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Deceptive Copulation Calls Attract
Female Visitors to Peacock Leks

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abstract: Theory holds that dishonest signaling can be stable if it is rare. We report here that some peacocks perform specialized copulation calls (hoots) when females are not present and the peacocks are clearly not attempting to copulate. Because these solo hoots are almost always given out of view of females, they may be dishonest signals of male mating attempts. These dishonest calls are surprisingly common, making up about a third of all hoot calls in our study populations. Females are more likely to visit males after they give a solo hoot call, and we confirm using a playback experiment that females are attracted to the sound of the hoot. Our findings suggest that both sexes use the hoot call tactically: females to locate potential mates and males to attract female visitors. We suggest that the solo hoot may be a deceptive signal that is acquired and maintained through reward-based learning.

Keywords: copulation call, signal honesty, eavesdropping, mate choice copying, learning, deception, courtship, peafowl.

In animal signaling systems, dishonesty can be evolutionarily stable if the average benefit of responding to the signal outweighs the average cost of being deceived (Maynard Smith and Harper 2003). Where the interests of signaler and receiver diverge, a dishonest signal can be maintained if it is rare (e.g., Batesian mimicry [Turner et al. 1984] and aggressive contests [Adams and Caldwell 1990]). When dishonest signals are common, however, they remain theoretically challenging to explain (Backwell et al. 2000; Rowell et al. 2006).

In peafowl (*Pavo cristatus*), males give a single high-pitched call as they rush toward a female and attempt to mount and inseminate her (Petrie et al. 1991; Takahashi and Hasegawa 2008; see video 1; videos 1 and 2 are available online). In contrast to the copulation calls of most birds, peacock hoot calls are loud enough to be heard from dis-

tances where the calling male cannot be seen. Thus, the call is a potential signal of copulatory activity to other peafowl that are out of sight of the calling male. In other species with noisy copulation calls, it is generally thought that these calls might advertise fertility (Maestripieri and Roney 2005), social rank (Clay et al. 2011), or mating success (Barclay and Thomas 1979; Barclay et al. 1979) to conspecific receivers. Recent experimental studies in both primates (Crockford et al. 2007; Pfefferle et al. 2008) and peafowl (Yorzinski and Anoop 2013) have shown that conspecifics other than the copulating pair respond to experimental playbacks of copulation calls, consistent with the idea that these calls serve a signal function to third parties.

Here we report that some males in free-living populations of peafowl in North America often give copulation hoot calls when they are alone and thus not attempting to copulate with a female (fig. 1; see video 2). These solo hoots are almost always performed when no females are in view, raising the possibility that such calls dishonestly advertise a mating attempt that did not occur. In this study, we use observation and experimental playback to test the function of this potentially deceptive call. In support of the hypothesis that hoot calls generally function as honest advertisements of male mating success, we show that preferred males attempt to copulate—and thereby give copulatory attempt hoots—more often than nonpreferred males. We then show that females are attracted to the sound of hoot calls. We also report that while some males in our study populations gave solo hoot calls frequently, others never did. We discuss the potential benefits to males of this dishonest signal and the factors that might help to maintain it at fairly high frequency in peafowl populations.
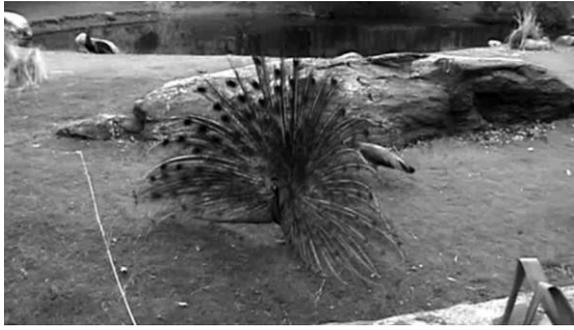
Methods

Study Populations

We studied *Pavo cristatus* peafowl at four sites between 2007 and 2010: (i) the Assiniboine Park Zoo (APZ: Man-

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Video 1: Still from video 1, available online, which shows precopulatory attempt hoots. The video, recorded at New York's Bronx Zoo in 2009, shows an example of a copulation attempt that was not successful, followed by an example of a successful copulation.

itoba, Canada; 50 ha), (ii) the Toronto Zoo (TZ: Toronto, Canada; 250 ha), (iii) the Los Angeles Arboretum (LAA: California, USA; 50 ha), and (iv) the Bronx Zoo (BZ: New York, USA; 100 ha). At all sites, the populations are self-sustaining, and birds mate on leks as described in studies of this species in its ancestral range in India (Harikrishnan et al. 2010). Study population sizes ranged from ~30 birds at TZ to >200 at both BZ and LAA. We captured males and marked them with numbered leg bands prior to the breeding season. At BZ, males were not captured but were identified by their unique plumage features and the locations of their display court territories.

In previous studies of peafowl, several traits involving the train ornament have been found to correlate with male mating success, including train length, the number of eyespots displayed in the train, and eyespot coloration (reviewed in Dakin and Montgomerie 2013). We measured train length and removed several eyespots from each captured male prior to the breeding season for a separate study of mate choice. We also photographed males performing their courtship displays during the breeding season so that we could count the number of eyespots actually displayed (see Dakin and Montgomerie 2011). Color traits measured from the eyespots included the iridescence, hues, and color contrasts of the blue-green, bronze, and purple regions (see Dakin and Montgomerie 2013 for details).

Focal Watches

We observed a total of 39 marked adult peacocks during the breeding season at APZ (May 2007, $n = 14$), TZ (June 2007, $n = 5$), and LAA (March–April 2008, $n = 20$), during 0.5–2.5-h focal watches of 1–4 marked males at a time, during peak daily lekking periods (0700–1200 and 1600–1800, local times) for a total of 355 h (80 h at APZ, 115 h at TZ, and 160 h at LAA). During focal watches, we recorded the period of attendance of each male at his display court as well as all hoot calls (both attempt hoots and solo hoots). Cloacal contact following an attempt hoot was assumed to be a successful insemination as females have not been observed ejecting sperm after they copulate. If there was at least one other male present on the lek when the attempt hoot was given, we scored this as an audience. In 2008, we also noted whether there were any females visible to the calling male during solo hoots.

To evaluate whether the hoot call might be a reliable signal of male mating success, we determined the rate of copulation attempts, successful copulations (cloacal contact), and both attempt hoots and solo hoots for each male by dividing the total number of these events by his total lek attendance time (mean $= 14.5$ h, 95% confidence interval [CI]: 12.6–16.4, $n = 39$ males) during focal watches. This allowed us to compare rates across males observed for different durations. To quantify female visitation rates as a measure of female interest in males, we counted the number of females within 5 m of each male at 5-min intervals during focal watches. We considered a female to be making a courtship visit when she was <5 m away from a male whose train was erect and not closer to any other adult male. For each male, we scored female visitation rate as the number of 5-min intervals when the male had a female visit divided by the total number of 5-min intervals he was observed on his display court.

Effect of Natural Solo Hoot Calls

To test whether solo hoot calls attracted females, we examined the two 5-min-interval observations of female visitation status before and after the call occurred to score female presence. These data were not available for all solo hoots, either because the male left the lek shortly after calling or because the hoot occurred close to the start or the end of a focal watch. Occasionally, males were observed giving several solo hoots during a focal watch. To avoid any overlap between a posthoot period and the next prehoot period, we included in this analysis only the first solo hoot that a male performed during a focal watch and any of his subsequent solo hoots that occurred >25 min later.

Playback Experiment

To test whether the sound of a hoot call would attract females independent of male behavior, we performed a playback experiment to compare the effect of a hoot with that of other typical male calls ("keow" and "ka"). Like the hoot, keow and ka are given only by adult males on their display court territories (Takahashi and Hasegawa 2008): keow is given by males when their trains are not erect; ka is given by males that are either displaying their

trains or are beginning to do so but only when females are not present (Takahashi and Hasegawa 2008; R. Dakin, personal observation). Ka and keow are always performed in bouts of repeated calls.

We recorded hoot, ka, and keow calls at LAA in March 2009 as 16-bit WAV files using a directional microphone (Audio-Technica AT-815a, Stow, OH) and an Edirol R-09 recorder (Roland, Los Angeles). We selected 15 recordings of each call type from at least five different males to use as stimuli in the playback experiment. Our hoot stimuli included both attempt hoots ($n = 10$) and solo hoots ($n = 5$). We found no significant difference in the fundamental frequency ($F_{1, 13} = 2.17$, $P = .16$) or duration ($F_{1, 13} = 2.34$, $P = .15$) of hoots given in these two different contexts (measured using Raven v1.3; Bioacoustics Research Program 2008). A separate study at APZ also found that there is no significant difference in the fundamental frequency of these two types of hoot calls (A. Freeman, unpublished data on 56 attempt hoots and 10 solo hoots). Mean fundamental frequencies for call stimuli used in the playback experiment (hoot = 756 Hz, ka = 687 Hz, keow = 800 Hz; $n = 15$ each) were nearly identical to those reported in an earlier study of peafowl calls in a population in Japan (Takahashi and Hasegawa 2008). The mean duration of hoot stimuli was 0.9 s (range 0.4–1.7), whereas ka and keow stimuli lasted an average of 3.1 s (range 1.2–7.3) and 5.6 s (range 2.8–8.0), respectively.

We used the normalizing function in Adobe Soundbooth CS3 (Adobe Systems, San Jose, CA) to amplify each stimulus recording to the same maximum level. We de-

Video 2: Still from video 2, available online, which shows six examples of solo hoots, all recorded at the Los Angeles Arboretum in 2012 by Kathy Kerran.

termined the appropriate levels for playback by measuring the peak sound pressure levels (SPLs) of peacock calls at LAA in March 2009 using a digital sound level meter (RadioShack 33-2055, C-weighting) at a distance (d) from the calling male, measured to the nearest meter after the call was recorded. We used these measured SPLs to calculate the SPL_{ref} at a distance of 1 m, according to the distance law:

$$SPL_{ref} = SPL - 20 \log_{10} \frac{d}{d_{ref}},$$

where $d_{ref} = 1$. The mean SPL_{ref} was 79 dB ($n = 14$) for the hoot, 92 dB ($n = 34$) for the ka, and 90 dB ($n = 12$) for the keow (note that these calls were not the same calls

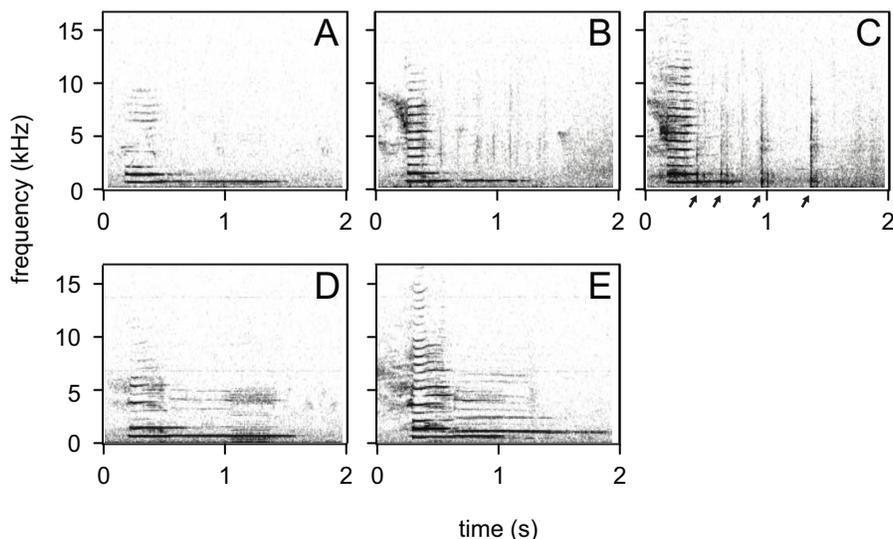**Figure 1:** Spectrograms for attempt hoot (*A–C*) and solo hoot (*D, E*) calls. The calls in *A, B* were given during unsuccessful copulation attempts, whereas the call in *C* was followed by a successful copulation. In *C*, arrows indicate the soft clucks given by the female during copulation. All spectrograms were made using Raven v1.3 with Hann windows (length = 0.0153 s, frequency spacing = 93.8 Hz).
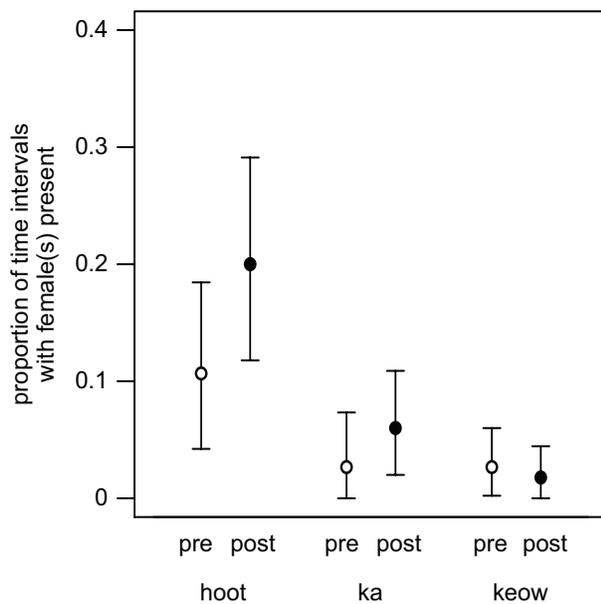
Figure 2: Response of females to experimental playback of hoot, ka, and keow calls, showing the mean proportion of 1-min time intervals where at least one female was noted near the playback speaker before (open circles) and after (filled circles) call playback. Data are means from 45 playback events across 15 experimental trials (with 3 repeated playback events per trial). Error bars show 95% confidence intervals calculated by bootstrapping (100,000 replicates).

recorded for playback stimuli). We used these estimates to adjust the volume of speaker playback to the approximate levels of natural peacock calls.

We selected 15 focal display courts ($n = 10$ at BZ; $n = 5$ at LAA) on eight different leks and conducted the playback experiment in May 2009 (BZ) and March 2010 (LAA). At each focal court, we ran a separate 60-min trial for each of the three call types (hoot, ka, keow) on three different days over a 3–8-d period, such that the experiment consisted of a balanced set of 15 replicates. The order of trials was rotated so that all possible orders were used about equally often. Trials were conducted between 0700–1200 and 1600–1800 local time and were begun only when the male on the focal display court was present. To account for differences in peak female visitation times between display courts, we began all trials at a given focal court at approximately the same time of day (mean span of start times per male = 42 min, range 3–91 min, $n = 15$ males).

The playback apparatus consisted of a single Pignose 7-100 speaker connected to a portable mp3 player (Apple iPod, Cupertino, CA) operated by an observer 6 m away. The speaker was positioned near the perimeter of the lek, 10–30 m from the focal display court, within the range of typical nearest-neighbor distances for peacock display courts (mean 23.3 m, range 9.4–35 m in the LAA population). We

played a single call at 10, 30, and 50 min after the start of each trial, selecting calls from a randomly ordered list such that each recording was used about equally often and no trial had duplicate stimuli. At 1-min intervals, we recorded the presence of any females within 30 m of the playback speaker, as this was the minimum distance of unobstructed visibility at all sites. We summarized these data into six 10-min periods per trial, representing pre- and postcall periods for each call played. We also noted any calls given by the male on the focal display court. On average, these focal males gave 0.6 (0.2–1.1) hoots/h, 5.8 (3.6–7.9) ka bouts/h, and 1.8 (0.1–2.5) keow bouts/h ($n = 45$ trials on 15 focal courts). Thus, three call playbacks per hour are realistic for a peacock lek, which typically has 1–10 males present (Petrie et al. 1991; Dakin and Montgomerie 2013).

Statistical Analysis

Analyses were performed using R 3.0.1 (R Development Core Team 2013). We used generalized linear models (GLMs) to test relations between hoot call rates and male mating success, as well as between hoot call rates and male traits, controlling for study site. We constructed generalized linear mixed models (GLMMs) using the R package lme4 with binomial error distributions to test the effect of natural solo hoots on females, including a random effect to account for repeated observations of the same focal male. We used similar methods to analyze binomial GLMMs for the playback experiment, including male ID as a random effect to control for repeated measures at each focal court. We controlled for study site and date in all GLMMs to account for the decrease in female activity on leks over the breeding season (Dakin 2013, p. 98). When analyzing the playback experiment, we also controlled for trial order. Dispersion parameters for binomial GLMMs were between 0.89 and 1.04, indicating that models were neither over- nor underdispersed (data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.vt562 [Dakin and Montgomerie 2014]).

Results

Attempt Hoots and Solo Hoots

We observed 432 hoot calls, of which 69% ($n = 298$) were attempt hoots (video 1). Only about 23% ($n = 68$) of these attempt hoots ended in cloacal contact, and thus most copulation attempts were not successful. The remaining 134 hoots (31%) were solo hoots, given by males with erect trains when they were not attempting to copulate with a female (fig. 1; video 2). Occasionally, solo hooting males picked up an object in their bill or pecked at the ground immediately after hooting, behaviors that

are similar to the stereotyped courtship feeding or tidbitting displays of other galliform birds (Williams et al. 1968; Stokes and Williams 1971; video 2).

Males were almost never observed solo hooting when females were visible nearby (e.g., only 3 of 80 solo hoots in 2008 were given in the presence of females). In contrast, the presence of other males did not seem to affect whether a male solo hooted, as other males were often present during solo hoots (70/132; 53%). There was no significant difference in the frequency of attempt hoots (162/298; 54%) and solo hoots in presence of other males (two-tailed Fisher's exact test, $P = .83$).

Hoot Rates and Male Mating Success

On average, males gave 0.67 (0.42–0.91) attempt hoots and 0.31 solo hoots (0.10–0.53) per hour ($n = 39$ males). However, the rate of solo hooting varied widely among males: 15/39 males were never seen solo hooting, whereas 1 male at APZ averaged 4.0 solo hoots/h. When this male was excluded, the average rate of solo hoots was 0.22/h (0.12–0.31) and the total hoot rate (attempt + solo) was 0.89/h (0.62–1.16; $n = 38$ males).

Successful males gave attempt hoots most often, as there was a significant positive relationship between attempt hoot rate and copulation rate among males (GLM controlling for study population, standardized $\beta = 0.92$, $F_{1, 35} = 63.4$, $P < .0001$, $n = 39$). There was also a significant positive relationship between attempt hoot rate and female visitation rate (standardized $\beta = 0.82$, $F_{1, 35} = 35.7$, $P < .0001$), indicating that preferred males more often gave attempt hoots. Preferred males were not more likely to solo hoot, however, as there was no significant relation between solo hoot rate and either copulation rate ($F_{1, 35} = 0.1$, $P = .76$) or female visitation rate ($F_{1, 35} = 1.0$, $P = .32$).

We used total hoot rate (attempt + solo) to assess whether the hoot signal is an honest indicator of male mating success. Total hoot rate (attempt + solo) was significantly positively related to both female visitation rate (standardized $\beta = 0.64$, $F_{1, 35} = 7.0$, $P = .01$) and copulation rate (standardized $\beta = 0.46$, $F_{1, 35} = 16.6$, $P = .0002$). Thus, despite nearly a third of all hoots recorded in our study populations being solo, a male's total hoot rate was a reliable signal of his mating success (and female preference). There was no relation between male solo hoot and attempt hoot rates ($F_{1, 35} = 1.00$, $P = .32$), so we conclude that solo hoots are not simply the result of a male having a tendency to give a lot of calls. Results of these analyses were the same when excluding the male with the highest solo hoot rate (i.e., 4.0 solo hoots/h).

Neither solo hoot rates nor attempt hoot rates were significantly related to any measures of male ornamentation that have previously been shown to be related to male mat-

ing success, including train length, number of eyespots displayed, and eyespot hue and iridescence (GLMs controlling for population, all $F_{1, 32} < 1.3$, all $P > .25$).

Effect of Natural Solo Hoot Calls

We compared the female visitation status of solo hooting males immediately before and after they gave the solo hoot call and found that males were more likely to attract at least one female visitor in the period following a solo hoot than during the immediately preceding period (binomial GLMM, $\beta = 1.36$, SE $= 0.58$, $z = 2.3$, $P = .02$, $n = 131$ solo hoots given by 24 males). On average, there was a 14.4% increase in the probability that a solo hooting male would attract a female in the fitted model. Males almost never copulated during the period in which they were observed after giving a solo hoot: only 2/78 solo hoots were followed by a copulation ($n = 24$ males, excluding repeated solo hoots given by the same male during a single observation period). Average copulation rates for solo hooting males in the 28.5 min (23.4–33.6) period observed after solo hooting were not significantly different from the baseline rates of copulation by those same males (paired t-test, $t = 0.89$, $P = .38$, $n = 24$).

Playback Experiment

During experimental trials, there were no females near the playback speaker during 90% (1,624/1,800) of 1-min intervals during observation periods, and copulations were rarely observed (only 5/45 trials). During trials where hoot calls were played, females were significantly more likely to approach the speaker in the 10-min period after call playback than during the 10-min period before (binomial GLMM, $\beta = 1.03$, SE $= 0.23$, $z = 4.5$, $P < .0001$; fig. 2). On average, there was a 9.4% increase in the probability of a female approaching in the fitted model. There was no significant effect of trial order in the experiment (likelihood ratio test, $\chi^2 = 1.9$, $P = .16$, df $= 1$). There was, however, a significant interaction between call type and call effect ($\chi^2 = 7.9$, $P < .02$, df $= 2$; fig. 2). Planned contrasts revealed that the hoot was significantly more likely to attract females than the keow ($\beta = 1.68$, SE $= 0.68$, $z = 2.5$, $P = .01$) but not the ka ($\beta = 0.08$, SE $= 0.62$, $z = 0.13$, $P = .90$) in this model.

Discussion

The hoot call that peacocks use when attempting to copulate can be heard at a distance and thus provides a signal to other individuals that a male has attempted to copulate with a female visitor. This call also provides a reliable signal that the calling male is a successful one, since the total

amount of calling by a given male is closely related to his female visitation and copulation rates. The results we present here demonstrate that distant females can hear and respond to this call, since hoot playbacks attracted female visitors at least as effectively as other calls that males gave during their courtship displays (fig. 2). These results suggest that social cues that indicate the presence of other females may be important for peahen mate search and choice (Gibson et al. 1991; Westneat et al. 2000; Danchin et al. 2004), although further study is needed to evaluate whether hoot calls actually influence mate choice in this species. As in other lek-breeding species, reproductive skew among peacocks tends to be very high, with few males obtaining most of the copulations in a given population (Loyau et al. 2005; Dakin and Montgomerie 2011). Petrie (1994) showed that the offspring of these preferred peacocks tend to grow faster and are more likely to survive their first 2 years than offspring of nonpreferred males, suggesting that peahens may gain considerable genetic benefits by mating with the most successful males—and, by extension, by copying other females. On the other hand, copying the choices of other females might entail a fertility cost if preferred males experience sperm depletion. The most successful peacock in our study achieved 0.9 copulations/h, a rate that could reduce his fertility, based on studies of other polygynous birds (Bakst and Cecil 1991).

We report here that some peacocks also used the copulatory hoot call when they were not attempting to mate with any female, a behavior that we observed often in four widely separated peafowl populations. We also showed here that solo hooters often attracted new female visitors after giving the call. Furthermore, we infer from our playback experiment that this effect on females is independent of factors affecting the motivation of males to give the call.

We argue that these solo hoots are a form of deception for three reasons: (i) the hoot most often indicates that a copulation attempt has taken place; (ii) females are rarely in view when males give solo hoot calls (i.e., these calls are heard and not seen by female receivers); and (iii) although total use of the hoot call (attempt + solo) is related to male mating success, the solo hoots are dishonest in this context. According to signal theory, deceit should also be costly for the receiver (Bradbury and Vehrencamp 2011); further study is needed to establish this for solo hoots. If females gain genetic benefits by mating with preferred males (Petrie 1994), then responding to solo hooting might lead to mate choice errors that incur a considerable cost. On two occasions, we observed females copulating with solo hooting males soon after they gave the call, but we cannot know for certain whether females chose these males because of their solo hoots. The two males who achieved copulation after solo hooting were relatively successful (one male obtained one other copulation, and the

other obtained three; they were the two most successful males in the TZ population). Females may also incur energetic or opportunity costs by visiting solo hooters, especially if females take longer to locate preferred, higher-quality males as a result of responding to those calls. This cost is likely to be small compared to the cost of mating with a low-quality male.

What are the benefits of solo hooting for males? There was no correlation between solo hoot rate and copulation rate overall, and as mentioned above, most solo hooters did not gain copulations immediately after giving the call, though they did temporarily increase their female visitation rates. Thus, we have no evidence of strong selection on this behavior, although we cannot rule out the possibility that solo hooters were visited more often than they would have been otherwise or that they obtained slightly greater paternity than they would have otherwise. The solo hoot (and also attempt hoots) may thus provide a small advantage to males by increasing the rate that females will visit and eventually copulate with them.

Interestingly, despite the fact that the solo hoot was fairly common (nearly a third of all hoot calls), 40% of the males in our study (15/39) were never seen solo hooting. Why don't more males use the solo hoot? One possibility is that this behavior is learned and that only some males have the opportunity to learn to use it. Experimental studies of birds and mammals have shown that increased access to opposite-sex individuals can reinforce behaviors, even if that access is purely visual and does not involve copulation (e.g., Gilbertson et al. 1975; see Crawford et al. 1993 for a review). In peafowl, if hoot calls encourage females to visit and if this experience is rewarding for males (in the sense of an internal, physiological reward, independent of any fitness benefit), then solo hooting may be reinforced as a result. Since female visits on leks tend to be rare and highly biased toward certain males, it is possible that some males never have the chance to learn the association between hoot calls and female visits. Learning could also explain why solo hooting is common in free-living populations but does not occur in some captive populations where males are limited in their exposure to females (e.g., Yorzinski and Anoop 2013).

We propose that reward-based learning—a powerful and ubiquitous mechanism in animals—may be involved in the acquisition of this and other dishonest signals, such as deceptive alarm calls (Munn 1986) that may be reinforced through food rewards (Flower 2011) or the presence of potential mates (Bro-Jørgensen and Pangle 2010). Such learning has not been considered in theoretical models to date but could have implications for signal honesty and evolutionary dynamics. Additional work is needed to establish whether the solo hoot is costly for females, whether reward-based learning is in fact involved in the acquisition

of this signal, and how learning might influence the maintenance of deception in this and other signal systems.

Acknowledgments

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