Multimodal signalling in an antelope: fluctuating facemasks and knee-clicks reveal the social status of eland bulls

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The evolution of status badges presents a challenge to animal communication theory because no obvious production costs prevent low-quality individuals from cheating. From mammals, evidence of visual status badges remains rare with most examples to date found in birds. Here we report that drastic fluctuations in the facial ornamentation of male eland antelope, *Tragelaphus oryx*, reliably indicated two aspects of social status: dominance in all-male herds and access to mates as the master bull in mixed-sex herds. The finding suggests that visual status badges may be more widespread in mammals than hitherto recognized, especially in taxa with complex social systems. The peak frequency of loud knee-clicks explained additional variation in male social status. Supporting a function as a body size indicator, the peak click frequency was in turn dependent on body depth and facemask darkness, the latter possibly related to testosterone levels and hence muscle development. Dewlap size reflected dominance in all-male herds but not master bull status in mixed-sex herds and, after controlling for the effect of age, no link with social status remained. Thus whether the primary function of the ungulate dewlap is in communication or rather in thermoregulation is still an open question.

Of particular interest to signalling theory is the occurrence of status badges, i.e. long-lasting, but reversible, signals of dominance defined by the absence of any significant production costs (Searcy & Nowicki, 2005). Status badges are intriguing to theoreticians because conventional theory predicts that inferior competitors would make the best of a bad job by faking inexpensive signals and thereby erode their information value. The most widely accepted explanation for the evolutionary stability of status badges is the social control hypothesis which posits that cheaters suffer disproportionate extrinsic costs from having to fight unevenly matched opponents (Rohwer, 1977). Still, in mammals evidence of visual status badges has been remarkably rare, with empirical examples so far coming mainly from birds (Senar, 2006; see also Berglund & Rosenqvist, 2009; Tibbetts & Dale, 2004; Whiting, Nagy, & Bateman, 2003 for examples from fish, insects and lizards, respectively). The few mammalian studies include investigations of the red muzzle, rump and genitalia of male mandrills, *Mandrillus sphinx* (Setchell & Dixson, 2001; Setchell, Smith, Wickings, & Knapp, 2008), the red chest of male gelada baboons,

Theropithecus gelada (Bergman, Ho, & Beehner, 2009) and the blue scrotum of vervet monkeys, *Chlorocebus aethiops* (Gerald, 2001).

The multifaceted communication system of male eland, *Tragelaphus oryx*, the world's largest antelope, offers a well-suited opportunity to investigate the dynamics of status signalling in ungulates. Signalling in this species is multimodal relying on several putative signal traits (Bro-Jørgensen, 2010; Partan, 2013), including facial ornamentation, a conspicuous dewlap and an unusual loud click sound, presumably produced by the carpal ('knee') joint in adult bulls (Estes, 1991; Hillman, 1979).

The facial ornamentation of eland bulls consists of two components: a brush of hair and a striking black facemask (Bro-Jørgensen & Dabelsteen, 2008; Fig. 1a). The face-brush ranges from practically absent to a mat of hairs up to ca. 10 cm long, covering the entire area from the insertion of the horns to just above the nostrils. The facemask, which depends on hair colour, ranges from white (i.e. absent) to jet black. Dark facemasks are not uncommon in ungulates (Stoner, Caro, & Graham, 2003); yet, detailed studies of their function are lacking. A well-established link exists between dark melanin-pigmented hair and high androgen levels in several mammalian species (Ducrest, Keller, & Roulin, 2008), alluding to the possibility that facemasks reflect testosterone-dependent traits such as aggression and muscle development.

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The loud clicking sound of mature eland bulls is a unique phenomenon (Hillman, 1979). We have previously shown that the peak frequency of clicks, which are audible up to more than 400 m away, descends as body depth increases (Bro-Jørgensen & Dabelsteen, 2008). This hints at a possible function as a signal of competitive ability, but again whether peak click frequency predicts social status is unknown. The function of the ungulate dewlap also remains poorly understood. One possibility is that it acts in intraspecific interactions, either by giving a deceptive illusion of large body size or by honestly signalling age-related fighting ability (Bro-Jørgensen & Dabelsteen, 2008).

To examine the function of the eland status-signalling system, we recorded dynamics in morphological, acoustic and dominance-related traits from more than 200 individually recognized adult bulls in the wild over an 8-year period. In eland, access to receptive females depends on the ability of males to acquire high dominance status and obtain the position as master bull in herds with females (Hillman, 1979; Underwood, 1975), and we therefore predicted that the traits hypothesized to act as status signals would reflect two indicators of social status: dominance status in dyads within all-male herds and priority of access to females as the master bull in mixed-sex herds (Hillman, 1979; Underwood, 1975). We also specifically tested the hypothesis that peak knee-click frequency was an indicator of body size by assessing its dependence on body depth and facemask darkness, where the latter, through its potential testosterone dependence, could reflect muscle development. To avoid any confounding effect of age, we controlled for this variable statistically in the analyses. As we established the developmental trends of all the potential signal traits, we were also able to test the predictions that status signals would develop at sexual maturity and their expression peak with maximum breeding success. Finally, we addressed the hypothesis that males actively produce knee-clicks by testing whether, when standing, adult males were more likely than females to lift their forelegs, an action that usually results in a click in males, but not in females.

METHODS

Study System

The eland is a nonterritorial, gregarious browser–grazer with pronounced sexual dimorphism (male mass: 450–942 kg; female mass: 317–470 kg; Estes, 1991). Mean home range size on East African savannahs has been reported as 48 km^2 for males and 222 km^2 for females (Hillman, 1988). In the present study, eland were studied between 2005 and 2013 in a 710 km^2 contiguous study area spanning parts of the Masai Mara National Reserve and Olare Orok, Motorogi and Naboisho conservancies in southwestern Kenya. The habitat consisted primarily of open, rolling grass plains interspersed with thickets. The eland population was estimated roughly at 400 individuals. The predominant social groups in the study area were (1) all-male herds with 2–20 individuals, (2) solitary males and (3) mixed-sex herds with one to four adult males, up to more than 50 females, and, in the larger herds, up to 25 calves and more than 50 juveniles/yearlings/subadults (Bro-Jørgensen, n.d.).

Data were collected annually during the wet season between February and May, and thus overlapped with the mating peak (Estes, 1991; Hillman, 1979). The study area was surveyed for eland in a four-wheel-drive vehicle on a total of 266 days (mean ± SE = 30 ± 5 days/year), resulting in a total of 908 social unit observations. For each observation, records were made of the GPS location, sex–age composition and the identity of males. Individuals were identified based on their highly distinctive stripe pattern, ear nicks, scars, and tail and horn abnormalities, with details recorded on paper sheets and in a photographic library. A total

of 2635 observations were recorded of 280 individually recognized male eland, for which morphometric measurements were obtained from 214. The vast majority of individuals were identified directly in the field with a small number identified later from photographs. Of the 214 males, 40 were seen as both master bulls and as solitary males or in all-male herds, 18 were seen only as master bulls and 156 were seen only as solitary males or in all-male herds.

Age Determination

Following the criteria listed in Table 1, absolute age was assigned to males ≤5 years when first seen (N = 169) whereas males above this age on first sighting (N = 45) were only assigned relative age initially; the absolute age of the latter was subsequently set to comply with the age structure of the population as determined from the estimated age-specific mortality rates (see below). Using this approach, the oldest males in the population were estimated at 11 years old which is consistent with a maximum life span of 10 years reported for males in the wild (Hillman, 1979; a similar age profile was reported in a field study of the close relative, the greater kudu, *Tragelaphus strepsiceros*, Owen-Smith, 1993). In captivity, where adult mortality is likely to be reduced in the absence of predation and food limitation, a life span of 21 years have been recorded in an exceptional case; however, only 8.7% of captive males that survived their first year lived longer than 12 years, and only 0.5% lived longer than 16 years (N = 183; Dolly, 2007). For the analysis presented in this paper, qualitatively similar results were obtained if we assumed a maximum age of 16 years in the wild or excluded all males that could not be aged directly because they were only seen when ≥6 years old.

Survival Rate Estimation

Focusing on adult males ≥3 years old, the probability of sighting a particular individual known to be alive in a given year was calculated to be 82% based on the proportion of individuals seen in year x that was resighted in year x + 1, including only those individuals known from subsequent resightings to be alive in year x + 2. Age-specific mortality rates were then estimated from the proportion of individuals that were not seen the following year, taking into account the calculated 18% probability of missing a live individual. For this analysis, only males that were first seen when ≤5 years old were included to allow direct determination of absolute age (Table 1). This approach may slightly overestimate mortality rates as individuals permanently vacating the main study area were not accounted for; however, the bias is likely to be modest as (1) the mean home range of 48 km^2 reported for males (Hillman, 1988) is significantly smaller than the 710 km^2 study area, (2) of 25 males identified during surveys in adjacent areas, only one was ever observed also inside the main study area and (3) none of the 40 males assessed to be older than 3 years in 2006 were observed to be alive after 2011 (these included 15 males estimated at 4 years old, all of which thus appear to have died before their 10th year).

Phenotypic Measurements

Acoustic and morphological measurements followed a protocol similar to that in Bro-Jørgensen and Dabelsteen (2008). Click sounds were recorded from a distance of ca. 75 m using a solid state recorder (Marantz PMD670) with a directional microphone (Sennheiser ME67), and the peak frequency was subsequently measured in Praat version 5.3.80 (http://www.fon.hum.uva.nl/praat/). For body depth, dewlap droop, face-brush size and horn length, pixel counts on digital photos of individuals standing in lateral orientation were converted to the metric system based on the distance to the animal measured by a laser rangefinder (Bushnell Yardage Pro

Figure 1. (a) An adult eland bull (left) and female in a tending bond. Note the black facemask, face-brush and dewlap of the male. (b) Reversibility of facial ornamentation within an individual. (i) 14 March 2010: as master bull in a mixed-sex herd (ca. 6 years old). (ii) 23 February 2011: in an all-male herd (ca 7 years old). (iii) 7 April 2012: again as master bull in a mixed-sex herd (ca. 8 years old). (iv) 6 April 2013: as a solitary male (ca. 9 years old).

800) and a reference scale (for repeatability analysis, see Bro-Jørgensen & Dabelsteen, 2008). Facemask darkness was scored on an eight-point scale by an observer naïve to the study system and validated by photometric measurements in Image J version 1.47 (http://rsbweb.nih.gov/ij/) as described in the Appendix.

Behavioural Observations

In mixed-sex herds, master bulls were identified either from being the only adult male present aged ≥4 years or, if several adult males were present, from the formation of tending bonds (i.e. persistent following of a female at close distance) and central location in the herd (Hillman, 1979; Underwood, 1975). In all-male herds, the outcome of dominance interactions was recorded during focal watches lasting 0.5—5 h. In order of increasing escalation, interactions included submissive mounting, supplanting, sparring, low horn threats, charging and fighting (Hillman, 1979; Underwood, 1975). In the dyads of males observed interacting, dominance was assigned to the winner of the majority of interactions at the most escalated level where an asymmetry was

Table 1
Typical developmental stages in male eland

Age (years)	Category	Horn rotation[1]	Average horn length[2]	Dewlap	Frontal brush	Nasal brush	Neck thickness	Neck fur	Shoulder mane
0	Calf/juvenile	Tips straight or pointed anteriorly (ca. 0°−45°)	Grows to longer than ear length	Absent; black hair tuft	−	−	−	−	+
1	Yearling	Tips pointed laterally (ca. 45°−135°)	Not measured	Appears; black hair tuft	−	−	−	−	+
2	Subadult	Tips pointed posteriorly (ca. 135°−225°)	55 cm	Growing; black hair tuft	−	−	−	−	+
3	Young adult	Tips pointed medially (ca. 225°−315°)	56 cm	Growing; black hair tuft/fringe	−	−	−	−	+
4	Adult	Tips pointed medially or anteriorly (ca. 315°−360°)	56 cm	Growing; black hair tuft/fringe	+	−	+	+	+
5		Tips pointed anteriorly or laterally (ca. 360°−450°)	55 cm	Growing; black hair tuft/fringe	+	+	++	+	+
ca. 6		Tips pointed anteriorly or laterally (ca. 360°−450°)	54 cm	Growing; greyish/white hair tuft/fringe	+	+	++	++	(−)
ca. 7		Tips pointed anteriorly or laterally (ca. 360°−450°)	53 cm	Growing; thinning white hair tuft/fringe	+	+	++	++	(−)
ca. 8		Tips pointed anteriorly or laterally (ca. 360°−450°)	52 cm	Growing; folded, less elastic; sparse white hairs	+	+	++	++	(−)
9≤		Tips pointed anteriorly or laterally (ca. 360°−450°)	≤51 cm; shortens with age	More pointed with age	+	+	++	++	(−)

Modified from Hillman (1979) with supplementary information from Underwood (1975) and the present study in which individuals first seen when ≤4 years old were followed for up to 8 years. Because individual deviations from the typical pattern are common, age is estimated most reliably from the combination of multiple traits (Hillman, 1979).

[1] Describing the clockwise rotation of the distal curve of the right horn.
[2] Distance from the horn insertion to the tip as measured in this study. Note that horns become progressively shortened by wear in adult bulls.

found; if no asymmetry was found at any level, the dyad was excluded from the analysis. The frequency with which males and females lifted their foreleg while in a standing position was recorded during 5 min focal watches of randomly selected individuals.

Statistical Analysis

In line with Murtaugh (2014), a null hypothesis significance testing procedure ($\alpha = 0.05$, two-tailed) was used to assess the predictive value of the candidate signal traits. Logistic regression mixed models were constructed of the two independently derived measures of social status: (1) dominant status within dyads in all-male herds (henceforth Dominance Model), and (2) master bull position in a mixed-sex herd (henceforth Master Bull Model). Specific dyads and individual males were included no more than once per year in the Dominance Model and Master Bull Model, respectively. For the dyads in the Dominance Model, males were assigned randomly to two equivalent roles (male I and male II), which were included as subjects for the residual covariance structure in order to account for nonindependence due to individual males occurring in multiple dyads. Similarly, in the Master Bull Model, individual males were entered as subjects due to their representation over multiple years. Individual males were included in the analysis only in years from which data were available on all the test variables, i.e. facemask darkness, face-brush size, dewlap droop, peak frequency of the click sound, body depth and age; this restricted the data set to adult males ≥4 years old as loud knee clicking was not recorded in younger males. The use of horn wear to estimate age precluded the inclusion of horn length in the analyses as it would violate the statistical assumption of independence between test variables. Explanatory variables were rejected by backward elimination in order of least significance until only significant variables remained. Age was represented by a linear and a quadratic expression in the Master Bull Model. In the Dominance Model, age was represented by the age difference within the dyad (age of male II subtracted from the age of male I), the absolute age of the reference male (male I) and the interaction between these terms. Variance inflation factors (VIFs) of the explanatory variables were all <2, except for age difference in the Dominance Model where VIF = 3.4; as VIFs in all cases were below 5, this indicates that multicollinearity was not affecting the results (Kutner, Nachtsheim, & Neter, 2004). In a separate generalized linear mixed model (GLMM), peak click frequency was modelled as a function of body depth, facemask darkness, face-brush size, age and age squared, with individual identity included as subject. An independent-samples t test was used to compare the mean frequency of foreleg lifts between the sexes. All analyses were done in SPSS version 21 (IBM, Armonk, NY, U.S.A.).

RESULTS

Phenotypic Development

The mean body depth of male eland increased until the age of 5 years and thereafter stabilized (Fig. 2a). Males were most likely to assume master bull status when 6–8 years old (Fig. 2b), and, mirroring this pattern, mean facemask darkness peaked in males 6–8 years old (Fig. 2c), mean face-brush size slightly later, at 7–8 years (Fig. 2d), and the mean peak frequency of the knee-clicks showed a descending trend from its onset at around 4 years of age until the age of 6 years, and then remained relatively stable with a tendency to increase again in males older than 8 years (Fig. 2e). By contrast, mean dewlap size increased monotonically through life (Fig. 2f).

Indicators of Social Status

Master bulls in herds with females were characterized by large body size, prolific face-brushes, dark facemasks and deep click sounds; however, in a multivariate analysis controlling for age, only facemask and peak click frequency were retained in the model (Table 2). In all-male herds, socially dominant males were likewise relatively large and had larger face-brushes, darker facemasks and deeper click sounds; in addition their dewlaps were relatively large and they were relatively old (Table 2). In the multivariate model of social dominance, only facemask, peak click frequency and age were retained as predictors (Table 2). Qualitatively similar results (not shown) were obtained if the analyses excluded 4-year-old males, an age group that had not attained full body size (Fig. 2a).

In years when seen as master bulls, individual males had significantly darker facemasks and larger face-brushes, and produced deeper click sounds, than in other years (including only males ≥4 years old seen in both contexts: Wilcoxon test: facemask: $T = 4.74$, $N = 37$ males, $P < 0.001$; face-brush: $T = 2.75$, $N = 30$ males, $P = 0.006$; peak click frequency: $T = -3.01$, $N = 23$ males, $P = 0.003$; Fig. 3). These differences were not explained by older age (Wilcoxon test: $T = 0.23$, $N = 37$ males, $P = 0.819$; Fig. 3). In a subset of males that could be monitored annually between 5 and 8 years of age a fully black mask was first observed at 5 years in 23%, at 6 years in 27%, at 7 years in 14%, at 8 years in 5% and never in 32% ($N = 22$ males; Fig. 4). Of the males developing black masks, 62% were confirmed to turn lighter again in subsequent years, and half were observed with a black mask in 1 year only. Repeated phases with dark facemasks were confirmed within individual males as were repeated phases as master bull (Figs. 1b and 4).

Body depth and facemask darkness were both strong predictors of peak click frequency in multivariate analysis (GLMM, $N = 227$ cases: body depth: coefficient = -34.1 ± 3.5, $t = 9.84$, $P < 0.001$; facemask darkness: coefficient = -32.7 ± 6.1, $t = 5.34$, $P < 0.001$; VIFs 1.01). Adult males were 10-fold more likely than adult females to lift their forelegs while standing (mean $\pm$ SE; males: 0.55 ± 0.12 lifts/min, $N = 23$ individuals; females: 0.046 ± 0.033 lifts/min, $N = 13$ individuals; t test, equal variances not assumed: $t_{25.3} = 4.09$, $P < 0.001$), thereby actively producing clicks (see Supplementary video).

DISCUSSION

This study shows that, in the eland, dark facemasks and large face-brushes characterize dominant bulls in all-male herds and master bulls in mixed-sex herds. These findings agree with the hypothesis that facial ornamentation acts as a dynamic status badge in the species. The general pattern of maximum expression at middle age when access to mates peaks, followed by attenuation in older bulls, has parallels in studies of sexually selected signals in other mammals, including the red sexual skin in mandrills (Setchell & Dixson, 2002) and vocalizations in fallow deer, *Dama dama* (Briefer, Vannoni, & McElligott, 2010), and the decline probably reflects the onset of reproductive senescence that is known to occur in wild ungulates (McElligott, Altwegg, & Hayden, 2002).

The facial ornamentation of eland shows significant structural and functional similarities to the mane of lions, *Panthera leo*. The lion mane reflects male competitive ability and serves as a target of female choice (West & Packer, 2002), and thus possibly qualifies as a status badge as well, although documented heat stress (West & Packer, 2002) could conceivably maintain honesty of this signal through condition-dependent costs according to the handicap principle (Zahavi, 1975). For both the lion mane and the eland facial ornamentation, darkness is due to black hairs and trait size
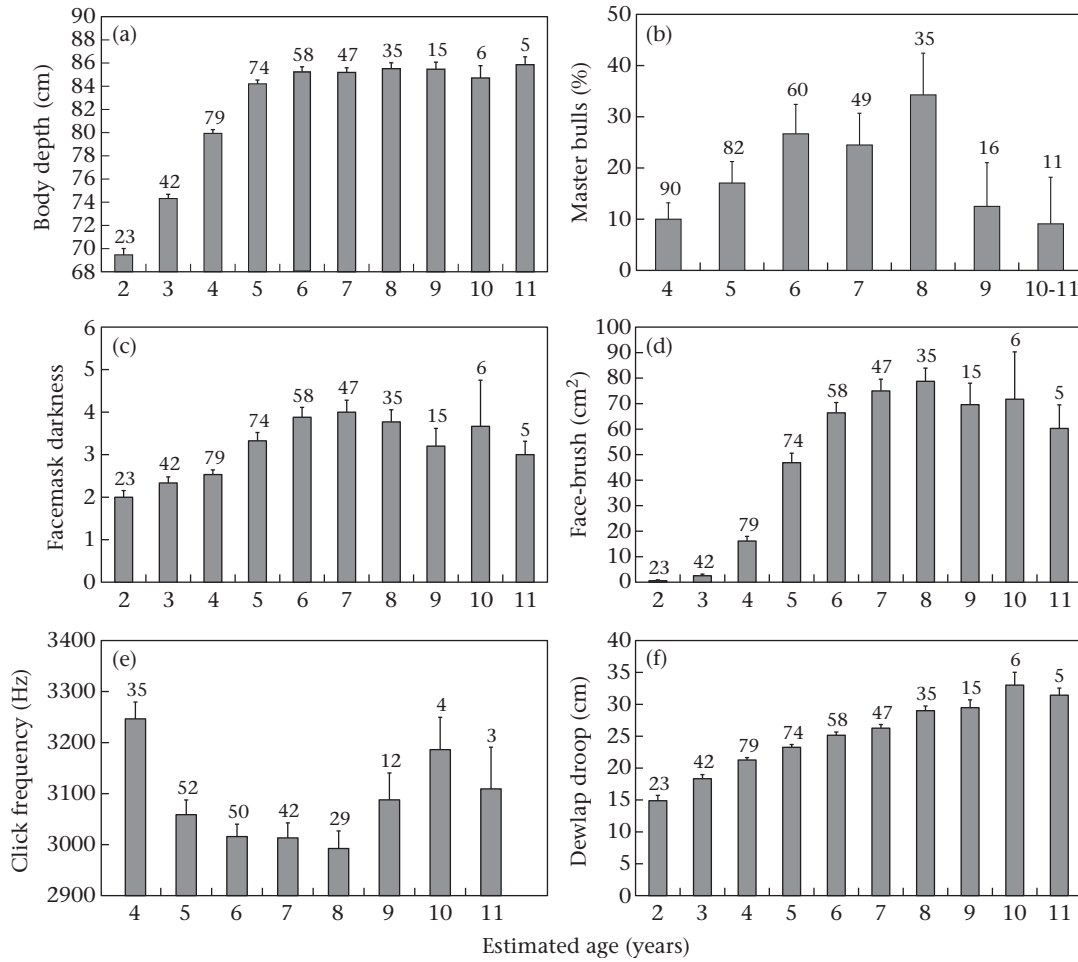
Figure 2. Development of phenotypic traits. (a) Body depth, (b) probability of master bull status, (c) facemask darkness, (d) face-brush size, (e) peak click frequency and (f) dewlap droop. Sample sizes are indicated above the columns. Error bars denote SE of the mean.

depends on hair length. However, a distinction is that, whereas the eland facemask typically peaks at middle age, the lion mane generally darkens with age (West & Packer, 2002). We speculate that this could reflect adaptive differences in male reproductive strategies. Although the two species are broadly similar in male life

span (usually ≤10 years in the wild) and male age at first reproduction (usually ≥5 years), only in lions do males practise infanticide. Infanticide could select for a terminal investment strategy with sustained investment in reproductive effort (Stearns, 1992): tenure of male lions must exceed 2 years before their own offspring

Table 2
Predictors of master bull status and social dominance in individual adult male eland ≥4 years old

	Variable	Bivariate			Multivariate			
		Coefficient±SE	t	P	Coefficient±SE	t	P	VIF
Master bull status[1]	Facemask darkness	0.69±0.11	6.28	<0.001	0.61±0.13	4.85	<0.001	1.34
	Click frequency (Hz)	−0.005±0.001	−4.74	<0.001	−0.003±0.001	−2.84	0.005	1.72
	Face-brush size (cm²)	0.022±0.005	4.31	<0.001	0.007±0.007	0.97	0.332	1.73
	Dewlap droop (cm)	0.007±0.035	0.20	0.844	−0.014±0.043	−0.33	0.740	1.43
	Body depth (cm)	0.13±0.06	2.22	0.029	0.018±0.080	0.23	0.819	1.58
	Age (years)	0.21±0.12	1.80	0.122	0.13±0.13	1.00	0.320	1.88
	Age+Age²	2.08±0.80/	2.60/	0.048/	0.52±0.62/	0.50/	0.617/	NA
		−0.14±0.06	−2.33	0.067	0.03±0.71	−0.37	0.709	
Social dominance within dyads[2]	Difference in facemask darkness	0.62±0.12	5.35	<0.001	0.52±0.13	4.09	<0.001	1.48
	Difference in click frequency (Hz)	−0.005±0.001	−4.98	<0.001	−0.003±0.001	−3.08	0.003	1.94
	Difference in face-brush size (cm²)	0.033±0.007	4.95	<0.001	0.012±0.007	1.69	0.094	1.74
	Difference in dewlap droop (cm)	0.10±0.04	2.89	0.005	−0.014±0.052	−0.27	0.790	1.88
	Difference in body depth (cm)	0.17±0.05	3.49	0.001	−0.002±0.068	−0.04	0.971	1.97
	Age difference (years)	0.51±0.12	4.32	<0.001	0.44±0.14	3.08	0.003	3.31
	Absolute age of reference male (years)	0.029±0.033	0.89	0.376	−0.035±0.039	0.89	0.375	1.93
	[Age difference]*[Age of reference male]	0.049±0.060	0.83	0.408	−0.030±0.077	−0.39	0.699	NA

VIF: variance inflation factor; NA: not applicable.
[1] $N = 227$ cases; 81.9% classified correctly.
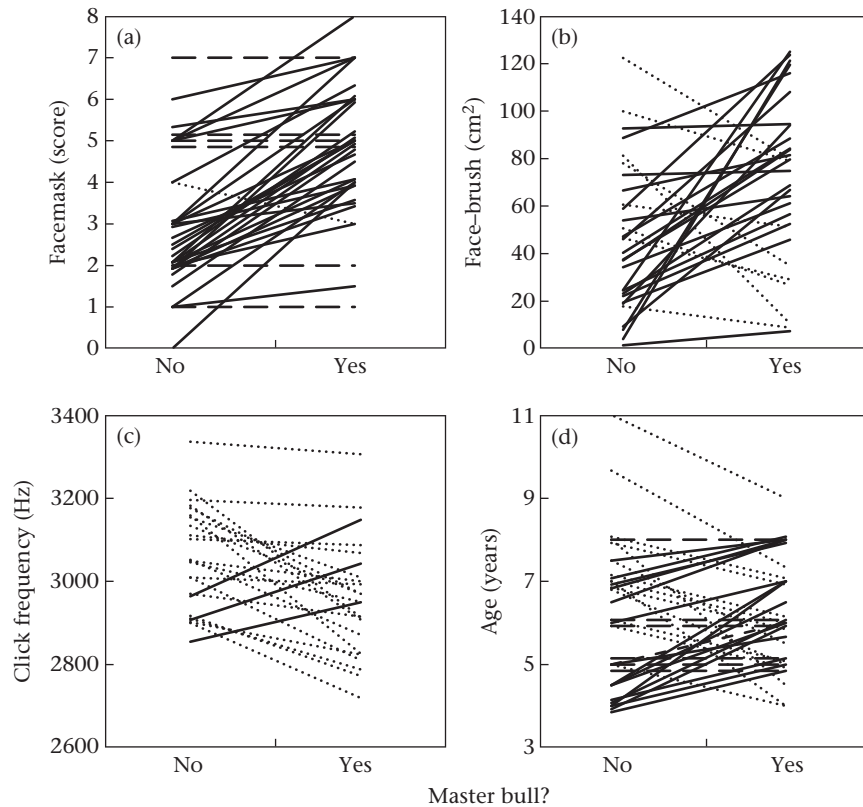[2] $N = 128$ dyads; 83.6% classified correctly.

Figure 3. Phenotypic changes in individual bulls (≥4 years old) between years in relation to whether or not they were observed as master bulls. (a) Facemask darkness, (b) face-brush size, (c) peak click frequency and (d) age. For males observed in the same role in multiple years, the mean value is shown. Solid line: increase; broken line: stable; dotted line: decrease.

are no longer vulnerable to infanticide by the incoming male coalition, and this restriction makes multiple successful reproductive bouts unlikely (Packer & Pusey, 1983; West & Packer, 2002). By contrast, in species with no paternal care such as the eland, male mating success translates more directly into reproductive success, and immediate rewards from success in male mate competition can select for multiple extreme peaks in reproductive investment, even if such investment is sustainable over shorter periods only. In captivity, the male eland is indeed reported to enter intermittent phases of heightened aggression referred to as 'ukali', which last from a few days to several months (Kingdon, 1982; compare 'musth' in elephants, *Loxodonta africana*, Hollister-Smith et al., 2007; Poole & Moss, 1981, and recently reported reproductive

cycles in male giraffes, *Giraffa camelopardalis*, Seeber, Duncan, Fritz, & Ganswindt, 2013). The expression of the dark facemasks of eland bulls may be a testosterone-dependent indicator of the ukali state; this would be consistent with documented links between dark hair pigmentation and testosterone level in white-tailed deer, *Odocoileus viginianus* (Bubenik & Bubenik, 1985) and between dark coat colour and dominance in a hybrid population of thinhorn sheep, *Ovis dalli* (Loehr, Carey, Ylönen, & Suhonen, 2008).

Why are visual status badges found in some mammals and not in others? It is noteworthy that the examples to date come from species living in groups that are among the very largest within their taxa and include multiple males, notably the mandrill and gelada within the primates, the lion within the felids and the eland within the bovids. Large group size increases the potential for conflict and can also render individual recognition more challenging, especially in societies with fission–fusion dynamics such as in the eland (Aureli et al., 2008). These factors are likely to provide a selective advantage for status badges as a generalized dominance indicator which allows conflicts to be resolved without costly fighting. In this context, the low incidence of fighting among male eland is noteworthy (Hillman, 1979; Underwood, 1975). Supporting a link between status badges and group size, Stoner et al. (2003) found a positive correlation between dark facemasks in ungulate species and their social group size, a finding that was indeed interpreted as evidence for a role of facemasks in intraspecific communication. However, an important distinction exists according to whether facemasks are dynamic, as in the eland, or individually fixed as, for example, in topi, *Damaliscus lunatus* (Bro-Jørgensen, 2002; Bro-Jørgensen & Durant, 2003): whereas fixed masks may function as static indicators of general phenotypic quality, only dynamic masks can reflect condition-dependent changes within individuals over time (Bro-Jørgensen, 2010).
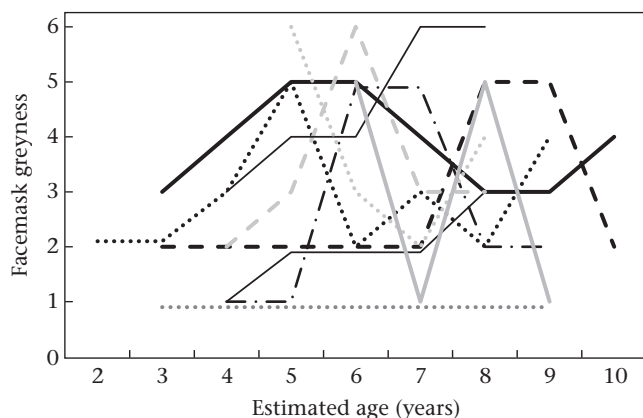

Figure 4. Age-related changes in facemask greyness (see Appendix) in 10 selected males.

It is clear that more studies of mammalian status badges are needed, and especially among bovid and primate species a rich diversity of striking sexually dimorphic visual traits still awaits investigation. The interest of such studies is emphasized by a recent comparative study of birds which found that sexually dimorphic traits hitherto presumed to be status badges were associated with nonbreeding rather than breeding contexts (Tibbetts & Safran, 2009). This finding was taken as evidence against a function in sexual signalling, and mammalian study systems, by providing some of the most clear-cut examples, may therefore be particularly important to our understanding of visual status badges in spite of the few examples at present.

Surprisingly, the audio frequency of the knee-click sound was a stronger predictor of social status than body depth. Possibly, clicks are a more accurate indicator of competitive ability than body depth because the mechanism by which they are generated encodes information not only about skeletal size, but also about muscular development. Hence, according to the proposition that clicks are produced by a tendon flipping over a carpal bone (Estes, 1991), Mersenne's law predicts that the acoustic frequency should descend with increasing length, mass and tension of the 'string', i.e. the tendon–muscle complex (Bro-Jørgensen & Dabelsteen, 2008). In this way, the negative correlation between peak click frequency and facemask darkness may be attributed to higher androgen levels in dark-faced males (Bubenik & Bubenik, 1985; Ducrest et al., 2008): the anabolic effect of androgens would be expected to increase muscle mass and thereby the thickness of the 'string', which in turn would decrease peak click frequency. However, further studies are needed to confirm exactly how the clicks are generated and how facemask darkness links to hormonal status in the eland. Mostly the clicks are produced during walking, but the finding that standing males also produce clicks by voluntarily lifting their foreleg hints at a possible benefit from active signalling as well.

No association was detected between dewlap size and master bull status. Larger dewlaps did, however, reflect dominance in dyadic relationships as older males, which were more likely to be dominant, had larger dewlaps. Still, we were unable to demonstrate an age-independent link between dewlap size and dominance status, and it is possible that the structure has evolved primarily to facilitate heat dissipation (Krumbiegel, 1979), similarly to the ears of the elephant (Phillips & Heath, 1992). Using infrared thermography, the temperature of the eland dewlap has indeed been confirmed as a site of heat loss (Kotrba, Knížková, Kunc, & Bartoš, 2007). The larger dewlaps of males than females is also consistent with a function in thermoregulation as males are markedly larger and therefore have a reduced capacity to dissipate heat due to their lower surface:body mass ratio; however, this sexual dimorphism could also reflect a role of sexual selection not detected here, and the function of the dewlap warrants further investigation.

In conclusion, this study illustrates how the integration of multiple putative signal traits in an analysis of a complex status-signalling system in the wild can help to pinpoint the distinct information value of each specific component. The finding that facial ornaments and click frequency in male eland predicted not only access to females, but also dominance in the absence of females, points mainly to their function in intrasexual communication; however, a role as indicators of indirect genetic benefits to mates should not be ruled out, and experimental evidence is now needed to further illuminate the signal functions suggested by the present results. More generally, the findings highlight that the conditions favouring the evolution of status badges are likely to be more widespread than previously realized, thereby stressing that dominance signals do not necessarily require high production costs.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2015.01.027.

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Appendix

Scoring of facemask darkness

The darkness of the facemask was quantified on a scale from 1 to 8 as follows: (1) the greyness of the mask was assigned a score between 1 (light/absent) and 6 (jet black) based on a library of reference photos for each score (Fig. A1); (2) the extension of the facemask beneath the chin was assigned a score of 0 if absent, 1 if present as a patch, or 2 if fully encircling the muzzle (Fig. A2); (3) the final facemask score was calculated as (1) + (2).

The reliability of the visual greyness score was objectively verified by photometric measurements of grey values on a subset of photos in Image J v. 1.47 (http://rsbweb.nih.gov/ij/); these were done blind to the visual greyness scores. First, the brightness of the photographs was adjusted to compensate for differences in illumination. We standardized the greyness scale by setting the contrasting black and white contrast markings on the back of the upper front legs as the extreme values; these markings, which possibly facilitate herd cohesion, are characterized by lack of variation in expression both between and within individuals (Kingdon, 1982; Fig. A3; for validation, see below). Next, we measured the mean grey value of the facemask area and of a reference area of the cheek, the latter to represent the base colour of the face. We then calculated the difference between these measures to quantify the greyness of the facemask relative to the base colour. Finally, we correlated the photometric measures with the visual greyness scores which confirmed the reliability of the visual scores (Pearson correlation: $r_{64} = 0.952$, $P < 0.001$; Fig. A4).

To further validate the assumption that contrast markings on the front legs could be regarded as constant, we compared the grey values obtained for the facemask of individual animals when brightness adjustment was based on their own contrast marking relative to when based on the contrast marking of another individual on the same photograph; repeatability was found to be very high (Cronbach's alpha 0.99; Pearson correlation: $r_{18} = 0.99$, $P < 0.001$). We also confirmed that differences in illumination between photos did not affect the results by comparing the measures obtained for individual animals in particular years when using two photographs under contrasting lighting conditions; again, repeatability was found to be very high (Cronbach's alpha 0.97; Pearson correlation: $r_{12} = 0.94$, $P < 0.001$).

The validation of the visual facemask scores was based on a subset of males; photometric measurements could not be performed on all males because grass sometimes obscured the contrast marking and because lighting conditions sometimes differed between the contrast marking and the face (specifically, when one was in shade and the other in sunlight).

Figure A1. Reference photos for facemask greyness scores. Scores 5 and 6 are referred to as black facemasks.
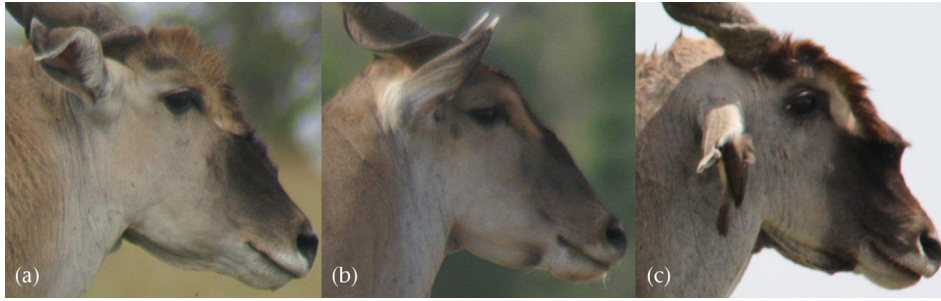
Figure A2. Reference photos for scoring the extension of the facemask beneath the chin. (a) Absent: score 0; (b) a patch: score 1; and (c) a continuous band: score 2.

Figure A3. Black-and-white contrast marking on the upper front leg of (a) a light-faced and (b) a dark-faced adult male.
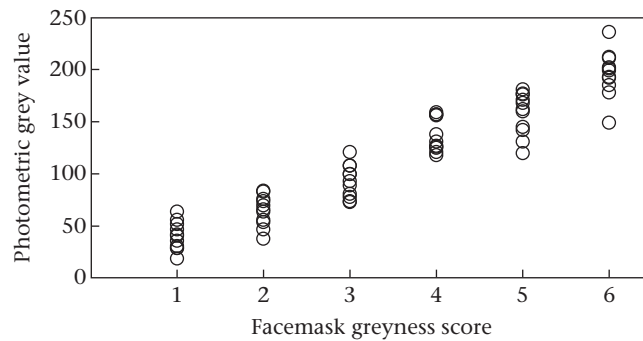

Figure A4. Photometric grey values in relation to visual scores of facemask greyness by a naïve observer. The increased variation for the higher scores can be explained by the procedure of calculating the difference in grey value between the base colour and the facemask: this prevents males with darker base colour from obtaining maximum scores even if their facemask is jet black. Although it may therefore seem more appropriate to use the grey value of the facemask directly for darker males, this procedure was not adopted because it would be inappropriate for males with lighter or no facemasks: their scores would then depend on the base colour of their face.