverse set of fleshy excrescences pending from the neck

45   in several taxa (e.g. cassowaries and galliformes). Like in lizards, they are more pronounced in males

46   than females and are thought to function as sexual signals of male quality [6]. The dewlap in

47   ungulates has so far evaded rigorous investigation and its function remains a puzzle. In spite of some

48   structural similarity with the dewlaps of lizards and birds, whether ungulate dewlaps have evolved as

49   a result of the same selective pressures remains an open question.

50   As in lizards and birds, sexual dimorphism is pronounced in the dewlap of ungulates, but both sexual

51   and natural selection could have affected the sexes differently to create this pattern. According to the

52   'Sexual Selection Hypothesis', the dewlap of ungulates, like in lizards and birds, has evolved because

53   of a function in intra- and/or intersexual signalling. Different scenarios can be imagined. Firstly, the

54   dewlap may be an honest signal of age-related fighting ability. Evidence from the common eland

55   (*Tragelaphus oryx*) shows that dewlaps increase monotonically in size with age and the dewlap could

56   thus provide meaningful information about fighting skills gained through experience [7,8]. Another

57   possibility is that the dewlap serves a deceptive function during rival assessment by exaggerating the

58 body size perceived by opponents [3,9]. Here it is worth noting that agonistic encounters in many

59 ungulate species involve broadside displays in which males assess the body size of rivals in lateral

60 view, the perspective from which the two-dimensional dewlap creates the most convincing illusion

61 (Fig. 1).

62 Alternatively, according to the 'Predator Deterrent Hypothesis', the dewlap has its selective advantage

63 in communication with predators rather than conspecifics [10]. Small ungulates are vulnerable to a

64 wider range of predators than large ungulates [11,12], and by enhancing apparent body size, dewlaps

65 could thus deter predator attacks. Similar intimidating effects can explain a wide range of antipredator

66 responses in vertebrates: piloerection in mammals, feather puffing in birds, anterior flattening in

67 snakes, and body inflation in toads, frogs and fishes (although the latter also interferes with

68 swallowing) [13]. Also conceivable is that the dewlap has evolved as a condition-dependent handicap

69 signal [14]. According to this idea, the dewlap makes it easier for predators to get a hold on their prey,

70 and because only 'high quality' individuals can develop large dewlaps without incurring prohibitive

71 predation costs, the structure signals that an individual will be difficult to kill, thereby discouraging

72 attacks. Such a condition-dependent handicap signal could also function as a 'quality' indicator that

73 intimidates rivals and/or attracts mates, hence showing a potential link to the Sexual Selection

74 Hypothesis.

75 Finally, according to the 'Thermoregulation Hypothesis', the selective advantage of the dewlap comes

76 from facilitating the dissipation of excess body heat by convection, an idea proposed to explain the

77 presence of dewlaps in dinosaurs [15,16]. Overheating is a particular challenge for larger species

78 owing to their lower surface/volume ratio, and the potential force of this selective pressure is

79 illustrated by the evolution of large ears in elephants [17], where it is also noteworthy that the larger

80 species has the proportionally largest ears (i.e. 6,300kg of large males in the African elephant

81 *Loxodonta africana* vs. 5,300kg in the Asian elephant *Elaphus maximus*). Infrared measurements have

82 confirmed the dewlap in the common eland as a site of high heat loss [18].

83   From these hypotheses follow various predictions at both the inter- and intraspecific level, and in this

84   paper, I therefore combine a comparative approach, investigating differences between species, with an

85   intraspecific field study on the common eland, a nomadic savannah antelope in which males develop

86   large dewlaps drooping up to more than 40cm beneath their necks. Quantifying predation is

87   notoriously difficult in ungulate field studies because attacks usually take place when observation is

88   difficult, i.e. at night and in dense vegetation. As a proxy measure, I therefore use claw-marks, the

89   usefulness of which as an indicator of predation attempts have recently been highlighted [19].

90   Because the dewlap in ungulates is sexually dimorphic, the analyses are focused on males, where the

91   structure is most pronounced.

92   According to the Sexual Selection Hypothesis, I predict that the presence of dewlaps among species is

93   linked to sexual body size dimorphism, a frequently used index for the intensity of sexual selection

94   [2,3,20]. According to the Predator Deterrent Hypothesis, where large dewlap size is associated with

95   reduced attack rate by predators, I predict a negative correlation between dewlap size and the

96   prevalence of claw-marks within species. Specifically, if dewlaps have evolved owing to the handicap

97   principle, I predict that scars from past predation attempts will be located on the dewlap, by which the

98   animal is hypothesized to be seized. According to the Thermoregulation Hypothesis, I predict that

99   dewlaps are associated with large-bodied species, and that a threshold exists above which the low

100   surface/volume ratio favours the evolution of dewlaps to facilitate heat dissipation.

101

102   METHODS

103   *Interspecific study: comparative analysis*

104   A dataset was compiled focusing on all extant bovids and cervids including the following variables:

105   presence/absence of dewlaps in males, mean male body mass, and sexual size dimorphism (SSD),

106   which was calculated as male body mass divided by female body mass. The data were obtained from

107   the sources: [9,20-27]. The presence of dewlaps in males was entered as the binary response variable

108   in a phylogenetic generalized linear mixed model for binary data (binary PGLMM). The analyses

109   were performed in R [28] with the packages 'ape' [29,30] and 'caper' [31]. The explanatory variables

110   were *male body mass* and *SSD* (both $\log_{10}$-transformed); these were tested in bivariate models as well

111   as in a multivariate model with backward elimination of non-significant predictors ($P < 0.05$). Control

112   for evolutionary dependence was based on the phylogenetic tree reported in [32].

113

114   *Intraspecific study: eland field study*

115   Study system: Eland males were studied between 2005 and 2013 in a 710 km^2 area within the Masai

116   Mara National Reserve and Olare Orok, Motorogi and Naboisho conservancies in Kenya. The habitat

117   was dominated by open grass plains with only scattered thickets and hence good visibility. The eland

118   is a large, sexually dimorphic antelope (males: 450–942 kg, females: 317–470 kg [33]), foraging on

119   both grass and browse [34]. They are non-territorial and gregarious, their main social units being

120   solitary males, male herds of 2–20 individuals, and larger mixed herds with up to more than a hundred

121   individuals [8]. The main predator of male eland in the study area is the lion (*Panthera leo*); younger

122   animals are occasionally killed by spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*) and,

123   even more rarely, cheetahs (*Acinonyx jubatus*) [35-38].

124   Data collection: As part of a larger study, data were collected annually between February and May

125   during the wet season by surveying the study area for eland in a four-wheel-drive vehicle on a total of

126   266 days. For each observation, the identity of males were recorded based on their distinctive stripe

127   pattern, ear nicks, scars, and tail and horn abnormalities, with identification details stored on paper

128   sheets and in a digital library of bilateral photographs. For morphological measurements using

129   photometry, individuals were photographed while standing relaxed, and their distance was measured

130   by laser rangefinder (Bushnell Yardage pro 800). The measurements in pixels on the photographs

131   were converted to the metric scale using a calibrated reference scale based on photographs of a 1 m

132   pole at a range of distances [7]. Body size was measured as the body depth, i.e. the maximum vertical

133   girth of the chest. Dewlap size was measured by the maximum vertical droop beneath the neck.

134   Repeatability was high [7]. Scars from the claws of big cats, distinctive in the alignment of 4–5

135 scratches [19] (Fig. 2), were recorded as present/absent in the field, with supplementary observations

136 in the digital photo library. Age was estimated upon first sighting of an individual, primarily based on

137 horn rotation, horn wear, and development of hair fringes and hair tufts, following the protocol

138 described in [8]. Complete measurements were obtained for 212 individual males.

139 Statistical analysis: The presence/absence of claw-marks was modelled as the response variable in two

140 multivariate logistic regression models, a generalized linear mixed model (GzLMM) and a

141 generalized linear model (GzLM). In the GzLMM, male identity was entered to control for correlated

142 random effects owing to multiple measurements from the same individuals, whereas only one,

143 randomly selected, observation per male was included in the GzLM. In both models, dewlap droop

144 was included as a predictor variable, together with age and body size in order to control for

145 confounding effects. Non-significant predictors were excluded by backward elimination ($P < 0.05$),

146 and results relating to the non-significant predictors refer to their separate inclusion in the final model.

147 Variance inflation factors (VIFs) were calculated to assess the potential for multicollinearity between

148 dependent variables to affect the results [39]. These analyses were performed in SPSS version 21

149 (IBM, Armonk, NY, U.S.A.).

150

151 RESULTS

152 *Interspecific study: comparative analysis*

153 Among species, the presence of dewlaps in males was predicted by large male body mass, but not by

154 large SSD (Table 1). These results agree with the Thermoregulation Hypothesis and speak against the

155 Sexual Selection Hypothesis. All the species in which males had dewlaps were characterized by a

156 mean male body mass above 400 kg, i.e. gaur (*Bos frontalis*, 848kg), kouprey (*Bos sauveli*, approx.

157 800 kg), banteng (*Bos javanicus*, 750 kg), giant eland (*Tragelaphus derbianus*, 680kg), common

158 eland (647 kg), and moose (*Alces alces*, 440 kg); in less than 3% of the species without dewlap did

159 males weigh above this threshold (i.e. five out of 171 species; see Discussion).

7

160

161   *Intraspecific study: eland field study*

162   The incidence of claw-marks was positively, rather than negatively, related to dewlap size (logistic

163   GzLMM: N = 381 observations on 212 males [34 of which were observed both with and without

164   scars]; intercept: 3.67, P < 0.001; dewlap: t = 4.96, P < 0.001, VIF = 2.144; age: t = 1.553, P = 0.122,

165   VIF = 2.596; body size: t = 0.385, P = 0.700, VIF = 2.118; logistic GzLM: N = 212 males: intercept:

166   3.05, P < 0.001; dewlap: : χ^2 = 8.53, P = 0.004, VIF = 2.178; age: χ^2 = 0.823, P = 0.364, VIF = 2.602;

167   body size: χ^2 = 0.028, P = 0.868, VIF = 2.113; Figure 3a). This speaks against the Predator Deterrent

168   Hypothesis and rather suggests a predation cost of large dewlaps. The robustness of the results to

169   multicollinearity between dependent variables is supported by all VIFs being significantly below the

170   threshold of 5. Contrary to the proposition that dewlaps may be condition-dependent handicaps, scars

171   were not observed on the dewlap itself, with the majority of claw-marks located on the rump and

172   flanks. The incidence of claw-marks increased from below 20% at 2 years to above 50% in animals of

173   9 years and above (Figure 3b).

174

175   DISCUSSION

176   On the balance of the current evidence, benefits from thermoregulation emerge as a plausible main

177   driver of the evolution of the ungulate dewlap (Table 2). Dewlaps have evolved independently among

178   the very largest species within several ungulate radiations, namely the bovines, the tragelaphines and

179   the cervids. Overheating is a particular problem for large species in hot climates, and the five species,

180   in which males weigh above the 400 kg threshold but have not evolved dewlaps, either live in cold

181   areas or have evolved alternative, behavioural, cooling mechanisms. The African buffalo (*Syncerus*

182   *caffer*, 643 kg) and the water buffalo (*Bubalis bubalis*, 1,200 kg) regularly cool their body

183   temperature by wallowing, and the wild yak (*Bos grunniens*, 591 kg), American bison (*Bison bison*,

184   795 kg) and European bison (*Bison bonasus*, 718 kg) inhabit boreal and temperate climates.

185   Neither the present interspecific study, nor our earlier results from the intraspecific study, provides

186   support for the Sexual Selection Hypothesis. In male eland antelopes, we found no link between

187   dewlap size and status as master bull in mixed-sex herds, and an association with dominance status in

188   all-male herds disappeared after controlling for age [8]. Consistent with this, in the present study

189   dewlaps were not found to have evolved more often in those species where pronounced sexual size

190   dimorphism suggests intense sexual selection. While the sexual dimorphism of the dewlap itself,

191   which is often minimal or absent in female ungulates, is consistent with the Sexual Selection

192   Hypothesis, it is also consistent with the Thermoregulation Hypothesis as females are markedly

193   smaller than males in all species with dewlaps; females are indeed close to the 400 kg threshold with

194   weights around 350–450 kg in all species except the gaur (702 kg) and possibly the kouprey (no data).

195   At present, the most parsimonious interpretation of the link between claw-marks and large dewlap

196   size is that benefits of large dewlaps in other contexts trade off against costs from increased predation

197   risk, possibly because of lower running speed. However, conceivable is also an alternative

198   explanation derived from the idea of the dewlap as a sexually selected handicap: rather than signalling

199   the ability to flee, the dewlap could signal the ability to successfully fight off predators, in which case

200   an association between large dewlaps and the presence of scars would indeed be expected. Still,

201   against expectation remains the absence of scars on the dewlap itself since this is where the animals

202   are hypothesized to be seized. At 30%, the proportion of adult eland males with claw-marks,

203   presumably primarily from lions, was comparable to figures found in another large savannah

204   herbivore which share the lion as its main predator: the prevalence of claw-marks on adult female

205   giraffes (*Giraffa camelopardalis*) in three study areas within the Serengeti-Mara ecosystem was found

206   to be 4%, 26% and 32% [19]. The prevalence of claw-marks may be related to the observation that

207   eland do not usually flee from lions [33].

208

209   CONCLUSIONS

210   All in all, the present evidence suggests that the dewlap in ungulates may be the result of convergent

211   evolution under different selective pressures than those thought to underlie dewlaps in lizards and

212   birds. Attaining very large body sizes in hot environments, the ungulate species in which dewlaps

213   have evolved face a significant challenge to dissipate excess body heat. The structure is thus likely to

214   facilitate temperature regulation, but a trade-off in terms of enhanced predation risk is suggested by

215   the higher incidence of claw-marks in individuals with large dewlaps. Ruling out a communicative

216   function of the dewlap on the basis of the present study would be premature and this remarkable trait,

217   which has attracted considerable scientific attention in other taxa, warrants further study in ungulates.

218

219   DECLARATIONS

227

228   REFERENCES

229   1. Darwin C. The descent of Man. 2nd ed. New York: Prometheus Books; 1874.

230   2. Andersson M. Sexual selection. Princeton, NJ: Princeton University Press; 1994.

231   3. Ord TJ, Klomp DA, Garcia-Porta J, Hagman M. Repeated evolution of exaggerated dewlaps and

232   other throat morphology in lizards. J Evol Biol. 2015;28:1948-1964.

233   4. Driessens T, Vanhooydonck B, Van Damme R Deterring predators, daunting opponents or drawing

234   partners? Signaling rates across diverse contexts in the lizard *Anolis sagrei*. Behav Ecol Sociobiol.

235   2014;68:173-184.

236   5. Driessens T, Huyghe K, Vanhooydonck B, Van Damme R. Messages conveyed by assorted facets

237   of the dewlap, in both sexes of *Anolis sagrei*. Behav Ecol Sociobiol. 2015;69:1251-1264.

238   6. Ohlsson T, Smith HG, Raberg L, Hasselquist D. Pheasant sexual ornaments reflect

239   nutritional conditions during early growth. Proc R Soc Lond B. 2002;269:21-27.

240   7. Bro-Jørgensen J, Dabelsteen T. Knee-clicks and visual traits indicate fighting ability in eland

241   antelopes: multiple messages and back-up signals. BMC Biol. 2008;6:e47.

242   8. Bro-Jørgensen J, Beeston J. Multimodal signalling in an antelope, fluctuating facemasks and knee-

243   clicks reveal the social status of eland bulls. Anim Behav. 2015;102:231-239.

244   9. Bro-Jørgensen J. Dense habitats selecting for small body size: a comparative study on bovids.

245   Oikos. 2008;117:729–737.

246   10. Vanhooydonck B, Herrel A, Meyers JJ, Irschick DJ. What determines dewlap diversity in Anolis

247   lizards? An among-island comparison. J Evol Biol. 2009;22:293-305.

248   11. Sinclair ARE, Mduma S, Brashares JS. Patterns of predation in a diverse predator-prey system.

249   Nature. 2003;425:288–290.

250   12. Hopcraft JGC, Olff H, Sinclair ARE Herbivores, resources and risks: alternating regulation along

251   primary environmental gradients in savannas. Trends Ecol Evol. 2010;25:119-128.

252   13. Caro T Antipredator deception in terrestrial vertebrates. Curr Zool. 2014;60:16–25.

253   14. Zahavi A, Zahavi A. The handicap principle: a missing piece of Darwin's puzzle. Oxford: Oxford

254   University Press; 1997.

255   15. Krumbiegel I Biological viewpoints for the reconstruction of Sivatherium. Säugetierkd

256   Mitt. 1979;27:292-300.

257   16. Briggs DEG, Wilby PR, Perez-Moreno BP, Sanz, JL, Fregenal-Martinez M. The mineralization of

258   dinosaur soft tissue in the lower Cretaceous of Las Hoyas, Spain. J Geol Soc. 1997;154:587-588.

259   17. Phillips PK, Heath JE. Heat-exchange by the pinna of the African elephant (*Loxodonta africana*).

260   Comp Biochem Physiol A. 1992;101:693-699.

261   18. Kotrba R, Knížková I, Kunc P, Bartoš L. Comparison between the coat temperature of the

262   eland and dairy cattle by infrared thermography. J Thermal Biol. 2007;32:355-359.

263   19. Strauss MKL, Packer C. Using claw marks to study lion predation on giraffes of the Serengeti. J

264   Zool. 2013;289:134-142.

265   20. Bro-Jørgensen J. The intensity of sexual selection predicts weapon size in male bovids. Evolution.

266   2007;61:1316–1326.

267   21. Mead JI *Nemorhaedus goral*. Mamm Species. 1989;335:1–5.

268   22. Kingdon J. The Kingdon field guide to African mammals. San Diego: Academic Press; 1997.

269   23. Brashares JS, Garland T, Arcese P. Phylogenetic analysis of coadaptation in behaviour, diet, and

270   body size in the African antelope. Behav Ecol. 2000;11:452–463.

271   24. Polak J, Frynta D. Sexual size dimorphism in domestic goats, sheep, and their wild relatives. Biol

272   J Linn Soc. 2009;98:872–883.

273   25. Plard F, Bonenfant C, Gaillard JM. Revisiting the allometry of antlers among deer species: male-

274   male sexual competition as a driver. Oikos. 2011;120:601–606.

275   26. Sibly RM, Zuo W, Kodric-Brown A, Brown JH. Rensch's rule in large herbivorous mammals

276   derived from metabolic scaling. Am Nat. 2012; 79:169–177.

277   27. Holman L, Bro-Jørgensen J. Ornament complexity is correlated with sexual selection. Am Nat. in

278   press (early online).

279   28. R Development Core Team. R: A language and environment for statistical computing. R

280   Foundation for Statistical Computing, Vienna. 2012. http://www.R-project.org. Accessed 16 March

281   2016.

282   29. Paradis E, Claude J, Strimmer K. Ape: Analyses of phylogenetics and evolution in R language.

283   Bioinformatics. 2004;20:289-290.

284   30. Paradis E. Package 'ape': Analyses of phylogenetics and evolution. R package version 3.4. 2015.

285   https://cran.r-project.org/web/packages/ape/ape.pdf. Accessed 13 March 2016.

286   31. Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N et al. Caper: Comparative analyses

287   of   phylogenetics   and   evolution   in   R.   R   package   version   0.5.   2012.   http://CRAN.R-

288   project.org/package=caper. Accessed 13 March 2016.

289   32. Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, et al. The

290   delayed rise of present-day mammals. Nature. 2007;446:507-512.

291   33. Estes RD. The behavior guide to African Mammals. Berkeley, CA: University of California Press;

292   1991.

293   34. Hillman JC. The biology of the eland (*Taurotragus oryx* Pallas). (Unpublished doctoral thesis).

294   Nairobi, Kenya: University of Nairobi; 1979.

295   35. Hayward MW, Kerley GIH. Prey preferences of the lion (*Panthera leo*). J Zool. 2005;267:309-

296   322.

297   36. Hayward MW Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary

298   overlap with the lion (*Panthera leo*). J Zool. 2006;270:606-614.

299   37. Hayward MW, Henschel P, O'Brien J, Balme G, Kerley GIH. Prey preferences of the leopard

300   (*Panthera pardus*). J Zool. 2006a;270:298-313.

301 38. Hayward MW, Hofmeyr M, O'Brien J, Kerley GIH. Prey preferences of the cheetah (*Acinonyx*

302 *jubatus*) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable

303 prey before kleptoparasites arrive? J Zool. 2006b;270:615-627.

304 39. Kutner MH, Nachtsheim CJ, Neter J. Applied linear regression models. 4th ed. Irwin: McGraw-

305 Hill; 2004.

306   Tables

307   Table 1 Predictors of the presence of dewlaps in males within the Bovidae and Cervidae (binary

308   PGLMM: N = 133 species; phylogenetic signal: male body mass [$\log_{10}$]: s2=3.19, P < 0.001)

	Bivariate analyses			Multivariate analysis		
	Coefficient (±SEM)	z	P	Coefficient (±SEM)	z	P
Male body mass ($\log_{10}$)	3.59±1.55	2.32	0.021	3.59±1.55	2.32	0.021
Sexual body-size dimorphism ($\log_{10}$)	0.984±2.538	0.39	0.698	-620±6.32	-0.98	0.326

309   Table 2 Predictive framework and results

Predictions	Support?	Source
SEXUAL SELECTION HYPOTHESIS		
P1: SSD predicts the presence of dewlaps (interspecific)	No	This study
P2: Dewlap size predicts dominance status (intraspecific)	'Yes', but not after control for age	Bro-Jørgensen & Beeston (2015)
P3: Dewlap size predicts master bull status (intraspecific)	No	Bro-Jørgensen & Beeston (2015)
PREDATOR DETERRENCE HYPOTHESIS		
P1: Large dewlap size predicts the absence of claw-marks (intraspecific)	No, the opposite	This study
P2: If condition-dependent handicap, scars from predation attempts present on dewlaps (intraspecific)	No	This study
THERMOREGULATION HYPOTHESIS		
P1: Large body size predicts the presence of dewlaps (interspecific)	Yes (threshold approx. 400kg)	This study

310   FIGURE CAPTIONS

311   Fig. 1: Broadside display between two eland bulls.

312   Fig. 2: (a) A young male eland with claw-marks on his flank still bleeding. (b) An older male with

313   claw-mark scars on his flank and hindquarters. (c) Claw-mark scars on the rump of a male estimated

314   at 3 years old (2007). (d) The same scar six years later (2013).

315   Fig. 3: (a) Dewlap droop in males with and without claw-marks according to age. (b) Prevalence of

316   claw-marks in relation to age. Columns and error bars indicate the mean and its standard error;

317   numbers above columns refer to sample sizes.