



Peacock copulation calls attract distant females

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Abstract

Males often continuously emit vocalizations during the breeding season that attract female mates. They can also emit calls that are specifically associated with copulations but the function of these copulation calls is often unknown. We explored the function of male copulation calls in wild and captive peafowl (*Pavo cristatus*) to test whether these calls attract female mating partners. By broadcasting male copulation calls, we assessed whether these playbacks affected female behavior. Females approached and spent more time near the speaker in response to copulation playback trials compared to control trials (no sound broadcast) in the wild and compared to control trials (American crow (*Corvus brachyrhynchos*) calls broadcast) in captivity. Our results, therefore, suggest that peacock copulation calls function to attract additional female mating partners. Because peafowl live in habitats with dense vegetation, loud copulation calls may help females locate potential mates.

Keywords

acoustic communication, copulation calls, mate choice, *Pavo cristatus*.

1. Introduction

Males in many species repeatedly emit songs to attract potential mates during the breeding season (Andersson, 1994). Singing can be costly, as it can be energetically expensive (Vehrencamp et al., 1989), attract predators (Zuk & Kolluru, 1998), and incite aggression (Searcy & Andersson, 1986). Despite these costs, males can benefit from singing by attracting females and advertising their quality (Andersson, 1994). When mates are difficult to detect,

males that sing can alert females to their locations (Hedrick, 1986). Temporal and acoustic aspects of male song (such as rate, amount of time spent calling, pitch, duration and type) can then influence female mating decisions (Andersson, 1994).

In addition to singing, males can also emit copulation calls immediately before, during, or after copulation (e.g., Grady & Hoogland, 1986; Alatalo et al., 1987; Hohmann, 1989). The function of these copulation calls, however, has been experimentally examined in only a few species. Male rhesus macaque (*Macaca mulatta*) copulation calls attract the attention of additional females (Hauser, 2007) and males that emit these calls obtain more copulations (Hauser, 1993); because copulation calls can be costly, they may serve as honest indicators of male quality (Hauser, 1993). Male copulation calls in ring-billed gulls (*Larus delawarensis*; Fetterolf & Dunham, 1985) and little blue penguins (*Eudyptula minor*; Waas, 1988) increase the mating activity of surrounding males and females. These calls may, therefore, function to reduce interference during copulation (copulating birds are less likely to interfere with other birds that are copulating; Fetterolf & Dunham, 1985) or help synchronize breeding activity (Waas, 1988).

Peafowl (*Pavo cristatus*) are an ideal species in which to further study the function of copulation calls. Peacocks form exploded leks, in which males display on scattered arenas, and females choose among males. Peacocks emit loud courtship vocalizations during the breeding season (Petrie et al., 1991; Takahashi & Hasegawa, 2008). Immediately prior to attempting a copulation, peacocks perform a hoot-dash display in which they move quickly toward a female while emitting a loud 'hoot' vocalization (Petrie et al., 1991, 1992). If the female chooses to mate, she crouches down as the male approaches and allows the male to mount her (but she can avoid if she does not decide to mate; Petrie et al., 1992). This hoot copulation call is almost exclusively associated with female courtship and is always associated with male display behavior (in a captive population in Durham, NC, USA, 97 observed hoots were emitted while males were performing hoot-dashes toward females but only two hoots were emitted when a peacock (in the presence of a female) performed a hoot-dash toward a squirrel and toward no obvious target; J.L.Y., unpublished data). We tested whether peacock copulation calls function to attract distant females. Because peafowl live in dense habitats, such as scrubland and forests (Kannan & James, 1998), it may be difficult for peahens to visually locate potential mates. Peahens could, therefore, use loud auditory signals from males to find mates.

2. Methods

2.1. Study site and animal subjects

We explored the function of male population calls (Figure 1) in wild peafowl during July and August 2011 at Keoladeo National Park (27°7.6'N, 77°33.2'E) in Bharatpur, Rajasthan, India. The peafowl were unmarked and not habituated to people. The park consists of marshy land as well as scrub woodland scattered with thickets and medium-sized trees (Sharma & Chatterjee, 2006). The peafowl live in the scrubland sections of the park (J.L.Y. & K.R.A., pers. obs.), which cover approximately 18 km² (Sharma & Chatterjee, 2007). Given that peafowl density can range from 30–65 birds/km² in other wild populations (Sharma, 1969), the peafowl population in this park likely had more than 500 birds. One researcher (J.L.Y.) conducted all trials. The trials lasted four hours each (except for one trial which was aborted early due to heavy rain) and were conducted approximately one hour after sunrise from exactly 07:00 to 11:00 h. Previous studies indicate that peafowl exhibit peak mating activity during this time period (Petrie et al., 1991; de Silva et al., 1996).

Because of limitations associated with the experiments conducted in the wild (such as small sample sizes, lack of a heterospecific control and unmarked individuals), we followed-up our experiments in the wild using a captive population during April 2012 in Durham, NC, USA (36.01°N, 79.02°W). The females were housed (without any males) in an outdoor enclosure (46 m perimeter) within a wooded area. For each trial, a female was captured from this enclosure and immediately transported to an outdoor testing cage (2.78 km away; 20 × 7 m; Figure 2) within a wooded area of the Duke Forest Teaching and Research Laboratory. Due to transport time and experimental set-up, females were tested approximately 30 min after they were captured. Because the females were regularly transported from their

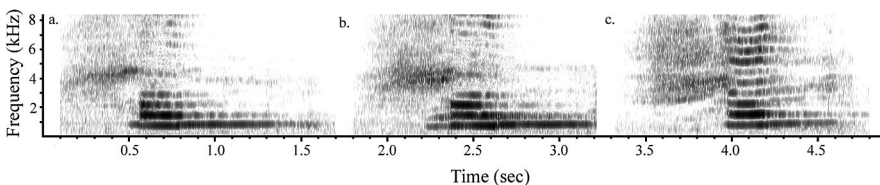


Figure 1. Example spectrograms of hoot vocalizations emitted by three different males (a–c; spacing between calls is not meaningful) that were used in the playback experiments.

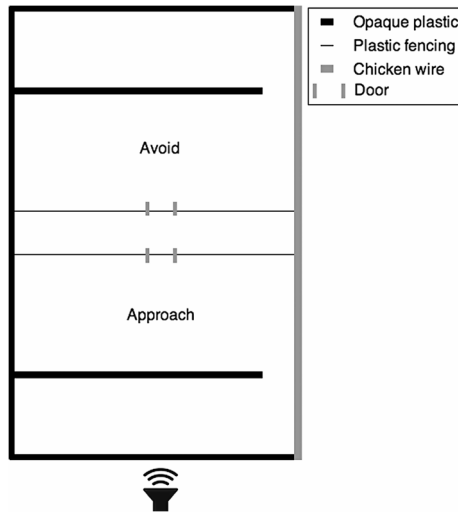


Figure 2. The testing cage for the captive playback experiments. A peahen began in the middle of the cage and was allowed to exit through either of the doors to approach or avoid the sound stimulus.

enclosure to additional cages (for use in other studies), they were familiar with this process; furthermore, females exhibited normal behavior during the pre-testing period (see below) by consuming food (such as leaves and insects) that was inside the cage (females in 92% and 75% of the control and copulation trials, respectively, consumed food during the pre-testing period). Further details on this captive population are described in Yorzinski & Platt (2012).

2.2. *Playback experiments in the wild*

Playback experiments were conducted in locations randomly-selected throughout the park in areas where peafowl were present and where small clearings (at least 20×20 m) existed (so that approaching peafowl could be visually detected). Because we did not know where male territories were located, it is unlikely that our trial locations were positioned near existing territories. No peafowl were ever within 20 m of the speaker at the start of the trials. The locations were at least 330 m apart from each other (mean: 441 ± 46 m); because peafowl have small ranges (though no quantitative data exists on their movement patterns; Kannan & James, 1998) and peacocks defend small territories during the breeding season (0.05–0.5 ha; Ridley, 1985), it is unlikely that we re-sampled many of the same birds.

The researcher entered a blind and setup equipment at least 15 min before the trial began. A speaker (Anchor mini-vox PB-25 speaker (frequency response: 100 Hz to 12 kHz) connected to a Sansa clip mp3 player) was positioned on the ground just outside the blind. Playback and control trials were identical except that male copulation calls were broadcast during copulation playback trials but no sound was broadcast (i.e., the speaker was turned off) during control trials. At each site, a playback and control trial were conducted (paired design; order randomized across trials) with 1–2 days separating the trials. The male copulation calls consisted of three hoots (emitted by three different adult males; recorded from captive peacocks in Durham, NC with a Sony SR-47 camcorder) that were broadcast at sound levels similar to natural calls (95 dB SPL at 1 m; ExTech 407730 Sound Level Meter; A weighting; fast setting). We used calls from multiple males for a given trial because previous work in a related species (*Tetrao tetrix*) demonstrated that females were more attracted to copulation call playbacks in which the calls were emitted by multiple males (Hovi et al., 1997); furthermore, male territories can be quite small (as little as 0.05 ha; Ridley, 1985) and displaying males can, therefore, be relatively close together. The three hoots were randomly scattered throughout a 1-min period and were then followed by 1 min of silence; 10 of these 2-min sequences were created and strung together into a single 20-min clip. A second 20-min clip was created (using different hoots from the same males as above). One of the 20-min clips (randomly selected for each copulation playback trial) was continuously broadcast throughout the duration of the trial by looping the clip. All trials were continuously recorded with a camcorder (Sony SR-47) that was located inside the blind; the researcher was constantly scanning the area and focused the camcorder on birds as soon as they were detected. The researcher remained concealed within the blind for the duration of the trials.

2.3. *Playback experiments in captivity*

Birds were tested individually in a testing cage (Figure 2). A speaker (Anchor Audio AN-MiniU1; frequency response: 100 Hz to 15 kHz) was placed (0.4 m above the ground; 1 m from the edge of the cage) on one side of the cage (randomly assigned for each trial). A bird was put into the middle of the testing cage (2 × 7 m), which was made of black plastic fencing, and was allowed to adjust to the novel environment for 10 min (pre-testing period). The researcher then initiated the playback (using an Anchor Audio Wireless Belt Pack connected to a Sansa clip mp3 player).

Playback and control trials were identical except that male copulation calls were broadcast during copulation playback trials and heterospecific calls (medium caws from American crows (*Corvus brachyrhynchos*); Verbeek & Caffrey, 2002) were broadcast during control trials. We used crow caws as control stimuli because these calls are regularly heard throughout the study area and are normally emitted at amplitude levels similar to the copulation calls. We chose not to use a different vocalization of peacocks as a control stimuli because peacock courtship vocalizations may function to attract females (see Discussion), peacock alarm calls may attract females because peafowl tend to mob predators (Yorzinski & Platt, 2012), and the function of other types of peacock vocalizations are not well characterized and could not be expected to elicit neutral responses. The male copulation calls were identical to those used in the playback experiments in the wild (three hoots randomly scattered throughout a 1-min period followed by a 1-min period of silence and then repeated) except that they were broadcast at slightly quieter levels (80 dB SPL at 1 m). Rather than only having two different clips of the copulation calls to use in the experiments (which were randomly selected for each trial in the wild), we used five different copulation clips (produced by calls from five different males; the clips were randomly selected for each trial) to avoid any problems associated with pseudoreplication; in each trial, however, females only heard the calls from one clip (and, therefore, from three different males). Even though the captive females were not normally housed with males, they had some familiarity with the males that provided the copulation call stimuli; the females were allowed to temporarily interact with some of the males in mate choice experiments that occurred in previous years.

The control (caw) playback stimuli were created using the same structure (three caws randomly scattered throughout a 1-min period followed by 1-min period of silence and then repeated). We used five different clips of the caw calls (produced by calls from six different crows; the clips were randomly selected for each trial); in each trial, however, females only heard the calls from one clip (and, therefore, from three different crows). The caw vocalizations were recorded in Ithaca, NY, USA from a banded crow population (Yorzinski et al., 2006) and likely function in territorial advertisement (Parr, 1997). One of these copulation or control clips (randomly selected for each playback trial) was continuously broadcast for one hour by looping the clip.

Three min after the playback was initiated, the researcher opened the two doors simultaneously (by pulling on clear fishing line) that were located on either side of the middle section of the cage, thus allowing the bird to approach (by moving into the side of the enclosure that was closer to the speaker) or avoid (by moving into the side of the enclosure that was farther from the speaker) the sound stimulus. A wall of black plastic was 5.0 m from each door so that the bird had to move behind these walls in order to see what was beyond them. The doors remained open for the remainder of the trial so that the bird could move between the sides of the cage. All trials were continuously recorded with a camcorder (Sony SR-47) and the researcher (J.L.Y.) was not visible to the bird during the trial.

2.4. Measurements and statistical analysis

For the playbacks in the wild, we analyzed the amount of time that females spent near the playback speaker. For each bird that approached to within 20 m of the speaker (a distance which enabled the researcher to clearly see approaching birds across testing sites given variation in understory coverage), we recorded the amount of time that the bird remained visible; we then summed this time across all females for each trial. All behaviors were analyzed based on video recordings supplemented by field observations. In one trial that was aborted early due to rain (18 min early), we analyzed data for a similarly reduced time period in its paired, control trial. Because our data was nonparametric, we analyzed differences between treatment and control conditions using Friedman tests that accounted for the paired trials.

For the playbacks in captivity, we analyzed the amount of time that females spent in the side of the cage that was closest to the playback speaker and the amount of time that females spent in the middle of the cage for the first 10 min after the female exited the middle of the cage using nonparametric Wilcoxon–Mann–Whitney tests (Proc NPar1WAY). We also examined the amount of time females spent in the side of the cage that was closest to the playback speaker compared to the amount of time females spent in the side of the cage that was farther from the playback speaker using Wilcoxon signed rank tests (testing whether the relative percentage of time spent in the side of the cage that was closest to the playback speaker was different from 50%). We only analyzed the first 10 min to avoid problems with the females habituating to the stimuli. We also analyzed whether the females first approached or avoided the sound stimulus using a chi-square analysis (Proc

FREQ). All statistics were performed with SAS (SAS Institute) or Minitab, and means \pm SE are reported. Although our sample sizes were relatively small, this did not prevent us from testing our hypothesis: we found statistically significant results that led to similar conclusions in both the wild and captive experiments (see Results).

3. Results

We conducted seven paired trials during the breeding season in the wild. Females spent more time near the speaker in response to the copulation compared to the control playback trials (copulation trials: 26.6 ± 15.9 min; control trials: 0.79 ± 0.79 min; $\chi^2 = 5.0$, $p = 0.023$; Figure 3a; see Video 1, which can be accessed via <http://booksandjournals.brillonline.com/content/1568539x>); they approached the speaker in five copulation playback trials but in only one control trial (Figure 3a).

We conducted 12 copulation and 12 control playback trials with 24 different captive peahens. The peahens were more likely to approach the copulation vocalizations compared to the control vocalizations ($\chi^2 = 13.59$, $df = 1$, $p < 0.0001$; odds ratio: 55.0; Video 1); in fact, only one female initially avoided the copulation calls whereas 10 females initially avoided the control vocalizations. The latency to approach or avoid (i.e., to first exit the middle section of the cage) did not differ between copulation and control trials (copulation trials: 13.06 ± 3.15 min; control trials: 18.69 ± 3.43 min; $z = 1.36$, $p = 0.17$). Females spent more time in the side of the cage that was closer to the playback stimulus in the copulation compared to the control trials (copulation trials: 8.80 ± 0.72 min; control trials: 3.57 ± 0.88 min; $z = 3.18$, $p = 0.0015$; Figure 3b); females spent the same amount of time in the middle of the cage in the copulation and control trials (copulation trials: 2.13 ± 1.19 min; control trials: 2.50 ± 0.74 min; $z = 1.08$, $p = 0.28$). Furthermore, in the copulation vocalization playbacks, females spent more time in the side of the cage that was closer to the playback stimulus compared to chance expectation ($T = 75.0$, $p = 0.005$); in contrast, in the control vocalization playbacks, females spent equal time in both sides of the cage ($T = 21.5$, $p = 0.18$).

4. Discussion

Our results support the hypothesis that copulation calls function to attract female mating partners: females approached the playback area in response to

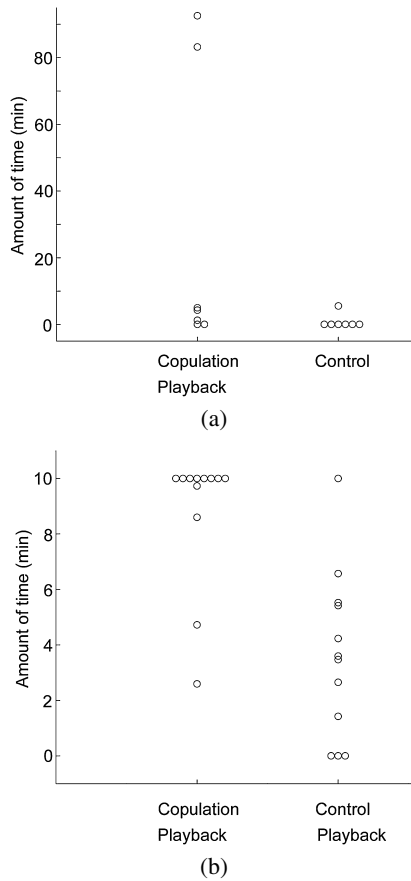


Figure 3. The amount of time that females spent near the playback speaker in (a) the wild and (b) captivity depending on whether copulation or control stimuli were broadcast. Each open circle represents a single trial.

male copulation calls in the wild and captivity. Females also spent more time near the speaker in response to copulation playback trials compared to control trials. The females’ responses in the wild and captive experiments were similar even though the experiment in the wild was based upon small sample sizes. Even though the captive peafowl were initially averse to approaching the heterospecific control (potentially because they gain no benefit by interacting with these heterospecifics and, therefore, have no immediate motivation to approach), they ultimately exhibited no preference for spending time closer or farther from these control stimuli.

Because peafowl often live in visually-occluded habitats and males establish display arenas that are scattered throughout the habitat (reviewed in Kannan & James, 1998), it may be difficult for females to locate potential mates. Females that listen to distant male copulation calls, therefore, can learn where potential mates are displaying and then approach those areas to assess males. Furthermore, because peacock copulation calls are loud and have low frequency components, females can likely hear them from relatively large distances (Bradbury & Vehrencamp, 1998). Acoustic properties of copulation calls (such as frequency) may also reveal information about the quality of the signaling male (Andersson, 1994). Females in other lekking species are similarly attracted to male courtship vocalizations. Female sage grouse (*Centrocercus urophasianus*; Gibson, 1989) and black grouse (*Tetrao tetrix*; Hovi et al., 1997) approach the area where male display vocalizations are broadcast.

In addition to copulation calls, peacocks emit other courtship vocalizations that females could use to locate males (Takahashi & Hasegawa, 2008). One such call is the 'keow' vocalization, which is primarily emitted when females are not yet present on a lek (Petrie et al., 1991; Takahashi & Hasegawa, 2008). Interestingly, the number of notes in this vocalization is correlated with mating success and may, therefore, provide females with information about male quality or age (Yasmin & Yahya, 1996; Loyau et al., 2005). Aside from the keow and hoot vocalization, another five peafowl vocalizations have been identified that are only produced by males (Takahashi & Hasegawa, 2008) and could likewise provide females with important information during the breeding season. Playback experiments could examine whether females use these other courtship vocalizations to locate mates. Because these courtship calls are emitted at different amplitudes (Takahashi & Hasegawa, 2008), it would be interesting to assess at what distances females use information from these calls. It is also possible that the identity of the male caller plays a role in female attraction (females in our wild study were completely unfamiliar with the males that produced the copulation call stimuli and females in our captive study had only minimal interaction with the males that produced the copulation call stimuli). Future playback experiments could compare the responses of females to copulation calls from familiar and unfamiliar males to determine whether male identity influences females' attraction.

Furthermore, peahens could learn about males' courtship behavior by attending to male copulation calls. Because copulation calls usually signify that males are attempting or successfully copulating with females, distant females can assess which males are most active by listening to the occurrence of copulation vocalizations. Females could then favor those popular males through mate-choice copying (Dugatkin, 1992; Pruett-Jones, 1992; Yorzinski & Platt, 2010). Because males could potentially benefit by emitting copulation calls at a higher rate, they could emit false copulation calls to give the impression that they are engaging in mating activities at higher rates than they actually are. Studies that explore what factors, such as social pressures (Hauser, 1993), maintain the honesty of this signal would be informative.

Future studies that performed playbacks at existing male display sites would reveal whether male copulation calls also function to repel male intruders (Kroodsmas & Byers, 1991) or whether they inadvertently attract unwanted competitors (Petrie et al., 1991). Males establish their display arenas nearby each other (Petrie et al., 1992) and would, therefore, benefit by warning potential competitors not to interfere with matings. However, males could be eavesdropping on their neighbors' copulation calls and attempt to interrupt matings.

Even though males in many species exhibit highly conspicuous ornaments, such as the bright feathers of the peacock's train, it can still be difficult for females to locate these males. Males can, therefore, adopt additional strategies to alert females to their locations. They can use visual tactics to gain female attention. For example, male lesser floricans (*Sypheotides indicus*) live in grasslands and perform complex displays in which they repeatedly leap out of the tall grass while fluttering their wings (Ali & Ripley, 1980). Males can also emit auditory signals to announce their locations. Loud copulation calls, such as those emitted by peacocks, clearly signal the location of displaying males. Further examination of the strategies that males use to signal their locations to females would help clarify how females find their mates.

Supplementary video

Video 1 A female in the wild approaches to within 20 m of the playback speaker and looks around after hearing a peacock copulation call

(00:10). A female in captivity exits the middle of the enclosure (00:42) to enter into the left side of the enclosure where the playback speaker is broadcasting peacock copulation calls (00:36). This video is available as part of the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/1568539x>.

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