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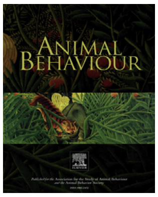

Multimodal signalling in an antelope: fluctuating facemasks and knee-clicks reveal the social status of eland bulls

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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