Peahens can differentiate between the antipredator calls of individual conspecifics

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Animals of many different species discriminate among individuals based on acoustic properties of vocalizations. These vocalizations are produced in different contexts, including territorial defence and parent–offspring interactions. They are also produced in response to predators, but we know less about whether animals, especially birds, are able to discriminate among individuals based on antipredator calls. We therefore examined whether an avian species (peafowl, *Pavo cristatus*) is able to differentiate between the antipredator calls of different individuals. Using a habituation–discrimination playback paradigm, we habituated peahens to the antipredator calls of a given individual and then examined their responses to additional calls from that individual and to calls from a novel individual. We found that peahens responded more strongly to calls from the novel individual than from the original individual, demonstrating that they are able to differentiate between individuals based on the acoustic properties of antipredator calls. The ability to differentiate between individual callers may be useful to peahens in modifying their antipredator behaviour based on signaller reliability.

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Individuals in many species discriminate among individuals based on vocalizations (Beecher, Beecher, & Hahn, 1981; Candiotti, Zuberbühler, & Lemasson, 2013; Hoffmann, Musolf, & Penn, 2011; Mumm, Urrutia, & Knörnschild, 2014; Sayigh et al., 1998; Sharpe, Hill, & Cherry, 2013). Sufficient variation in acoustic signals is the foundation for individual recognition based on these signals (Falls, 1982). If there is more variation between the calls of individuals than within one individual's calls, then the species has the potential for call-based individual recognition. While recognizing individuals is clearly important in many contexts (such as territorial interactions and parent–offspring interactions), the importance of recognizing individuals based on their antipredator calls is less clear (Pollard, 2011).

Recognizing individuals based on their antipredator calls may allow receivers to respond differently to alarm calls based on the perceived reliability of the signaller (Cheney & Seyfarth, 1988). While discrimination based on signaller reliability has been found in some studies (Hare & Atkins, 2001), other studies have found that animals do not discriminate based on signaller reliability (Schibler & Manser, 2007). The cost of responding to unreliable individuals may be outweighed by the fatal cost of not responding to a genuine predator alarm (Schibler & Manser, 2007).

Antipredator calls can only be used for individual recognition if they, like other call types, contain sufficient variation in acoustic parameters (Falls, 1982). This variation in antipredator calls has been found in many species, such as yellow-bellied marmots, *Marmota flaviventris* (Blumstein & Munos, 2005), Canada geese, *Branta canadensis* (Cowan, 1974), white-tailed hawks, *Buteo albicaudatus* (Farquhar, 1993), ground squirrels, *Spermophilus citellus* (Schneiderová & Policht, 2011), peafowl, *Pavo cristatus* (Yorzinski, 2014), silky sifaka lemurs, *Propithecus candidus* (Patel & Owren, 2012) and chacma baboons, *Papio cynocephalus ursinus* (Fischer, Hammerschmidt, Cheney, & Seyfarth, 2002). With the potential for individual recognition established, playback experiments are a powerful method for determining whether individuals use the variation in acoustic signals to differentiate among individuals. Individual differentiation based on calls has been shown in many different species, including bottlenose dolphins, *Tursiops truncatus* (Sayigh et al., 1998), house mice, *Mus musculus musculus* (Hoffmann et al., 2011), bank swallows, *Riparia riparia* (Beecher et al., 1981), giant otters, *Pteronura brasiliensis* (Mumm et al., 2014), dwarf mongooses, *Helogale parvula* (Sharpe et al., 2013) and mixed-species groups of African forest monkeys (Candiotti et al., 2013).

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While these studies utilized contact or contest calls, individual differentiation or discrimination has also been shown using playbacks of alarm calls in ground squirrels and primates (Blumstein & Daniel, 2004; Cheney & Seyfarth, 1988; Hare, 1998). Individual differentiation based on antipredator calls has rarely been demonstrated in birds. Only one study has shown that birds can differentiate among the mobbing calls of different individuals (McDonald, 2012).

Peafowl are an appropriate avian species in which to further investigate individual differentiation based on antipredator vocalizations. Because social group size is hypothesized to be a major evolutionary driver of individuality in social alarm calls (Pollard & Blumstein, 2011), we might expect peafowl to demonstrate individual recognition abilities because they often form large social groups. Their groups can be as large as 18 individuals, but the organization of these groups (e.g. the stability and age composition) is largely unknown (de Silva, Santiapillai, & Dissanayake, 1996). Peafowl are omnivorous ground-dwelling birds indigenous to the Indian subcontinent. They produce antipredator calls in response to aerial and terrestrial predators (Kannan & James, 1998). In particular, they produced their 'bu-girk' vocalization (Takahashi & Hasegawa, 2008) when a predator is detected and continue producing it while they mob the predator (Yorzinski & Platt, 2012). The 'bu-girk' antipredator vocalization contains sufficient variation among individuals to permit individual recognition (Yorzinski, 2014). Females produce 'bu-girk' calls that consistently vary among individuals in frequency, harmonicity and duration.

We tested whether peahens are able to differentiate among individuals based on acoustic features of their antipredator vocalizations using a habituation—discrimination paradigm. Habituation—discrimination paradigms have been successfully used to determine whether animals can differentiate among individual conspecifics (Blumstein & Daniel, 2004; Hardouin, Tabel, & Bretagnolle, 2006; Hare, 1998; McDonald, 2012; Sproul, Palleroni, & Hauser, 2006; Trefry & Hik, 2009). Using this paradigm, a focal animal is habituated to the antipredator calls of one individual ('individual A') and is then presented with antipredator calls from that same individual ('individual A') and from a novel individual ('individual B'). After habituation is complete, if the focal is able to differentiate among individual callers, then it should respond more strongly to the antipredator calls produced by 'individual B' compared to 'individual A.'

METHODS

Animals and Housing

We examined whether birds differentiate among individual alarm callers by studying a captive population of peahens, *P. cristatus*, between April and July 2013. The birds (33 adult females) were housed in an outdoor enclosure (46 m perimeter; 132 m^2) in temperate pine forest in Durham, North Carolina (36°0′35″N, 79°1′11″W). All of the subjects had been housed together for at least 2 years. They were marked with numbered plastic and metal leg bands for individual identification.

Acoustic Stimuli

The antipredator vocalizations ('bu-girk') used as stimuli were recorded during a previous study (Yorzinski, 2014). They were produced by peahens from the same population as studied here and were elicited by a researcher attempting to capture the peahens. This antipredator call consists of two elements: 'bu' (mean duration ± SE: 175.9 ± 1.4 ms) and 'girk' (mean duration ± SE: 402.1 ± 5.9 ms; Yorzinski, 2014). We only used antipredator

vocalizations produced by females because the acoustic properties of male and female antipredator vocalizations differ (e.g. male calls have a lower fundamental frequency than female calls; Yorzinski, 2014). If we had also used antipredator vocalizations produced by males, then the peahens may have differentiated among calls based on the sex of the caller rather than the individual identity.

Acoustic stimuli were created using Raven Pro v.1.4 (www.birds.cornell.edu/raven). After selecting bu-girk calls with low background noise, we filtered out frequencies below 100 Hz; the fundamental frequency of peahen antipredator calls is above this level (bu: 234.32 ± 1.0 Hz; girk: 552.55 ± 1.9 Hz; Yorzinski, 2014). For each trial, we created a habituation loop and two stimulus sets. For the habituation loop, we randomly selected 10 calls from one peahen ('individual A'). We then created a 20 min playback loop in which these calls were randomly ordered (randomized using an algorithm based on atmospheric noise; www.random.org/integer-sets) and separated by silence (mean ± SE intercall interval = 18.1 ± 0.1 s; range 12—24 s). Most of the calls were repeated multiple times within the habituation loop so that there were a total of 60 calls within the loop (mean ± SE = 6.00 ± 0.16 times; range 0—16 repetitions). One stimulus set was created using five randomly selected calls from individual A (different calls than those used in the habituation loop). The other stimulus set was created using five randomly selected calls from another peahen ('individual B'). The order of calls within each stimulus set was randomized. The calls from nine different peahens were used to create the stimulus sets. The number of trials in which the calls from a particular individual were used ranged from one to eight. Except for one individual's calls that were used in two trials and another individual's calls that were used in one trial, the calls from the other individuals were used in both 'individual A' and 'individual B' stimulus sets. Calls were broadcast at 85 dB SPL at 1 m (Extech Instruments Sound Level Meter 40773; Extech Instruments, Waltham, MA, U.S.A.).

Experimental Setting

For each trial, a peahen was transported to an indoor room (2.75 × 3.35 × 2.35 m) at the Duke University Research Farm (36°2′23″N, 78°55′12″W), 9.6 km from the study population, and placed within an enclosure (1.60 × 1.80 × 2.20 m) constructed of a PVC structure with cloth walls and a plastic mesh roof. This was done at least 3 h (mean ± SE = 6.6 ± 0.5 h) before playback in order to allow the bird to habituate to the surroundings. The enclosure had a wooden perch (width: 0.76 m; height 0.92 m) that was placed only 0.33 m from one wall of the enclosure so that the bird was most likely to face in the opposite direction towards the speaker. We placed a speaker (Anchor mini-vox PB-25 speaker; frequency response: 100 Hz to 12 kHz) outside of the enclosure (1.55 m from the perch and 0.5 m high) such that it was in front of the perch and pointed directly towards it. The speaker was connected to a digital media player (Sansa Clip; SanDisk Corporation, Milpitas, CA, U.S.A.). We positioned two cameras in small openings on either side of the enclosure (1.4 m high) in order to record the responses of each of the bird's eyes (Sony Handycam DCR-SR42 and DCR-SR40 with Nightshot Plus enabled; Sony Corp., Tokyo, Japan). We recorded the left and right eye separately because peahens (Yorzinski & Platt, 2012), like other birds (Rattenborg, Lima, & Amlaner, 1999), asymmetrically close their eyes during sleep. Infrared lights (Clover Electronics IR045; Clover Electronics U.S.A., Cerritos, CA, U.S.A.) were located above each camera at the top of the enclosure. An experimenter (M.R.N.) observed the bird from outside the room through monitors connected to the camcorders. Sunrise and sunset were simulated in the enclosure with timers that switched from bright light (using a compact fluorescent lamp bulb; model no. 28942 ES42; TCP, Inc., Aurora, OH, U.S.A.; 95 lx at perch level) to

moonlight (using a dimmable incandescent bulb; model no. 11664; Osram Sylvania, Danvers, MA, U.S.A.; 0.7 lx at perch level) at the same time sunrise and sunset were in Durham, North Carolina on that trial day. The birds were given water and feed ad libitum.

Playback Procedure

We utilized a habituation−discrimination procedure in which a habituation phase was followed by stimulus sets designed to detect differential responses (e.g. Sproul et al., 2006). The experimenter arrived at the enclosure between 2200 and 2350 hours, when the bird was roosting for the night and it was dark. After turning on the equipment, he waited 20 min. The habituation phase involved broadcasting the habitation loop at least two times (mean ± - SE = 2.24 ± 0.12 times). He recorded the bird as responding to a given call if either of the bird's eyes opened within 2 s of the call's end or if either of the eyes were already open. If the bird responded to more than 50% of the calls during the second playback of the habituation loop, the loop was played a third or fourth time until responses were less than 50%. After this habituation period ended and both of the bird's eyes were closed for at least 5 s, he broadcast the first stimulus set. After the first call of the first stimulus set was broadcast, at least 18 s elapsed before the next call was broadcast. This interval was chosen to be the same as the mean interval between calls during the habituation phase. If the bird opened either of its eyes within this 18 s interval, then the next call would not be played until both of the bird's eyes had been closed for at least 5 s. After the first five-call stimulus set was played, he broadcast the other stimulus set using the same protocol. The order of the stimulus set (calls from individual A or B) was randomized across trials. Trials were aborted if the bird did not habituate according to the above criteria, the bird moved to a location in which neither of its eyes was visible, or outside disturbances interrupted the trial. Birds were removed and returned to their housing the following morning. After the trial, videos were analysed using Final Cut Express v.4.0.1 (Apple Inc., Cupertino, CA, U.S.A.). The birds' responses to each call, which were initially recorded in real-time during the trials (see above), were confirmed through video playback. We only analysed trials in which peahens habituated to more than 50% of antipredator calls during the final habituation loop that was broadcast to them (mean ± SE = 69.7 ± 0.024%).

We conducted 32 trials using 32 different birds. We tested all birds in the flock except one individual; this one individual was not tested because she escaped from the indoor testing room before she could be tested. Eleven of these trials were aborted because the bird did not habituate according to our criteria (see above). Within the successful trials ($N = 21$), we were able to analyse 96.7% of the stimulus A calls and 95.7% of the stimulus B calls (in the remaining calls, the bird's eye was not visible or opened before the call was played). The intercall intervals within the stimulus sets were similar (stimulus set of 'individual A': mean ± SE = 34.1 ± 3.6 s; stimulus set of 'individual B': mean ± SE: 37.6 ± 6.1 s; paired *t* test: $t_{20} = 0.76, P = 0.46$). Most of the trials (80.9%) had two habituation loops, while 14.3% had three, and 4.8% had four.

Acoustic Analysis

We also examined the acoustic properties of the antipredator calls used in the stimulus sets to determine whether they were related to the strength of the focal birds' responses to these calls (Beecher, Stoddard, & Loesche, 1985). The acoustic features were analysed from Fourier-based spectrograms using Luscinia sound analysis software (Lachlan, 2007; 150 Hz high-pass filter; 15 kHz maximum frequency; 20 ms Gaussian analysis window; 1 ms time step; 44.1 kHz sample rate). The software automatically calculated

the mean of the fundamental frequency, mean frequency and harmonicity as well as the duration of the 'bu' and 'girk' elements of the antipredator vocalizations (see Yorzinski, 2014, for further description of acoustic analysis and variables). These acoustic features vary consistently across individuals (Yorzinski, 2014). We calculated the overall mean and standard deviation of each of these four acoustic features for both the 'bu' and 'girk' elements using all of the calls from the stimulus sets ('overall mean' and 'overall standard deviation'). We then calculated a standard score for each call by taking the absolute value of the difference between the 'overall mean' and the value for that call and dividing by the 'overall standard deviation'. For each of the five calls within a stimulus set for each trial, we averaged these standard scores. For each trial, we then calculated the absolute value of the difference between the averaged standard score for the calls produced by 'individual A' and 'individual B' for each acoustic feature ('standardized difference').

Statistical Analysis

We ran a mixed linear model to test whether peahens differentiated between individual alarm callers. The independent variables included the caller ID (individual A or B), the order in which the stimulus sets were broadcast and the number of habitation loops broadcast (two, three or four; categorical variable); the focal ID and caller ID were included as a random variable. The dependent variable was the percentage of antipredator calls to which the focal bird responded. Because both eyes of the focal birds exhibited similar responses to the stimuli (paired *t* test: individual A calls: $t_{20} = 1.72, P = 0.10$; individual B calls: $t_{20} = 1.13, P = 0.27$), we averaged the responses between eyes.

We performed a stepwise selection procedure and generalized linear model to test whether peahens' responses depended on the acoustic features of the playback stimuli. We used a selection procedure (PROC STEPDISC) to select which acoustic features (using the 'standardized difference' acoustic values for each of the four acoustic parameters for the 'bu' and 'girk' elements) to enter into the linear model. The dependent variable was calculated by subtracting the percentage of antipredator calls to which the focal bird responded when the calls were produced by 'individual A' from the percentage of antipredator calls to which the focal bird responded when the calls were produced by 'individual B.' We analysed our data using SAS (v.9.3; SAS Institute Inc., Cary, NC, U.S.A.).

RESULTS

Peahens ($N = 21$) responded to a larger percentage of antipredator calls that were produced by the novel individual ('individual B'; mean ± SE =33.5 ± 5.4%) compared to the individual that produced the calls in the habituation loop ('individual A'; mean ± SE = 21.6 ± 4.6%; $F_{1,19.6} = 4.88, P = 0.039$; Fig. 1, Supplementary Movie S1). The order in which the calls were broadcast ($F_{1,17} = 0.30, P = 0.59$) and the number of habituation loops ($F_{2,17} = 1.08, P = 0.36$) did not influence focal responses. Peahens showed a greater response to calls produced by 'individual B' compared to 'individual A' when the difference in duration of the 'girk' element was greater ($F_{1,19} = 4.43, P = 0.0489$); the differences in the other acoustic features did not influence the peahens' magnitude of response to the calls.

DISCUSSION

We found that peahens differentiate between the antipredator calls of different individuals. When habituated to the antipredator calls of one individual, the birds responded less frequently to different calls from that individual compared to calls from a novel
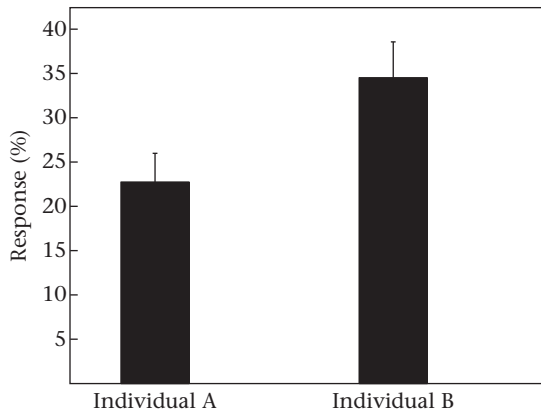
Figure 1. Responses (%) of peahens to stimulus calls produced by the individual that called during the habituation loops ('individual A') and to calls produced by a novel individual ('individual B'). Means ± SE are displayed.

individual. The strength of their response to the novel individual's call was greater when the call's duration was different from the duration of the other individual's call. This study is among the first to demonstrate that avian species are capable of differentiating among individuals based on antipredator calls (see also McDonald, 2012).

We used a habituation—discrimination playback paradigm to test the peahens' ability to discriminate between individual callers. We found that peahens showed a heightened response to the calls from a novel peahen (compared to a control), suggesting they are able to differentiate among individual callers. Previous studies that also used a habituation—discrimination playback paradigm found that the animals showed similar levels of responsiveness to calls from novel individuals as we found in the peahens (e.g. Hardouin et al., 2006; Wilson & Mennill, 2010). It would be interesting to evaluate whether levels of responsiveness to novel calls change depending on the sex of the callers (in this study, all calls used for playback were produced by females).

Our playback results are consistent with previous work showing that peafowl antipredator calls encode information about signallers (Yorzinski, 2014). Based on acoustic classification algorithms, peahen antipredator calls can be correctly classified to an individual with over 90% accuracy, and similar results have been found for the antipredator calls of other species (Cowan, 1974; Farquhar, 1993; Fischer et al., 2002; Patel & Owren, 2012; Schneiderová & Policht, 2011). Some studies have found a difference in response to antipredator calls based on signaller reliability (Blumstein, Verneyre, & Daniel, 2004; Hare & Atkins, 2001). In yellow-bellied marmots, individuals foraged less after hearing calls from unreliable individuals compared to reliable individuals, suggesting that they were becoming more vigilant and assessing the danger level directly rather than relying on information from the unreliable signaller (Blumstein et al., 2004). In contrast, Richardson's ground squirrels, *Urocitellus richardsonii*, become less vigilant after hearing calls from unreliable versus reliable signallers (Hare & Atkins, 2001). These opposing results indicate that species may use their ability to discriminate among conspecifics in different ways. It is possible that variation in predation pressure across species and classes influences these responses.

Importantly, social rank is encoded in peafowl antipredator calls (Yorzinski, 2014). Individuals may respond differentially to antipredator calls based on the dominance status of the caller (Hegner, 1985; Hogstad, 1986; Krams, 1998; Waite, 1987). In some species, dominant individuals express different antipredator behaviour than subordinate individuals and this information may be useful to

receivers (e.g. Hegner, 1985). Individuals may also use information encoded in antipredator calls to assess potential mates. Male domestic fowl, *Gallus gallus*, that produced alarm calls at higher rates had greater reproductive success than males that produced alarm calls at lower rates (Wilson, Bayly, Nelson, Gillings, & Evans, 2008).

Another benefit of individually distinctive alarm calls is that receivers can modify their responses based on the number of unique signallers. If multiple individuals are producing antipredator calls, there is likely to be a high probability that a predator is actually present. Blumstein et al. (2004) found that yellow-bellied marmots were more vigilant after hearing alarms calls produced by multiple individuals rather than a single individual. Antipredator calls produced by individuals that are widely dispersed could also indicate that multiple predators are present. Multiple predators in the area would increase risk levels and should lead to higher vigilance levels by prey.

Lastly, it would be valuable for peafowl to communicate about potential threats through acoustic signals. Given that peafowl live in dense scrubland habitat (Kannan & James, 1998), they are often not within visual range of each other. Because they can differentiate among signallers based on antipredator calls and potentially recognize individuals based on those calls, they could adjust their antipredator behaviour based on signaller identity without even seeing the caller. They may even be able to extract additional information based on the acoustic properties of the calls, such as the type of threat (Seyfarth, Cheney, & Marler, 1980). Their ability to differentiate between individuals provides a foundation for further investigations into the information that their antipredator and other vocalizations contain.

Social group size and complexity are likely evolutionary drivers of individuality in alarm calls. In sciurid rodents, the level of individuality in their alarm calls is positively related to group size but not social complexity (Pollard & Blumstein, 2011). These rodents have relatively stable social groups and individual discrimination is important. Little is known about the social structure of peafowl in the wild (Kannan & James, 1998). The average group size is 3.54 individuals, but groups can be as large as 18 individuals (de Silva et al., 1996) and vary with the season (Ali & Ripley, 1969). These groups are composed of both sexes, but females generally outnumber the males (de Silva et al., 1996). Because of their potentially large group sizes, we might expect peafowl to discriminate among individuals based on antipredator calls. However, we do not know whether their groups are stable (no study has tracked individual peafowl) and therefore the relationship between group size and strength of acoustic individuality that was found in rodents may not apply (Pollard & Blumstein, 2011).

Even though we found that peahens can differentiate among individual callers using antipredator calls, additional research is needed to assess whether they recognize individuals based on these calls. Recognition has been demonstrated in other avian species. White-throated sparrows, *Zonotrichia albicollis*, respond more strongly to playbacks of their neighbour's songs than to playbacks of a stranger's songs, indicating that they are differentiating between the songs and recognizing which songs belong to their neighbour (Brooks & Falls, 1975). Cliff swallows, *Hirundo pyrrhonota*, that are close to fledging also show acoustic recognition. These chicks respond more strongly to the calls of their parents than they do to unrelated birds (Beecher et al., 1985). These studies show that birds are able to recognize groups of individuals (e.g. neighbours versus others or parent versus others), but they may not be recognizing individuals per se (Rendall, Rodman, & Emond, 1996; Wiley, 2012). Similarly, peafowl may be able to recognize groups of individuals, especially since their antipredator calls encode information about the sex, size and social rank of caller (Yorzinski, 2014). If simpler mechanisms exist (recognizing groups

of individuals rather than each individual based on vocalizations) that are sufficient to meet the behavioural needs of animals in different contexts, then it may not be necessary for animals to use more complex mechanisms (Wiley, 2012).

In some species, the ability to recognize each individual (rather than groups of individuals) is important. Research on primates has shown that animals can recognize the individual identity of callers. Chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*, correctly match the vocalizations of conspecifics to photographs of those individuals (Kojima, Izumi, & Ceugniet, 2003; Sliwa, Duhamel, Pascalis, & Wirth, 2011). By conducting such an auditory-visual matching-to-sample paradigm in birds, we could better understand their recognition abilities.

Acknowledgments

Supplementary Material

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2015.11.016.

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