# Peafowl antipredator calls encode information about signalers

Jessica L. Yorzinski[a)]

*Duke Institute for Brain Sciences and Center for Cognitive Neuroscience, Duke University, Durham, North Carolina 27710*

Animals emit vocalizations that convey information about external events. Many of these vocalizations, including those emitted in response to predators, also encode information about the individual that produced the call. The relationship between acoustic features of antipredator calls and information relating to signalers (including sex, identity, body size, and social rank) were examined in peafowl (*Pavo cristatus*). The "bu-girk" antipredator calls of male and female peafowl were recorded and 20 acoustic parameters were automatically extracted from each call. Both the bu and girk elements of the antipredator call were individually distinctive and calls were classified to the correct signaler with over 90% and 70% accuracy in females and males, respectively. Females produced calls with a higher fundamental frequency ($F_0$) than males. In both females and males, body size was negatively correlated with $F_0$. In addition, peahen rank was related to the duration, end mean frequency, and start harmonicity of the bu element. Peafowl antipredator calls contain detailed information about the signaler and can potentially be used by receivers to respond to dangerous situations. © *2014 Acoustical Society of America.*
[http://dx.doi.org/10.1121/1.4861340]

## I. INTRODUCTION

Animals frequently emit vocalizations in response to external events. They often call when encountering a predator, discovering food, or interacting with conspecifics (Cheney and Seyfarth, 1990; Bradbury and Vehrencamp, 2011). Receivers that decipher these vocalizations learn about the contexts in which the calls were produced (Marler, 1977). In addition to providing contextual information, these vocalizations can also encode information about the signaler (Bradbury and Vehrencamp, 2011). They can reveal the sex and identity of the caller (Falls, 1982) as well as information about body size and social status (Vannoni and McElligott, 2008). The current study investigated the information that the antipredator vocalizations of peafowl (*Pavo cristatus*) encode about the signaler.

### A. Sex and identity

Many vocalizations encode the sex and individual identity of callers. These vocalizations are emitted in different situations, including parent-offspring interactions, territorial defense, courtship, and group cohesion (reviewed in Falls, 1982). The antipredator calls of some species also contain sex and individual identity information (Farquhar, 1993; Fischer *et al.*, 2001; McCowan and Hooper, 2001; Fischer *et al.*, 2002; Randall *et al.*, 2005; Yorzinski *et al.*, 2006; Kennedy *et al.*, 2009; Schneiderová and Policht, 2010; Matrosova *et al.*, 2011; Patel and Owren, 2012) and receivers can use this information to discriminate among callers (Hare and Atkins, 2001; Blumstein and Daniel, 2004; Sproul *et al.*, 2006).

Individuals that can distinguish the sex or identity of alarm callers may differentially respond to danger. If individuals also emit antipredator calls to advertise their quality to potential mates (Slagsvold, 1984), males may preferentially respond to the antipredator calls of females. Animals that discriminate among alarm callers can differentially respond to reliable and unreliable signalers (Cheney and Seyfarth, 1988; Hare and Atkins, 2001; Blumstein *et al.*, 2004). Furthermore, receivers can better evaluate danger levels by assessing how many different individuals are emitting alarm calls. If multiple individuals are emitting alarm calls, it is more likely that a predator is present than if only a single individual is emitting the calls (Blumstein *et al.*, 2004).

### B. Body size

Vocalizations emitted in many different contexts contain information about a caller's body size. Acoustic features of calls can be constrained by the size of callers. Larger individuals of frogs, toads, and birds emit calls with lower fundamental frequencies ($F_0$) than smaller individuals (e.g., Davies and Halliday, 1978; Brown *et al.*, 1996; Appleby and Redpath, 1997; Bee *et al.*, 1999; Barbaud *et al.*, 2000; de Jong *et al.*, 2007; but see Cardoso *et al.*, 2008). $F_0$ is the rate at which the vocal folds of the larynx open and close, which can be influenced by the length of the vocal folds (Titze, 1994). Body size can also be reflected in formant frequencies, resonances of the vocal tract that are determined by the shape and length of the vocal tract (Fitch, 1997).

In some species, courtship vocalizations reveal the body size of males. Both males and females could potentially use this size information to adjust their courtship behavior (Vannoni and McElligott, 2008). In fact, red deer stags were more attentive in response to synthetic calls that indicate larger compared to smaller rivals (Reby *et al.*, 2005).

[a)]Author to whom correspondence should be addressed. Electronic mail: jly5@duke.edu

Vocalizations produced during direct aggressive interactions can also reflect body size and provide critical information to competing males. Acoustic properties of fish vocalizations during competitive feeding reflected the size of callers and could influence rates of agonism (Amorim and Hawkings, 2005).

It is not known whether antipredator vocalizations also encode body size information. Body size is a key factor that influences predator-prey relationships (Wilson, 1975; Peters, 1983). If antipredator vocalizations contain body-size information, it is possible that conspecifics use this information when responding to dangerous situations. Conspecifics may preferentially respond to the calls of individuals that are similar in size to themselves because risk levels may likewise be similar (Gotmark and Post, 1996).

### C. Rank

Acoustic signals can encode an individual's position within the dominance hierarchy (Fischer *et al.*, 2004; Vannoni and McElligott, 2008). Information about an individual's social rank can reflect aspects of the caller's quality. Acoustic properties of baboon advertisement calls are related to dominance and change when individuals fall within the hierarchy. Receivers can potentially listen to these advertisement calls to learn about a caller's competitive abilities (Fischer *et al.*, 2004). Courtship calls in fallow deer contain information about male rank. Because male dominance is tightly linked to mating success, females may be evaluating male courtship calls to assess rank relationships and inform their mating decisions (Vannoni and McElligott, 2008).

Antipredator calls may also contain information about rank that receivers can use when responding to dangerous situations. An individual's social rank can influence its antipredator behavior. Subordinate individuals often take greater risks when responding to predators (Hegner, 1985; Hogstad, 1986). Compared to high-ranking individuals, low-ranking willow tits were quicker to approach an area where a predator was previously located and were therefore exposing themselves to greater danger (Hogstad, 1986). Dominance status can also influence vigilance levels. In some species, high-ranking individuals allocate more time to scanning for predators compared to subordinate individuals (Krams, 1998) but the opposite may be true in other species (Waite, 1987).

Because high- and low-ranking individuals differ in their antipredator strategies, receivers that can distinguish antipredator calls based on the dominance status of the signaler may learn additional information about the antipredator context.

### D. Current work

Peafowl are an appropriate species in which to examine the information encoded in antipredator vocalizations. Peafowl are a lekking species, in which males display on scattered arenas during the breeding season, but they also form flocks that consist of multiple males and females (Ali and Ripley, 1969; de Silva *et al.*, 1996). They emit a variety of antipredator calls in response to potential threats (Johnsingh and Murali, 1978; Takahashi and Hasegawa,

2008; Yorzinski and Platt, 2012). One of their most commonly emitted antipredator vocalizations is the "bu-girk" call, a relatively loud call emitted by both sexes that includes two elements ("bu" and "girk"; Takahashi and Hasegawa, 2008; Yorzinski and Platt, 2012).

The acoustic features of the bu-girk antipredator call of peafowl were examined to determine whether they encode information about the signaler. In particular, the calls were analyzed to assess whether they revealed information about the sex and identity of the caller. In addition, the calls were examined to determine whether they contained information about the size and social rank of the callers.

## II. METHODS

### A. Animals and housing

The acoustic properties of bu-girk antipredator calls were investigated in a captive population of peafowl from June to August 2012 (post-breeding season) in Durham, North Carolina (36.01 N, 79.02 W) during the daytime between 7:00 and 14:00. The females and males were housed in outdoor enclosures (female enclosure: 46-m perimeter, 33 birds; male enclosure: 92-m perimeter, 14 birds) within a wooded area. For each trial, a bird was captured from its enclosure and immediately transported to an outdoor cage (2.78 km away; 45-m perimeter) within a wooded area of the Duke Forest Teaching and Research Laboratory. Due to transport and experimental setup time, the recording sessions began approximately 30 min after the birds were captured. Because the birds were regularly transported from their enclosure to additional cages (for use in other studies), they were familiar with this process. The body size of each bird was determined by measuring the length of the tarsus and metatarsus (using a Neiko digital caliper, Neiko Tools, Wenzhou, Zhejiang, China; model number: 01409 A; ±0.03 mm accuracy). The tarsus is a good predictor of overall body size in birds (Senar and Pascual, 1997). The tarsus and metatarsus were measured by taking the sum of the tarsus and largest metatarsus (excluding the claw) for each leg (Petrie *et al.*, 1991) and then averaging these two values. Further details on this captive population are described in Yorzinski and Platt (2012) and Yorzinski and Anoop (2013).

### B. Acoustic recording and analysis

The antipredator vocalizations of nine adult females and nine adult males were recorded to test whether the calls varied by sex, individual, and body size. For each trial, the researcher elicited antipredator vocalizations by approaching the bird and attempting to capture it. When the bird began emitting antipredator vocalizations, the researcher stopped pursuing the bird and only resumed pursuit if the bird stopped emitting vocalizations. The vocalizations were recorded with a Sennheiser K6 microphone (Sennheiser electronic cooperation, Wedemark, Germany) with an ME62 omnidirectional capsule that was connected to an M-audio Microtrack II audio recorder (Cumberland, RI) (sample rate: 44.1 kHz; sample size: 16 bit width; audio format: wav). Each trial lasted approximately 15–30 min. Each bird was

tested in at least four trials that were separated by several weeks [mean ± standard error (SE): 17 ± 2 days; range: 1–55 days]. Five of these birds failed to vocalize during one of the first four trials, so their vocalizations were recorded in a fifth trial.

The acoustic features of the bu-girk calls (see Fig. 1) were analyzed from Fourier-based spectrograms using Luscinia sound-analysis software (Lachlan, 2007; 150-Hz, high-pass filter; 15 kHz max. frequency; 20-msec, Gaussian analysis window; 1-msec time-step; 44.1-kHz sample rate). High-pass filtering at 150 Hz removed low-frequency background noise, and this cutoff was lower than the minimum
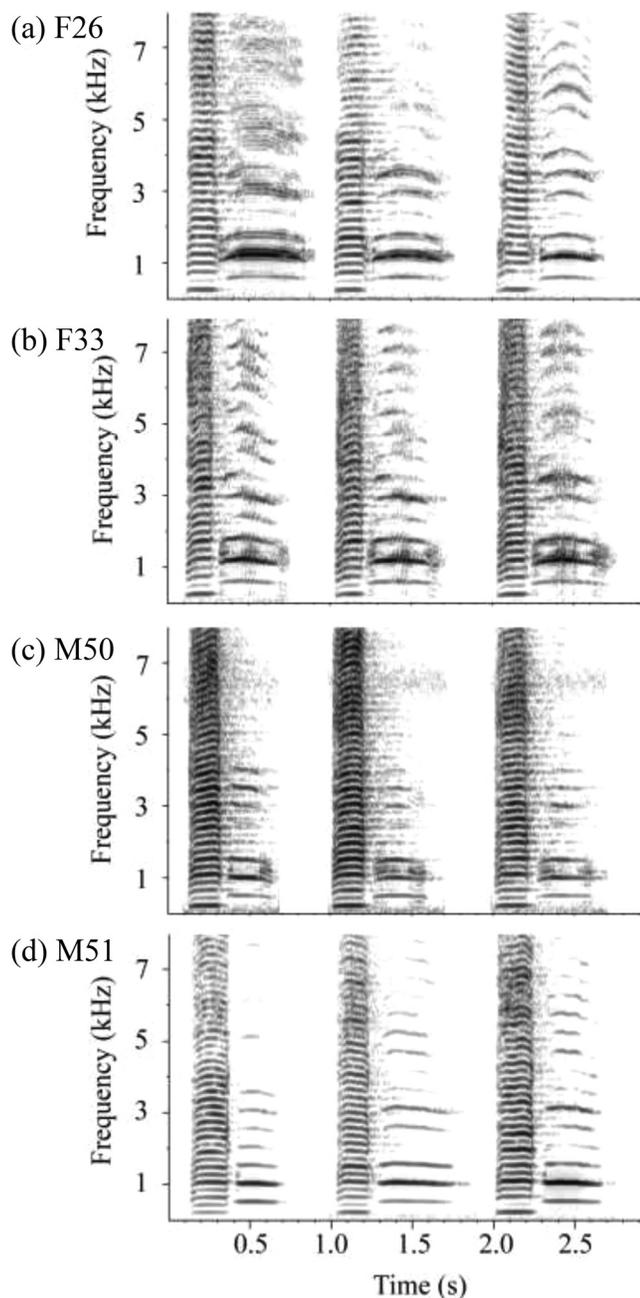


(a) F26

(b) F33

(c) M50

(d) M51

FIG. 1. Example spectrograms of the bu-girk calls (Lachlan, 2007; 150 Hz high-pass cutoff filter; frame length: 20 msec; time step: 1 msec; Windowing function: Gaussian) of four peafowl (the spacing between the calls is not meaningful). Two individuals are females [(a): F26; (b): F33] and two individuals are males [(c): M50; (d): M51].

frequency of the calls (see Table I). Using a 20-ms Gaussian analysis window provided 65-Hz frequency resolution.

The birds emitted many bu-girk vocalizations during each of their four trials (mean ± SE: 38 ± 3 calls; range: 10–147 calls) but only 5 calls from each trial were randomly selected for the analyses. Therefore, 20 calls from each bird that were recorded on 4 different days were used in the analyses and all of these calls were emitted when the bird was on the ground (i.e., neither flying nor immediately landing after flight). Because the vocalizations of a given bird were sampled across multiple days and during different times of the day, background noise did not likely vary systematically within the calls from a particular bird. The two elements of the bu-girk call (bu and girk) were analyzed separately.

For each element, the software automatically calculated 20 acoustic measurements. It calculated the element duration as well as the mean, maximum, minimum, start, and end values of the mean frequency, $F_0$, and harmonicity. The $F_0$ was estimated through a spectrogram-based, harmonic-peak search algorithm. Harmonicity measured the noisiness of the element by testing how well the signal fits a harmonic model based on $F_0$. Harmonicity values close to zero indicate that the sound is noisier while values close to one indicate that the sound is less noisy. The software also calculated the upper bandwidth limit (frequency at which 5% of the total energy of the element lies above), lower bandwidth limit (frequency at which 5% of the total energy of the element lies below), median peak frequency (median of the peak frequency measures, which are the frequencies of highest amplitude taken at each time slice within the element), and overall peak frequency (frequency at which there is the most energy in the power spectrum across the entire element).

## C. Rank

An additional study was conducted from September to October 2012 during the daytime between 7:00 and 19:30 to investigate whether the antipredator calls encode information related to rank. Because of limitations in the number of male birds, rank relationships were only investigated in females. Antipredator vocalizations were elicited using the same methods as above, except that each female was only sampled in one trial; five of the resulting bu-girk calls were randomly selected for each individual ("rank dataset").

Because the peahens had been housed together for nearly 2 years, it was assumed that their dominance hierarchy was stable. Rank observations (46 h total) were made during times when the birds were fed. A bird was considered dominant when it pecked, displaced, or jumped atop another bird. In cases where the dominance order between two birds had not yet been determined, these birds were isolated together so that their interactions could be observed. Rank order between every dyad in the flock was determined. Because there were reversals within the dominance hierarchy, rank was calculated using David's score (Bang et al., 2010). Antipredator calls and rank order were collected from all of the females (n = 33) within the flock. To ensure that harmonicity was correlated with rank (see Sec. III) and not simply with background noise (cf. Blumstein and Chi, 2012), a 50-msec period

Jessica L. Yorzinski: Peafowl antipredator calls

TABLE I. Descriptive statistics (mean ± SE) for the 20 acoustic parameters of the bu and girk elements of peafowl antipredator calls.

| | bu | | girk | |
| | Female | Male | Female | Male |
|---|---|---|---|---|
| Duration (msec) | 175.9 (1.4) | 181.2 (2.0) | 402.1 (5.9) | 378.4 (7.5) |
| Mean frequency (Hz) | | | | |
| Mean | 4987.6 (63.4) | 4756.0 (65.2) | 2982.6 (46.1) | 2636.0 (36.5) |
| Maximum | 5748.8 (70.8) | 5531.5 (73.5) | 3804.4 (58.0) | 3541.4 (46.0 |
| Minimum | 2241.4 (56.9) | 1765.9 (54.8) | 1566.9 (28.6) | 1493.6 (30.9) |
| Start | 2241.6 (56.9) | 1771.4 (54.8) | 3232.9 (54.2) | 3410.9 (52.0) |
| End | 4511.9 (46.1) | 4423.5 (49.8) | 1625.2 (31.0) | 1572.4 (34.4) |
| $F_0$ (Hz) | | | | |
| Mean | 234.32 (1.0) | 214.0 (0.9) | 552.6 (1.9) | 509.8 (1.5) |
| Maximum | 241.9 (1.1) | 221.2 (1.0) | 578.4 (2.4) | 538.1 (2.3) |
| Minimum | 207.4 (1.1) | 190.1 (0.9) | 501.0 (2.4) | 481.1 (1.6) |
| Start | 210.0 (1.2) | 194.6 (1.0) | 527.3 (2.9) | 513.9 (2.9) |
| End | 239.7 (1.0) | 218.3 (0.9) | 525.1 (2.7) | 494.3 (1.7) |
| Harmonicity | | | | |
| Mean | 0.70 (0.0034) | 0.69 (0.0026) | 0.79 (0.0053) | 0.81 (0.0058) |
| Maximum | 0.79 (0.0036) | 0.76 (0.0028) | 0.92 (0.0044) | 0.92 (0.0050) |
| Minimum | 0.58 (0.0027) | 0.57 (0.0016) | 0.55 (0.0032) | 0.59 (0.0055) |
| Start | 0.64 (0.0046) | 0.62 (0.0031) | 0.58 (0.0046) | 0.61 (0.0058) |
| End | 0.63 (0.0038) | 0.60 (0.0029) | 0.67 (0.0071) | 0.78 (0.0111) |
| Bandwidth limit (Hz) | | | | |
| Lower | 851.2 (25.5) | 780.0 (24.4) | 1014.4 (12.1) | 917.3 (12.7) |
| Upper | 6939.0 (115.0) | 6565.0 (126.0) | 2555.6 (66.3) | 2126.7 (63.1) |
| Peak frequency (Hz) | | | | |
| Median | 2029.0 (59.5) | 1998.5 (55.5) | 1158.4 (10.9) | 1070.2 (10.1) |
| Overall | 2001.3 (69.2) | 1907.2 (55.4) | 1170.9 (11.8) | 1068.6 (9.9) |

immediately before the onset of each of the five bu elements from each bird was also analyzed and the mean harmonicity parameter from this background noise was calculated.

## D. Statistical analysis

Stepwise discriminant-function analyses and generalized linear models were used to assess which of the 20 acoustic parameters differed among sex, individuals, body size, and rank. Discriminant-function analysis uses a classification procedure to identify a linear combination of quantitative predictor variables that most accurately characterizes differences among groups. The percentage of cases correctly categorized by the classification procedure (correct classification) is compared to the percentage of cases that would be correctly classified by randomly assigning the cases into categories (prior probability). The stepwise procedure reduces the number of variables used in the discriminant-function analysis by selecting those that have the best discriminatory power. Because the data being categorized are used to build the classification function, the error rate may be biased. To reduce this bias, a leave-one-out cross-validation procedure was used. This procedure excludes the first observation from the data set, builds a classification function based on the remaining observations, and then classifies the first observation. Next, the first observation is returned to the data set, the second observation is removed, and the process is repeated until all of the observations have been classified (Tabachnick and Fidell, 2001).

Seven main analyses were performed on the antipredator calls. First, a stepwise discriminant-function analysis with cross-validation was performed on each of the call elements to determine if the calls could be distinguished by sex; a follow-up discriminant-function analysis was performed using the acoustic parameters from both of the call elements that were selected by the stepwise discriminant-function analyses. Second, a stepwise discriminant-function analysis with cross-validation was performed on each of the call elements for male and female vocalizations to determine if the calls were individually distinctive. Another discriminant-function analysis was performed on the male and female vocalizations using the acoustic parameters from both of the call elements that were selected by the stepwise discriminant-function analysis; the centroid plots of the first and second canonical variables from these discriminant-function analyses were created. An error reduction rate (Bachorowski and Owren, 1999) was calculated as follows:

$$\text{Error reduction} = \frac{(100 - \text{chance rate}) - (100 - \text{observed rate}) \times 100}{(100 - \text{chance rate})}.$$

Third, a factor analysis with a principal components method of extraction and varimax rotation was performed to reduce the 20 acoustic parameters to orthogonal factors (Tabachnick and Fidell, 2001) for each of the call elements. Nine factors were extracted for the bu element analysis but

only eight factors were extracted for the girk element analysis because none of the acoustic parameters loaded strongly on the ninth factor for the girk element. A repeated measures generalized linear model analysis was performed on each orthogonal factor so that sex effects were controlled [$y$ = sex + individual(sex) with individual as a random variable].

Fourth, a generalized linear model [with individual identity (ID) as a repeated measure] investigated the relationship between mean $F_0$ and body size (measured using the tarsus and metatarsus). Fifth, a generalized linear model (with individual ID as a repeated measure) explored the relationship between acoustic parameters and rank. A stepwise model selection procedure first identified which of the 20 acoustic parameters best predicted rank and those parameters were then entered into the generalized linear model. Sixth, a generalized linear model (with individual ID as a repeated measure) examined the relationship between body size, $F_0$, and rank. Finally, a generalized linear model (with individual ID as a repeated measure) examined the relationship between rank and the three acoustic features of the bu element (see Sec. III) that were related to rank. The discriminant-function analyses and generalized linear models were performed in SAS (version 9.3), the factor analyses were performed in Minitab (version 15.1), and the canonical plot was generated in JMP (version 10.0).

## III. RESULTS

### A. Acoustic properties of bu-girk call

The antipredator call of peafowl was approximately 570 msec in duration (Fig. 1; Table I). The girk element (390 msec) was nearly twice as long as the bu element (179 msec). The mean frequency at the start of the bu element (2.0 kHz) was less than the mean frequency at the end of the bu element (4.5 kHz) but the start mean frequency of the girk element (3.3 kHz) was higher than the end mean frequency of the girk element (1.6 kHz). The girk element had a $F_0$ (531 Hz) that was more than 2 times higher than the $F_0$ of the bu element (224 Hz). The $F_0$ of female calls was higher than the $F_0$ of male calls. The $F_0$ increased and then decreased within each of the call elements. Mean harmonicity values were similar in the bu (0.7) and girk elements (0.8). The lower bandwidth limits were wider and the peak frequencies were lower in the girk (lower bandwidth: 966 Hz; overall peak frequencies: 1.1 kHz) than the bu elements (lower bandwidth: 816 Hz; overall peak frequencies: 2.0 kHz).

### B. Sex and identity

The first and second call elements were assigned to the sex of the callers at levels greater than chance by using a linear combination of acoustic variables (bu: Wilks' Lambda: $F_{10\,349} = 37.6$, $p < 0.0001$; girk: Wilks' Lambda: $F_{11\,348} = 60.8$, $p < 0.0001$). A cross-validated discriminant-function analysis correctly classified 88.3% of the bu elements (unvalidated = 88.6%; 50% prior probability of random correct assignment) and 90.8% of the girk

elements (unvalidated = 91.4%). A cross-validated discriminant-function analysis correctly classified 93.9% of the calls when both elements were used in the analysis (unvalidated = 95.0%). Since there was a 50% probability of correct assignment, the error reduction was 87.8%.

The first and second call elements (bu and girk) were also assigned to the individual caller at levels greater than chance by using a linear combination of acoustic variables in females (bu: Wilks' Lambda: $F_{128\,1137.6} = 11.1$, $p < 0.0001$; girk: Wilks' Lambda: $F_{112\,1119.6} = 9.1$, $p < 0.0001$) and males (bu: Wilks' Lambda: $F_{112\,1119.6} = 9.3$, $p < 0.0001$; girk: Wilks' Lambda: $F_{112\,1119.6} = 5.6$, $p < 0.0001$). For the female vocalizations, a cross-validated discriminant-function analysis correctly classified 78.3% of the bu elements (unvalidated = 88.3%) and 68.9% of the girk elements (unvalidated = 81.7%). A cross-validated discriminant-function analysis correctly classified 91.1% of the calls when both elements were used in the analysis [unvalidated = 98.3%; Fig. 2(a)]. Since there was an 11.1% probability of correct assignment, the error reduction was 90.0%. For the male vocalizations, a cross-validated discriminant-function analysis correctly classified 65.6% of the bu elements (unvalidated = 81.1%) and 53.3% of the girk elements (unvalidated = 69.4%). A cross-validated
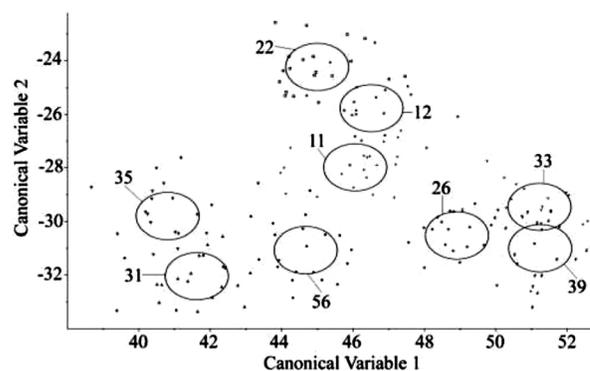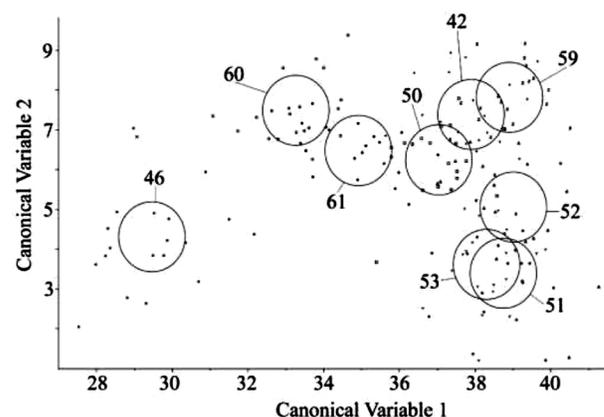


FIG. 2. Location of all of the bu-girk calls on the first two canonical functions for (a) females and (b) males. Circles represent 95% confidence intervals for the estimate of the mean centroid location and are labeled with the identification numbers of individual birds.

Jessica L. Yorzinski: Peafowl antipredator calls

discriminant-function analysis correctly classified 72.8% of the calls when both elements were used in the analysis [unvalidated = 89.4%; Fig. 2(b)]. Given the 11.1% probability of correct assignment, the error reduction was 69.4%.

The factor analysis accounted for over 85% of the variation in acoustic variables. It extracted nine factors for the bu element and eight factors for the girk element. The acoustic variables of a given measurement often loaded on the same factor (e.g., the mean, maximum, minimum, start and end of the $F_0$ all loaded on the same factor) and the factors therefore provided meaningful composite variables (Table II). Peafowl bu-girk calls varied by the sex of the caller. The $F_0$ in both the bu and girk elements was statistically-significantly lower in males compared to females. In the girk element, some acoustic features were also statistically different between the sexes: Duration was longer, peak frequency was higher, and start and minimum harmonicity were lower (i.e., noisier) in females compared to males (Table II). A repeated-measures generalized linear model indicated that all of the factors significantly contributed to distinguishing individual peafowl except the peak frequency factor of the bu element (Table II).

## C. Body size

Because males had larger body sizes (tarsus + metatarsus) than females (females: $177.26 \pm 1.86$ mm; males: $204.34 \pm 2.09$ mm), body-size analyses were conducted separately for female and male calls. The bu and girk elements had a lower mean $F_0$ in birds with larger body sizes in females (bu: $F_{1,7} = 14.6$, $p = 0.0066$, $R^2 = 42.1\%$; girk: $F_{1,7} = 22.56$, $p = 0.0021$, $R^2 = 58.0\%$) and males (bu: $F_{1,7} = 5.8$, $p = 0.047$, $R^2 = 13.3\%$; girk: $F_{1,7} = 9.46$, $p = 0.018$, $R^2 = 33.4\%$; Fig. 3).
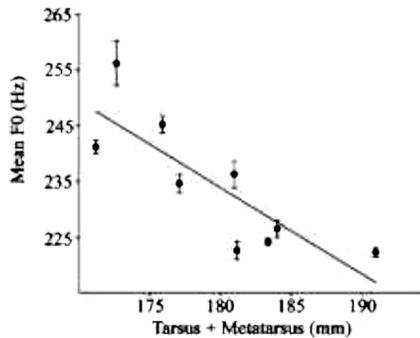
## D. Rank

The duration, end mean frequency, and start harmonicity of the bu element were positively related to rank (duration: $F_{1,129} = 26.7$, $R^2 = 14.2\%$; $p < 0.0001$; end mean frequency: $F_{1,129} = 34.7$, $R^2 = 17.7\%$; $p < 0.0001$; start harmonicity: $F_{1,129} = 18.0$, $R^2 = 10.0\%$; $p < 0.0001$; Figs. 4(a)–4(c) using the rank dataset. The other acoustic measurements made on the bu element, including those related to $F_0$, were unrelated to rank based on the model-selection procedure. No acoustic features of the girk element were found that correlated with rank. The relationship between rank and the duration, end mean frequency, and start harmonicity of the bu element remained the same when the analysis was rerun including only individuals ($n = 19$) that formed a linear dominance hierarchy (duration: $F_{1,73} = 16.6$, $R^2 = 15.4\%$; $p = 0.0001$; end mean frequency: $F_{1,73} = 29.8$, $R^2 = 24.7\%$; $p < 0.0001$; start harmonicity: $F_{1,73} = 18.4$, $R^2 = 16.8\%$; $p < 0.0001$). The relationship between harmonicity and rank was not simply driven by background noise: Rank was not correlated with the mean harmonicity of the background noise immediately preceding the onset of the bu element ($F_{1,126} = 0.6$, $R^2 = 0.3\%$; $p = 0.46$).

Because the $F_0$ of the calls was related to body size (see body-size results above), the relationship between body size, $F_0$, and rank were examined in this rank dataset as well. Similar to the body-size analysis above, the calls of larger peahens had lower $F_0$ than the calls of smaller peahens (bu: $F_{1,131} = 12.0$, $p = 0.0007$, $R^2 = 6.7\%$; girk: $F_{1,131} = 71.3$, $p < 0.0001$, $R^2 = 30.6\%$). Unexpectedly, larger peahens had lower ranks than smaller peahens (bu: $F_{1,31} = 40.1$, $R^2 = 19.9\%$; $p < 0.0001$; girk: $F_{1,31} = 38.9$, $p < 0.0001$; $R^2 = 19.3\%$; Fig. 4(d). An additional analysis was run to examine whether the acoustic properties that related to rank

TABLE II. Summary of analyses of acoustic measurement factors extracted from the bu-girk calls of 18 individual peafowl. Each orthogonal factor was analyzed separately in a multivariate model that included sex and individual identity (nested within sex). Variance explained by each factor, $F$ statistic, degrees of freedom, and $p$ values are shown.

| Factor | Acoustic feature | Explained variance (%) | Sex $F_{1\,342}$ ($p$) | Individual (Sex) $F_{16\,342}$ ($p$) |
|---|---|---|---|---|
| bu | | | | |
| 1 | Mean, max., min., start and end $F_0$ | 23.7 | 18.24 (0.001)* | 17.49 (<0.0001) * |
| 2 | Mean and max mean frequency and upper bandwidth limit | 15.5 | 0.94 (0.35) | 2.74 (<0.0001) * |
| 3 | Mean, max., min., and start harmonicity | 13.7 | 0.20 (0.66) | 8.40 (<0.0001) * |
| 4 | Min. and start mean frequency | 10.1 | 3.0 (0.10) | 7.31 (<0.0001) * |
| 5 | Median peak frequency and overall peak frequency | 8.6 | 0.01 (0.94) | 1.45 (0.12) |
| 6 | End mean frequency | 6.3 | 0.27 (0.61) | 8.51 (<0.0001) * |
| 7 | End harmonicity | 5.6 | 2.07 (0.17) | 4.35 (<0.0001) * |
| 8 | Duration | 5.3 | 0.58 (0.46) | 91.11 (<0.0001) * |
| 9 | Lower bandwidth limit | 4.3 | 0.83 (0.38) | 3.23 (<0.0001)* |
| girk | | | | |
| 1 | Mean, max., min., start and end $F_0$ | 19.5 | 9.91 (0.006)* | 28.68 (<0.0001)* |
| 2 | Mean, max. and start mean frequency and upper bandwidth limit | 15.1 | 0.11 (0.74) | 6.65 (<0.0001)* |
| 3 | Mean, max., and end harmonicity | 11.7 | 0.73 (0.41) | 9.96 (<0.0001)* |
| 4 | Min. and end mean frequency | 10.4 | 1.92 (0.19) | 4.27 (<0.0001)* |
| 5 | Median peak frequency and overall peak frequency | 9.8 | 8.53 (0.01)* | 3.10 (<0.0001)* |
| 6 | Min. and start harmonicity | 9.7 | 7.72 (0.01)* | 4.65 (<0.0001)* |
| 7 | Duration | 6.5 | 9.33 (0.008)* | 7.36 (<0.0001)* |
| 8 | Lower bandwidth limit | 4.9 | 0.01 (0.93) | 2.03 (0.01)* |

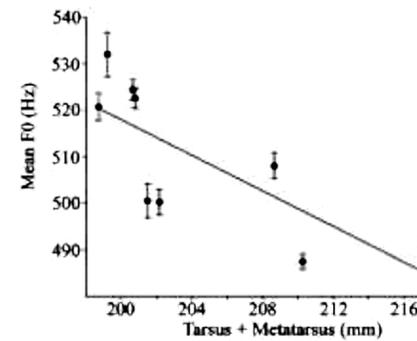(a) Females: bu   (b) Females: girk
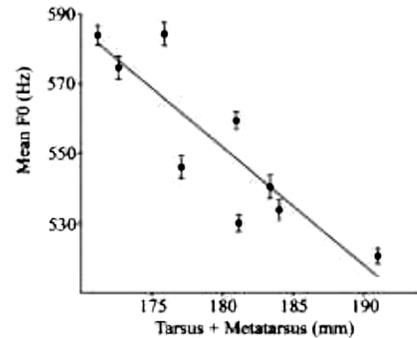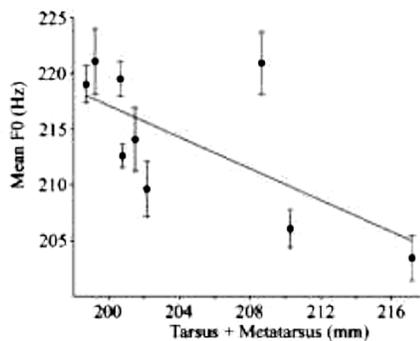
(c) Males: bu   (d) Males: girk

FIG. 3. The relationship between mean $F_0$ (Hz) and body size (as measured by tarsus + metarsus) in females [(a): bu element; (b): girk element] and males [(c): bu element; (d): girk element]. Means $+/-$ SE are displayed.

(duration, end mean frequency, and start harmonicity of the bu element) were directly related to body size. The end mean frequency of the bu element was unrelated to body size ($F_{1,129} = 0.9$, $p = 0.34$, $R^2 = 0.6\%$) but the duration and start harmonicity were negatively related to body size (duration: $F_{1,129} = 7.2$, $p = 0.008$, $R^2 = 4.3\%$; harmonicity: $F_{1,129} = 10.5$, $p = 0.0015$, $R^2 = 6.1\%$).

## IV. DISCUSSION

Peafowl bu-girk antipredator calls contained detailed information about the signalers. They encoded information about the sex of the callers. The vocalizations of male callers had a lower $F_0$ than those of female callers. The vocalizations also contained information related to the identity of callers. Nearly all of the acoustic features varied among individuals. Furthermore, the $F_0$ of the calls was negatively related to body size. In addition, peahen rank was related to the duration, end mean frequency, and start harmonicity of the bu element. Surprisingly, larger peahens had lower dominance ranks than smaller peahens.

### A. Sex

Peafowl antipredator calls could be categorized by the sex of the caller with a low error rate. Calls were classified to the correct sex in 93.9% of cases, which translates to an 87.8% reduction in error rates compared to chance expectation. One major difference in acoustic structure between male and female calls was the $F_0$. The $F_0$ of the call was lower in males compared to females. Because males are larger than females, variation in $F_0$ may be driven by body-size differences (see below). In other species, the $F_0$ is often lower in male calls compared to female calls (e.g., Fischer et al., 2002; Patel and Owren, 2012).

Males emitted girk elements that had higher harmonicity (less noise) than females. Harmonicity may reflect the arousal state of the bird (reviewed in Blumstein and Chi, 2012). The exact relationship between harmonicity and level of arousal, however, may vary by species. For example, calls with lower harmonicity indicate a higher level of arousal in some species (Manser, 2001) but may indicate the opposite in others (Blumstein and Chi, 2012). Future experiments that examine the exact relationship between harmonicity and arousal level would help clarify this difference in harmonicity between peacocks and peahens.

Because the acoustic features of bu-girk calls varied between the sexes, peafowl may be able to detect the sex of alarm callers. Individuals in other species are able to distinguish male and female signalers and respond differentially to their vocalizations (e.g., Hoelzel, 1986; Levin, 1996; Morton and Derrickson, 1996; Bard et al., 2002). Peafowl may likewise respond differently to the antipredator calls of males
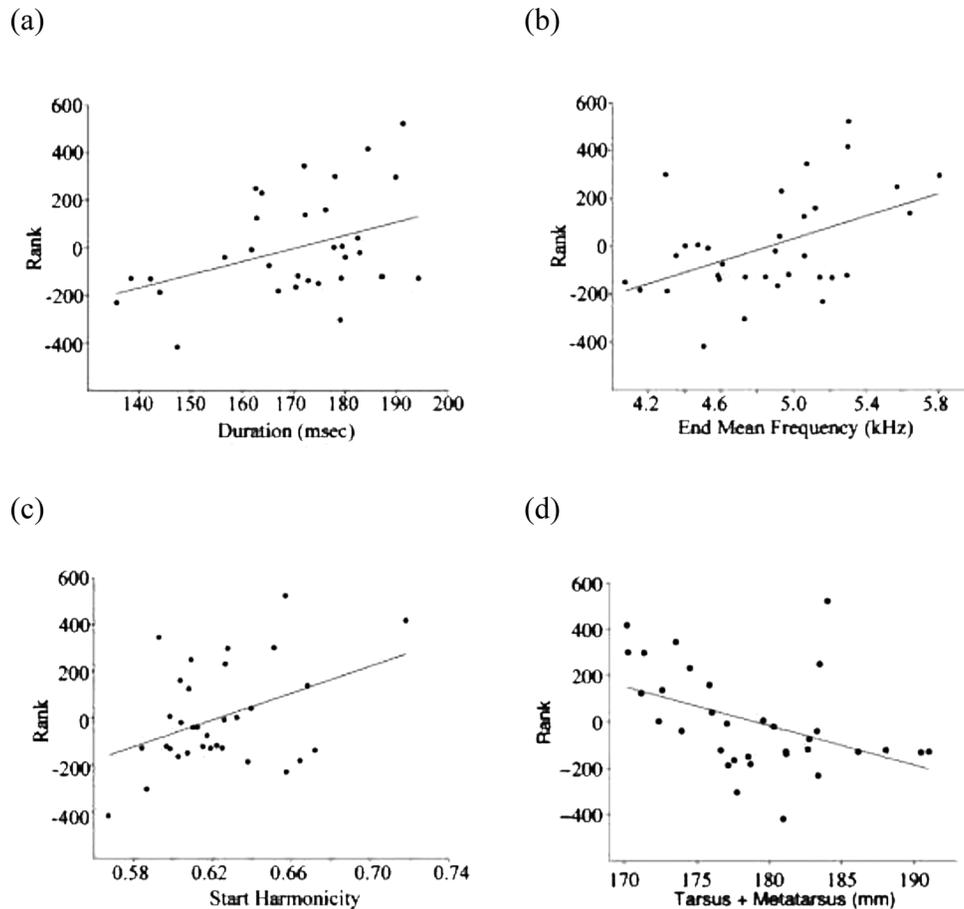
FIG. 4. The relationship between peahen social rank and (a) duration, (b) end mean frequency, and (c) start harmonicity of the bu element. Each dot represents the mean acoustic value for each female. (d) The relationship between peahen social rank and body size.

compared to females. Because antipredator behavior may also serve as self-advertisement signals (Slagsvold, 1984), it is possible that peacocks preferentially respond to the antipredator calls of females, especially during the breeding season.

## B. Identity

Both elements of the bu-girk antipredator call exhibited sufficient consistency within individuals and sufficient variation among individuals for identification of individuals on the basis of the calls. Female and male calls were classified to the correct individual in 91.1% and 72.8% of cases, respectively, which translates to a 90.0% and 69.4% reduction in error rates compared to chance expectation, respectively. The classification accuracy was higher for female calls compared to male calls. Since there are generally more females within a flock than males (Ali and Ripley, 1969), there would be a greater probability of mistaking female versus male identities. Female calls may therefore be more distinctive than male calls to compensate for potentially higher rates of mistaken identities.

Nearly all of the acoustic features that were measured contributed to differentiating among individuals. The only exception was the peak frequency factor of the bu element, which was not significantly different among individuals. Many different aspects of the calls are therefore varying

across individuals and unique combinations of these acoustic aspects are contributing to the classification of individual callers. It is possible that additional (unmeasured) acoustic features also contribute to individual identity (such as amplitude modulation and nonlinear properties).

The identity information encoded in the bu-girk vocalization potentially contains redundant information. Both the bu and girk element of the vocalization provided information about identity that led to reasonably high levels of individual discrimination. Classification rates in males and females were even higher when both elements of the bu-girk vocalization were simultaneously used in the analysis. These two elements of antipredator calls may therefore supply receivers with redundant information. Because environmental features can negatively affect signal transmission (e.g., causing attenuation and reverberation; Richards and Wiley, 1980), these redundant signals could minimize receiver errors (Bradbury and Vehrencamp, 2011) and allow receivers to identify individual callers with a higher certainty (Jouventin et al., 1999).

Previous work in other species has also found that antipredator vocalizations contain information related to individual identity (Farquhar, 1993; Fischer et al., 2001; McCowan and Hooper, 2001; Fischer et al., 2002; Randall et al., 2005; Yorzinski et al., 2006; Kennedy et al., 2009; Schneiderová and Policht, 2010; Matrosova et al., 2011; Patel and Owren, 2012). Future experiments could test whether peafowl detect

differences in the acoustic structure of vocalizations across individuals (e.g., Dooling and Saunders, 1975) and then use this information to discriminate among callers (e.g., Blumstein and Daniel, 2004; Sproul et al., 2006).

Individually distinctive antipredator calls can help receivers respond more appropriately to potential threats (reviewed in Pollard, 2010). Receivers can learn to ignore the alarm calls of unreliable signalers (Cheney and Seyfarth, 1988; Blumstein et al., 2004). Because peafowl mob predators (Yorzinski and Platt, 2012), a receiver's decision to stop its current activity and approach a mobbing event (when it has not yet even seen the predator) may depend upon the reliability of the signaler. Because the antipredator calls in this study were recorded in social isolation, the calls may have functioned to recruit distant conspecifics to the dangerous situation. The identity of the caller may also be important if animals preferentially aid their relatives (Sherman, 1977) or flock mates (Krams et al., 2006). Peafowl form flocks, especially during the nonbreeding season (Ali and Ripley, 1969), and may selectively respond to the antipredator calls of their flock mates.

## C. Body size

Peafowl antipredator calls contained information related to body size. Peafowl with larger bodies had antipredator calls with lower $F_0$. Because larger vocal organs and vocal tracts generally produce lower frequency sound better than smaller ones (Bradbury and Vehrencamp, 2011), it was expected that $F_0$ would be negatively related to body size. This relationship between body size and fundamental frequency has been found in other species (e.g., Davies and Halliday, 1978; Brown et al., 1996; Bee et al., 1999; de Jong et al., 2007), including non-oscine birds (Appleby and Redpath, 1997; Barbaud et al., 2000). Previous studies have not shown a link between acoustic properties of antipredator calls and body size.

Peafowl (or their predators) may respond differentially to the antipredator calls of differently sized birds. Conspecifics may preferentially respond to the calls of similarly sized individuals because risk levels may be comparable for birds of similar sizes (Wilson, 1975; Peters, 1983). Because predator success rate can depend upon prey size (Gotmark and Post, 1996), predators may also use body-size information encoded in antipredator calls to select their targets. Finally, because peacocks are larger than peahens (15% larger), the relationship between body size and $F_0$ can also help explain the finding that peacocks produce antipredator calls with a lower $F_0$ than peahens (see above; male bu and girk elements have a mean fundamental frequency that is 9% and 8% lower than female bu and girk elements, respectively).

## D. Rank

The antipredator calls of peahens encoded rank information. Peahens that were higher ranked emitted bu elements with higher end mean frequencies, longer durations, and higher start harmonicity (less noise). These relationships held up even when considering only a subset of individuals that formed a linear dominance hierarchy. Both the duration and start harmonicity of the bu element were negatively correlated with body size. However, most of these acoustic and rank relationships had relatively weak effects ($R$-squares were mostly less than 20%). In addition, higher-ranked peahens had smaller body sizes than lower-ranked peahens. Surprisingly, no acoustic properties of the girk element were correlated with rank. The girk element may therefore not contain any rank information or additional (unmeasured) acoustic variables of the element may encode rank information. Future studies are needed to assess whether the antipredator calls of other species also contain rank information.

High-ranking peahens emitting bu elements with long durations may be indicating the perceived level of danger. If calls with longer duration reflect greater risk (e.g., Yorzinski and Vehrencamp, 2009), then higher-ranked peahens emitting calls with longer durations may be communicating a higher level of danger. In addition, the higher harmonicity values of higher-ranked birds could reflect higher quality (Ramig et al., 1988; Ferrand, 2002). Because low- and high-ranking individuals often exhibit different antipredator strategies (Hegner, 1985; Hogstad, 1986), playback experiments could demonstrate whether peafowl are able to distinguish between calls from high- and low-ranking birds (despite the relatively weak relationships found between rank and these acoustic measurements) and differentially respond to the calls of high-ranking compared to low-ranking birds. It is possible that rank information is also encoded in the antipredator vocalizations of males; the vocalizations of the highest ranking male [#46; Fig. 2(b)] were the most distinctive in the canonical plot.

Peahens with smaller body sizes were higher ranked than peahens with larger body sizes. This result is counterintuitive compared to previous studies showing positive relationships between body size and rank in many different animals (Petrie, 1988; Riechert, 1998), including peacocks (Loyau et al., 2005; but see Dakin, 2011). While larger-sized individuals usually have a competitive advantage over smaller-sized individuals, other selective pressures (such as energy demands) might have a greater effect on body size (Mueller, 1990). In some species, body size has no influence on rank (e.g., Arcese and Smith, 1985) while smaller individuals outrank larger individuals in other species (e.g., Convey, 1989; Hernández and Benson, 1998). Given the relatively weak negative association between body size and rank found in this study along with previous work in peahens that did not find a relationship between body size and dominance (exact dominance ranks were unknown; Dakin, 2011), additional studies can confirm the exact relationship between these traits in peahens. In addition, two acoustic properties that were related to peahen rank (duration and start harmonicity of the bu element) were also related to body size (although the relationship was not very strong) and may therefore provide information about multiple aspects of the caller.

Peahens do not normally form flocks as large as the captive flock studied here but instead tend to form flocks with up to seven birds (Ali and Ripley, 1969). However, very little is known about the non-mating behavior of peafowl and

it is possible that peafowl transfer between flocks or regularly interact with other flocks. Indeed, large flocks (up to 18 individuals) have been observed in the wild (de Silva et al., 1996). Therefore, in the wild, birds may also establish dominance relationships among many individuals, both within their flock and within the larger population, and produce vocalizations that reflect these relationships.

### E. Peafowl vocalizations

Apart from the bu-girk call, peafowl produce many other types of vocalizations (Johnsingh and Murali, 1978; Petrie et al., 1991; Takahashi and Hasegawa, 2008; Yorzinski and Platt, 2012) that may encode information about the signaler. Peafowl emit additional types of antipredator calls. In particular, the "pe-girk," "pe," "bu," and "kokok" antipredator calls are often interspersed within bu-girk calling bouts (Takahashi and Hasegawa, 2008; pers. obs.) and may provide additional cues to signaler attributes. Peacocks produce many different vocalizations during courtship as well (Takahashi and Hasegawa, 2008; Petrie et al., 1991; Yorzinski and Anoop, 2013) and these calls may contain information that females can use to assess mate quality. It would be informative to determine whether the acoustic properties that are important for individual discrimination in bu-girk calls are likewise important for individual discrimination in other call types.

## V. CONCLUSION

The information contained within antipredator vocalizations can provide receivers with valuable information about potentially dangerous situations (reviewed in Caro, 2005). Peafowl antipredator vocalizations, in particular, encode information related to the caller and receivers can potentially use this information when responding to threats. The antipredator calls of peafowl contain information about the sex and identity of the caller. The calls also reflect the body size of vocalizers, with larger individuals emitting calls with lower $F_0$ than smaller individuals. The antipredator calls of peahens even contain information about the social rank of the birds. Future playback experiments that assess the responses of peafowl to antipredator calls emitted by different individuals as well as those emitted by individuals of certain body sizes and ranks will help clarify the importance of this information.

Ali, S., and Ripley, S. D. (1969). Handbook of the Birds of India and Pakistan, Vol. 2 (Oxford University Press, Bombay), pp. 1–147.

Amorim, M. C. P., and Hawkings, A. D. (2005). "Ontogeny of acoustic and feeding behaviour in the Grey Gurnard, Eutrigla gurnardus," Ethology 111, 255–269.

Appleby, B. M., and Redpath, S. M. (1997). "Indicators of male quality in the hoots of tawny owls (Strix aluco)," J. Raptor Res. 31, 65–70.

Arcese, P., and Smith, J. N. M. (1985). "Phenotypic correlates and ecological consequences of dominance in song sparrows," J. Anim. Ecol. 54, 817–830.

Bachorowski, J. A., and Owren, M. J. (1999). "Acoustic correlates of talker sex and individual talker identity are present in a short vowel segment produced in running speech," J. Acoust. Soc. Am. 106, 1054–1063.

Bang, A., Deshpande, S., Sumana, A., and Gadagkar, R. (2010). "Choosing an appropriate index to construct dominance hierarchies in animal societies: A comparison of three indices," Anim. Behav. 79, 631–636.

Barbaud, C., Mariani, A., and Jouventin, P. (2000). "Variation in call properties of the snow petrel, Pagodroma nivea, in relation to sex and body size," Aust. J. Zool. 48, 421–430.

Bard, S., Hau, M., Wikelski, M., and Wingfield, J. C. (2002). "Vocal distinctiveness and response to conspecific playback in the spotted antibird, a neotropical suboscine," Condor 104, 387–394.

Bee, M. A., Perrill, S. A., and Owren, P. C. (1999). "Size assessment in simulated territorial encounters between male green frogs (Rana clamitans)," Behav. Ecol. Sociobiol. 45, 177–184.

Blumstein, D. T., and Chi, Y. Y. (2012). "Scared and less noisy: Glucocorticoids are associated with alarm call entropy," Biol. Lett. 8, 189–192.

Blumstein, D. T., and Daniel, J. C. (2004). "Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to calls from juveniles," Anim. Behav. 68, 1257–1265.

Blumstein, D. T., Verneyre, L., and Daniel, J. C. (2004). "Reliability and the adaptive utility of discrimination among alarm callers," Proc. R. Soc., London, Ser. B 271, 1851–1857.

Bradbury, J., and Vehrencamp, S. (2011). Principles of Animal Communication, 2nd ed. (Sinauer Associates, Sunderland, MA), pp. 1–697.

Brown, W. D., Wideman, J., Andrade, M. C. B., Mason, A. C., and Gwynne, D. T. (1996). "Female choice for an indicator of male size in the song of the black0horned tree cricket Oecanthus nigricornis (Orthoptera: Gryllidae: Oecanthinae)," Evolution 50, 2400–2411.

Cardoso, G. C., Mamede, A. T., Atwell, J. W., Mota, P. G., Ketterson, E. D., and Price, T. D. (2008). "Song frequency does not reflect differences in body size among males in two oscine species," Ethology 114, 1084–1093.

Caro, T. (2005). Antipredator Defenses in Birds and Mammals (University of Chicago Press, Chicago, IL), pp. 1–591.

Cheney, D. L., and Seyfarth, R. M. (1988). "Assessment of meaning and the detection of unreliable signals by vervet monkeys," Anim. Behav. 36, 477–486.

Cheney, D. L., and Seyfarth, R. M. (1990). How Monkeys See the World (University of Chicago Press, Chicago, IL), pp. 1–388.

Convey, P. (1989). "Influences on the choice between territorial and satellite behavior in male Libellula quadrimaculata Linn. (Odonata: Libellulidae)," Behaviour 109, 125–141.

Dakin, R. (2011). "The crest of the peafowl: A sexually dimorphic plumage ornament signals condition in both males and females," J. Avian Biol. 42, 405–414.

Davies, N. B., and Halliday, T. R. (1978). "Deep croaks and fighting assessment in toads (Bufo bufo)," Nature 274, 683–684.

de Jong, K., Bouton, N., and Slabbekoorn, H. (2007). "Azorean rock-pool blennies produce size-dependent calls in a courtship context," Anim. Behav. 74, 1285–1292.

de Silva, P. K., Santiapillai, C., and Dissanayake, S. (1996). "Some aspects of the population ecology of the blue peafowl, Pavo cristatus, in Ruhuna National Park, Sri Lanka," J. South Asian Nat. Hist. 2, 113–126.

Dooling, R. J., and Saunders, J. C. (**1975**). "Hearing in the parakeet (*Melopsittacus undulates*): Absolute thresholds, critical ratios, frequency difference limens, and vocalizations," J. Comp. Physiol. Psychol. **88**, 1–20.

Falls, J. B. (**1982**). "Individual recognition by sounds in birds," in *Acoustic Communication in Birds*, edited by D. H. Kroodsma and E. H. Miller (Academic Press, New York), pp. 237–278.

Farquhar, C. C. (**1993**). "Individual and intersexual variation in alarm calls of the white-tailed hawk," Condor **95**, 234–239.

Ferrand, C. T. (**2002**). "Harmonics-to-noise ratio: An index of vocal aging," J. Voice **16**, 480–487.

Fischer, J., Hammerschmidt, K., Cheney, D. L., and Seyfarth, R. M. (**2001**). "Acoustic features of female chacma baboon barks," Ethology **107**, 33–54.

Fischer, J., Hammerschmidt, K., Cheney, D. L., and Seyfarth, R. M. (**2002**). "Acoustic features of male baboon loud calls: Influences of context, age, and individuality," J. Acoust. Soc. Am. **111**, 1465–1474.

Fischer, J., Kitchen, D. M., Seyfarth, R. M., and Cheney, D. L. (**2004**). "Baboon loud calls advertise male quality: Acoustic features and their relation to rank, age, and exhaustion," Behav. Ecol. Sociobiol. **56**, 140–148.

Fitch, W. T. (**1997**). "Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques," J. Acoust. Soc. Am. **102**, 1213–1222.

Gotmark, F., and Post, P. (**1996**). "Prey selection by sparrowhawks, *Accipiter nisus*: Relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour," Phil. Trans. R. Soc. Lond. B **351**, 1559–1577. See: http://rstb.royalsocietypublishing.org/content/351/1347/1559.short

Hare, J. F., and Atkins, B. A. (**2001**). "The squirrel that cried wolf: Reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*)," Behav. Ecol. Sociobiol. **51**, 108–112.

Hegner, R. E. (**1985**). "Dominance and anti-predator behaviour in blue tits," Anim. Behav. **33**, 762–768.

Hernández, M. I. M., and Benson, W. W. (**1998**). "Small-male advantage in the territorial tropical butterfly *Heliconius sara* (Nymphalidae): A paradoxical strategy?" Anim. Behav. **56**, 533–540.

Hoelzel, A. R. (**2008**). "Song characteristics and response to playback of male and female robins *Erithacus rubecul*," Ibis **128**, 115–127.

Hogstad, O. (**1986**). "Social rank and antipredator behavior of Willow Tits *Parus montanus* in winter flocks." Ibis **130**, 45–56.

Johnsingh, A. J. T., and Murali, S. (**1978**). "The ecology and behaviour of the Indian peafowl (*Pavo cristatus*) Linn. of Injar," J. Bombay Nat. Hist. Soc. **75**, 1069–1079.

Jouventin, P., Aubin, T., and Lengagne, T. (**1999**). "Finding a parent in a king penguin colony: The acoustic system of individual recognition," Anim. Behav. **57**, 1175–1183.

Kennedy, R. A. W., Evans, C. S., and McDonald, P. G. (**2009**). "Individual distinctiveness in the mobbing call of a cooperative bird, the noisy miner *Manorina melanocephala*," J. Avian Biol. **40**, 481–490.

Krams, I. (**1998**). "Dominance-specific vigilance in the great tit," J. Avian Biol. **29**, 55–60.

Krams, I., Krama, T., and Igaune, K. (**2006**). "Alarm calls of wintering great tits *Parus major*: Warning of mate, reciprocal altruism, or a message to the predator?," J. Avian Biol. **37**, 131–136.

Lachlan, R. F. (**2007**). "Luscinia: A bioacoustics analysis computer program. Version 1.0," [Computer program]. Retrieved from luscinia.source-forge.net on October 8, 2012.

Levin, R. N. (**1996**). "Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: II. Playback experiments," Anim. Behav. **52**, 1107–1117.

Loyau, A., Saint Jalme, M., and Sorci, G. (**2005**). "Intra- and intersexual selection for multiple traits in the peacock (*Pavo cristatus*)," Ethology **111**, 810–820.

Manser, M. B. (**2001**). "The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency," Proc. R. Soc., London, Ser. B **268**, 2315–2324.

Marler, P. (**1977**). "Primate vocalization: Affective or symbolic?," in *Progress in Ape Research*, edited by G. H. Bourne (Academic Press, New York), pp. 85–96.

Matrosova, V. A., Blumstein, D. T., Volodin, I. A., and Volodina, E. V. (**2011**). "The potential to encode sex, age, and individual identity in the alarm calls of three species of Marmotinae," Naturwissenschaften **98**, 181–192.

McCowan, B., and Hooper, S. L. (**2002**). "Individual acoustic variation in Belding's ground squirrel alarm chirps in the High Sierra Nevada," J. Acoust. Soc. Am. **111**, 1157–1160.

Morton, E. S., and Derrickson, K. C. (**1996**). "Song ranging by the dusky antbird, *Cercomacra tyrannina*: Ranging without song learning," Behav. Ecol. Sociobiol. **39**, 195–201.

Mueller, H. C. (**1990**). "The evolution of reversed sexual dimorphism in size in monogamous species of birds," Biol. Rev. **65**, 553–585.

Patel, R. R., and Owren, M. J. (**2012**). "Silky sifaka (*Propithecus candidus*) 'zzuss' vocalizations: Sexual dimorphism, individuality, and function in the alarm call of a monomorphic lemur," J. Acoustic. Soc. Am. **132**, 1799–1810.

Peters, R. H. (**1983**). *The Ecological Implications of Body Size* (Cambridge University Press, Cambridge), pp. 1–344.

Petrie, M. (**1988**). "Intraspecific variation in structures that display competitive ability: Large animals invest relatively more," Anim. Behav. **36**, 1174–1179.

Petrie, M., Halliday, T., and Sanders, C. (**1991**). "Peahens prefer peacocks with elaborate trains," Anim. Behav. **41**, 323–331.

Pollard, K. (**2011**). "Making the most of alarm signals: The adaptive value of individual discrimination in an alarm context," Behav. Ecol. **22**, 93–100.

Ramig, L. A., Scherer, R. C., Titze, I. R., and Ringel, S. P. (**1988**). "Acoustic analysis of voices of patients with neurologic disease: rationale and preliminary data," Ann. Otol. Rhinol. Laryngol. **97**, 164–172.

Randall, J. A., McCowan, B., Collins, K. C., and Hooper, S. L. (**2005**). "Alarm signals of the great gerbil: Acoustic variation by predator context, sex, age, individual, and family group," J. Acoust. Soc. Am. **118**, 2706–2714.

Reby, D., McComb, K. E., Cargnelutti, B., Darwin, C., Fitch, W. T., and Clutton-Brock, T. (**2005**). "Red deer stags use formants as assessment cues during intrasexual agonistic interactions," Proc. R. Soc., London, Ser. B **272**, 941–947.

Richards, D. G., and Wiley, R. H. (**1980**). "Reverberations and amplitude fluctuations in the propagation of sound in a forest: Implications for animal communication," Am. Nat. **115**, 381–399.

Riechert, S. E. (**1998**). "Game theory and animal contests," in *Game Theory and Animal Behavior*, edited by L. A. Dugatkin and H. K. Reeve (Oxford University Press, New York), pp. 64–93.

Schneiderová, I., and Policht, R. (**2011**). "Alarm calls of the European ground squirrel *Spermophilus citellus* and the taurus ground squirrel *S. taurensis* encode information about caller identity," Bioacoustics **20**, 29–43.

Senar, J. C., and Pascual, J. (**1997**). "Keel and tarsus length may provide a good predictor of avian body size," Ardea **85**, 269–274.

Sherman, P. W. (**1977**). "Nepotism and the evolution of alarm calls," Science **197**, 1246–1253.

Slagsvold, T. (**1984**). "The mobbing behaviour of the hooded crow *Corvus corone cornix*: Anti-predator defence or self-advertisement?," Fauna Norv. C Cinc. **7**, 127–131.

Sproul, C., Palleroni, A., and Hauser, M. D. (**2006**). "Cottontop tamarin, *Saguinus oedipus*, alarm calls contain sufficient information for recognition of individual identity," Anim. Behav. **72**, 1379–1385.

Tabachnick, B. G., and Fidell, L. S. (**2001**). *Using Multivariate Statistics*, 4th ed. (Allyn and Bacon, Needham Heights, MA), pp. 1–966.

Takahashi, M., and Hasegawa, T. (**2008**). "Seasonal and diurnal use of eight different call types by Indian peafowl (*Pavo cristatus*)," J. Ethol. **26**, 375–381.

Titze, I. R. (**1994**) *Principles of Voice Production* (Prentice Hall, Englewood Cliffs, NJ), pp. 1–354.

Vannoni, E., and McElligott, A. G. (**2008**). "Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males," PLoS ONE **3**, e3113.

Waite, T. A. (**1987**). "Dominance-specific vigilance in the tufted titmouse: Effects of social context," Condor **89**, 932–935.

Wilson, D. S. (**1975**). "The adequacy of body size as a niche difference," Am. Nat. **109**, 769–784.

Yorzinski, J. L., and Anoop, K. R. (**2013**). "Peacock copulation calls attract distant females," Behaviour **150**, 61–74.

Yorzinski, J. L., and Platt, M. L. (**2012**). "The difference between night and day: Antipredator behavior in birds," J. Ethol. **30**, 211–218.

Yorzinski, J. L., and Vehrencamp, S. L. (**2009**). "The effect of predator type and danger level on the mob calls of the American crow," Condor **111**, 159–168.

Yorzinski, J. L., Vehrencamp, S. L., Clark, A. B., and McGowan, K. J. (**2006**). "The inflected alarm caw of the American crow: Differences in acoustic structure among individuals and sexes," Condor **108**, 518–529.