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The meaning of boom calls in a lekking bird: identity or quality information?

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In mating systems where sexual selection is intense, providing information on identity and quality to congeners may strongly influence reproductive success. In the lekking North African houbara bustard, *Chlamydotis undulata undulata*, males perform a spectacular courtship that includes highly visible displays and low-frequency vocalizations called booms. Booms are individualized and may play a role in individual recognition. However, this hypothesis is valid only if boom parameters are fixed phenotypes that do not change over time. It is also possible that they convey information about male quality. Using captive birds, we investigated whether the characteristics of booms vary over time, and whether they are related to physiological, physical and behavioural traits of the males. We showed that booming calls varied over the breeding season and that the males producing the lowest frequency booms were the heaviest and displayed the most. Using playback experiments in the field, we tested whether wild males use the frequency of rival booms as an indicator of their opponent's condition. We found that males' behavioural responses were significantly different according to the frequency of the signals played back. Males responded to booms simulating heavier intruders (lower frequency), which presumably represented a bigger threat, by increasing the duration of their running phase and by decreasing the duration of their booming phase, potentially bluffing on their own condition. Thus, booms convey information on male quality rather than identity, and are key acoustic signals in the agonistic relationships between lekking males.

Individual distinctiveness is widespread among taxa and can be signalled visually (Detto, Backwell, Hemmi, & Zeil, 2006; Tibbetts, 2002), acoustically (Charrier, Aubin, & Mathevon, 2010; Vergne, Avril, Martin, & Mathevon, 2007), chemically (Kent & Tang-Martínez, in press; Krause, Krüger, Kohlmeier, & Caspers, 2012) or electrically (McGregor & Westby, 1992) between signallers and receivers. The ability to identify individuals can have important roles in different social contexts, such as parent–juvenile interaction (Aubin & Jouventin, 1998; Charrier, Mathevon, & Jouventin, 2001), mate or kin recognition (Bergman, Beehner, Cheney, & Seyfarth, 2003; Speirs & Davis, 1991), neighbour–stranger discrimination (Bee & Gerhardt, 2002; Briefer, Aubin, Lehongre, & Rybak, 2008) or dominance interaction (Höjesjö, Johnsson, Petersson, & Järvi, 1998). The process of recognition relies on the existence of consistent variation in some signal parameters between individuals. However, individual variation does not necessarily mean individual discrimination, and signal parameters expressing a high degree of phenotypic variation between individuals may also indicate quality (Dale, Lank, & Reeve, 2001).

Signals of individuality and quality might both influence reproduction success, especially when sexual selection is intense. In the context of male competition, signals supporting signatures of identity or reflecting various qualities are exchanged between males and can be used to regulate their interactions (Bradbury & Vehrencamp, 2011). On the one hand, the ability to distinguish individuals (neighbour, stranger or kin) allows the territory holder to adapt its behavioural response (e.g. to run away, to fight or to tolerate) and optimize its expenditure of time and energy (Lovell & Lein, 2005; Temeles, 1994). On the other hand, the ability to distinguish between opponents of differing quality through reliable

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signals can help prevent costly confrontations (Tibbetts & Dale, 2004, 2007).

The North African houbara bustard, *Chlamydotis undulata undulata*, is a bird species with a lek mating system (Hingrat et al., 2004). Leks are defined as 'assemblies of adult males which females visit solely for the purpose of copulation' (Bradbury & Gibson, 1983, p 109). In the houbara bustard, males compete for display sites before females start to breed and remain faithful to their sites, which they defend for up to 5 months during the breeding season and also between years (Hingrat, Saint Jalme, Chalah, Orhant, & Lacroix, 2008). In this context, intrasexual competition is high and intrasexual communication might be of crucial importance for males to gather and hold a display site within the lek. Males perform courtship displays on sites separated by large distances, on average 550 m, within so-called 'exploded leks' (Hingrat et al., 2008). As a part of their courtship, males produce very low-frequency vocalizations called booms, with an average fundamental frequency of 46 Hz (Cornec, Hingrat, & Rybak, 2014). Given that producing low-frequency sounds is known to be an effective strategy for long-range communication (Garstang, Larom, Raspet, & Lindeque, 1995; Mack & Jones, 2003), we hypothesize that booms are involved in communication between houbara males within the exploded lek. Recent experiments in the field confirmed this assumption, with booms being detectable beyond 600 m (Cornec, Hingrat, Aubin, & Rybak, 2015). The parameters of booms have recently been shown to be individualized, especially the frequency parameters (Cornec et al., 2014). They may carry information about the individuality or the quality of the bird, both variables being potentially involved in the relationships between competing males. However, booms can only be good candidates for supporting identity recognition if they are constant over time and not condition dependent (Dale et al., 2001). Indeed, when traits are costly to elaborate and to maintain, they often are condition dependent. They are also often subject to change over time according to individual phenotype, its investment in reproduction and its response to social and environmental factors. In that case, traits may signal information not about identity but about quality (Briefer, Vannoni, & McElligott, 2010). Few studies have investigated the variability of individual acoustic signals over time (Gilbert, Tyler, & Smith, 2002; Kirschel et al., 2011; Lengagne, 2001; Peake et al., 1998). It is none the less a first criterion to show the potentiality for individual recognition to persist over a long period and is one way to disentangle real individuality from quality information (Tibbetts & Dale, 2007).

In this study we first investigated whether acoustic signals of houbara males are stable across the breeding season by recording and analysing the booms produced by the same individuals at three different times during the breeding season. We then examined the relationships between the acoustic parameters of booms and measurements of physical, physiological and behavioural traits that might reflect the sender's quality: age, body size and weight, courtship activity and sperm quality. As a large number of vocalizations were necessary to achieve precise analysis, and taking into account the difficulty and the potential uncertainty of recording in the field, these two aims were achieved using captive-bred houbara bustards. This allowed us to work on males raised and maintained in controlled conditions. Additionally, it also provided access to some traits impossible to measure in the field, such as sperm volume, motility and number of spermatozoids. Finally, we investigated, in the field, whether booms were effectively used by males to estimate the potential quality of their opponents in intrasexual competition. To that aim, booms differing in acoustic parameters and correlated with specific quality traits were played back to males holding display sites and their behavioural responses were compared.

METHODS

Study Species

The North African houbara bustard is classified as Vulnerable by the IUCN Red List of Threatened Species (Birdlife International, 2014) owing to excessive hunting pressure, poaching, human disturbance and habitat degradation (Le Cuziat et al., 2005). It inhabits steppe and semidesert areas with open and scattered vegetation (Hingrat, Saint Jalme, Ysnel, Le Nuz, & Lacroix, 2007). During the breeding season (January–May), males perform conspicuous and spectacular courtship displays (Gaucher et al., 1996). The courtship is a sequence of several distinct phases including a highly visual 'running' phase, where the bird runs in circular motions with the white feathers on the neck and the head fully erect, and a 'vocal' phase, during which the male produces low-frequency sounds called booms (Cornec et al., 2014). Males devote several hours per day to courtship activity, especially from dusk to dawn, and are faithful to their display sites over the season and from year to year (Hingrat et al., 2008).

Recordings in Captivity

We recorded captive males within the breeding station of the Emirates Center for Wildlife Propagation (Enjil, Morocco), between February and May 2012. In the station, breeding adults are housed outdoors in individual cages (2×2 m and 2 m high) arranged in rows (see Chargé et al., 2014 for details). Males might be in visual and acoustic contact with each other, but cannot see females, which are housed in separate breeding units. In the breeding station, all the birds are of known age.

Subjects

Individual and seasonal variation of booms

To study whether the acoustic parameters of booms vary over time, 13 males were chosen at random (4–13 years old) and were recorded at three different times during the breeding season in 2012: at the start (14–23 February), at the middle (28 March–10 April) and at the end of the season (18–25 May).

Relationships between acoustic parameters and male quality traits

To study the relationships between male quality traits and acoustic parameters, 25 males were recorded between 28 March and 10 April 2012. Since sperm quality varies with a male's age (Preston, Saint Jalme, Hingrat, Lacroix, & Sorci, 2011), we selected 13 'young' males between 2 and 5 years old and 12 'old' male between 9 and 13 years old. In birds, male vocalizations can be affected by their body weight (e.g. Mager, Walcott, & Piper, 2007). Therefore, within the 'young' male category six males were selected as 'light' (1630–1980 g) and seven males were selected as 'heavy' (2377–2500 g). Within the 'old' male category, six males were selected as 'light' (1830–2100 g) and six males were selected as 'heavy' (2126–2500 g).

Ethical Note

The birds used in the captive breeding part of the study were artificially bred in agreement with the 'Ministère de l'Agriculture, Développement Rural et des Pêches Maritimes, Direction Provinciale de l'Agriculture de Boulemane, Service Vétérinaire' (Nu DPA/48/285/SV) under permit N° 01-16/VV; OAC/2007/E; Ac/Ou/Rn. The birds were individually housed in cages 2×2 m and 2 m high (see Chargé, Saint Jalme, Lacroix, Cadet, & Sorci, 2010; Chargé et al., 2014). Bird handling and measurements were performed by