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# Risk-based alarm calling in a nonpasserine bird

Shailee S. Shah [a], Emma I. Greig [b], Sarah A. MacLean [c], David N. Bonter [b], *

[a] *Department of Neurobiology and Behavior, Cornell University, Ithaca, NY, U.S.A.*
[b] *Cornell Lab of Ornithology, Cornell University, Ithaca, NY, U.S.A.*
[c] *Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA, U.S.A.*

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Recent studies have demonstrated the presence of risk-based variation in alarm calling in many vertebrate species. Most of the studies on birds, however, have focused on passerine systems perhaps due to the traditional view that passerine vocalizations are more complex. We investigated the presence of a risk-based alarm calling system in a nonpasserine, the herring gull, *Larus argentatus*, by recording birds presented with varying degrees of threat, and experimentally exposing and quantifying responses to manipulated alarm calls. We found that herring gulls communicate threat urgency in their alarm calls using both frequency and time parameters. Sound recordings indicated that herring gulls change centre frequency modulation patterns of their alarm calls, generate frequency discontinuities in notes and increase the rate of calling with increases in perceived threat level. Playback experiments showed that conspecifics pay attention to both frequency and time parameters and respond most urgently to playbacks of high-threat calls at a high call rate. A less urgent response to high-threat calls at a low call rate and to low-threat calls at a high call rate suggests that threat urgency information is reinforced by both call type and call rate in the herring gull system. This study is one of the first demonstrations of a risk-based alarm calling system in a nonpasserine.

An organism faced with a potential threat typically engages in antipredator behaviour to increase its own chances of survival or those of other organisms in its vicinity (Bradbury & Vehrencamp, 2011). One such behaviour involves producing an alarm signal: an auditory, chemical or visual warning signal (Bradbury & Vehrencamp, 2011). Auditory alarm signals produced in a predator context are generally termed ‘alarm calls’ (Klump & Shalter, 1984). Alarm calls can be directed towards conspecific or heterospecific prey species and/or predators (Caro, 2005). When directed towards conspecific or heterospecific prey species, alarm calls elicit escape or predator defence behaviour in the receiver that also benefits the signaller in some way (Bradbury & Vehrencamp, 2011; Caro, 2005). Predator defence can be energetically costly (Caro, 2005), however, so an ability to judge the level of threat and respond in a manner commensurate with the risk is adaptive (Lima & Dill, 1990).

Recent studies have determined that some vertebrates have evolved alarm-calling systems in which alarm calls communicate specific information about the perceived threat. This information may communicate the type of threat (referential alarm-calling system) such as predator type (Gill & Sealy, 2003; Grieves, Logue, & Quinn, 2014; Gyger, Marler, & Pickert, 1987; Pereira & Macedonia, 1991; Seyfarth, Cheney, & Marler, 1980; Turner, 1973) or predator behaviour (e.g. flying versus perching; Griesser, 2008). Alarm calls can also encode information about the level of threat (risk-based alarm-calling system), such that the calls are modified depending upon the immediacy of the threat (Baker & Becker, 2002; Leavesley & Magrath, 2005; Owings & Hennessy, 1984; Templeton, Greene, & Davis, 2005; Welbergen & Davies, 2008). Some animals can communicate both types of information, type of threat as well as threat level, through different components of their alarm calls (Manser, Seyfarth, & Cheney, 2002; Murphy, Lea, & Zuberbühler, 2013; Sieving, Hetrick, & Avery, 2010; Suzuki, 2014).

In birds, various passerines have referential and/or risk-based alarm-calling systems. For example, Japanese great tits, *Parus major*, produce a ‘chicka’ call for crows (aerial predators) and a ‘jar’ call for snakes (terrestrial predators; Suzuki, 2012), and black-capped chickadees, *Poecile atricapillus*, vary the number of ‘dee’ notes in their ‘chick-a-dee’ alarm call to indicate the level of risk posed by the predator (Templeton et al., 2005). With the exception of studies on domestic fowl (Karakashian, Gyger, & Marler, 1988; Manser et al., 2002), however, little research attention has focused on referential or risk-based alarm calling in nonpasserines. This might

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* Correspondence: D. N. Bonter, Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Rd, Ithaca, NY 14850, U.S.A.
*E-mail address:* dnb23@cornell.edu (D. N. Bonter).

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be because passerine songs are often more complex than comparatively ‘simple’ nonpasserine songs (Beer, 1980). Passerines have a more developed syrinx than nonpasserines, allowing them to generate more complex vocalizations than nonpasserines (Bradbury & Vehrencamp, 2011). This difference in complexity of vocalizations, however, need not preclude complex alarm-calling systems in nonpasserines. Our study of risk-based variation in the alarm calls of herring gulls, *Larus argentatus*, investigates whether a nonpasserine species can have a sophisticated risk-based alarm-calling system similar to that found in many passerine species.

Herring gulls nest in colonies and communicate complex information using a rich repertoire of postures and vocalizations, which have been well documented by Tinbergen (1961) in a classic study of animal communication. Herring gulls respond to conspecific alarm calls by becoming alert and assuming a defensive posture as demonstrated in recent experiments (MacLean & Bonter, 2013). A signaller in a colony of nesting gulls may benefit by recruiting conspecifics to mob the potential predator (Caro, 2005; Clode, Birks, & MacDonald, 2000; Montgomerie & Weatherhead, 1988). Because antipredator defence by herring gulls involves energetically costly calling, grass pulling (a way of signalling aggression), pecking and dive bombing (Tinbergen, 1961), risk-based variation in their alarm calls could be adaptive so that gulls in a colony can adjust their response based on the level of threat encoded in the call. Previous work has shown that gulls can discriminate between auditory cues from different potential threats and react in a corresponding graded manner, yet the mechanisms for communicating threat level remain unknown (MacLean & Bonter, 2013). Here, we hypothesize that herring gulls encode risk-based variations in their alarm calls to communicate the level of threat, to which conspecifics respond in a graded manner.

To demonstrate the information conveyed by a signal, it is important to quantify both signal production and response (Evans, 1997). The goals of this study were, therefore, to (1) quantify differences in the structure of herring gull alarm calls given under varying degrees of threat and (2) experimentally expose conspecifics to playbacks of alarm calls with varying structures to test whether receivers perceive differences in urgency. If gulls communicate threats via a risk-based alarm-calling system, we predicted that gulls would (1) modify their alarm calls with increasing level of threat through a change in frequency and/or time parameters and (2) respond more urgently to playbacks of alarm calls with frequency and/or time parameters that reflected high-threat level than to playbacks with parameters reflecting low-threat level.

## METHODS

### Ethics Statement

This research was carried out in strict accordance with the Guidelines for the Use of Wild Birds in Research of the Ornithological Council and approved by the Cornell University Institutional Animal Care and Use Committee (protocol no. 2011-0036). Research was conducted on property managed by Cornell University for research and educational purposes. This work did not involve any threatened, endangered or protected species. No nests were abandoned as a consequence of our research and playback experiments were terminated before eggs hatched.

### Study Site and Population

We studied herring gulls nesting on the Isles of Shoals Archipelago (42.98°N, 70.61°W), approximately 11 km offshore of Portsmouth, New Hampshire, U.S.A. Alarm calls were recorded on Appledore Island (June–July 2012 and 2013) and playback experiments were conducted on Appledore and Smuttynose Islands (June–July 2012). Herring gulls in the Isles of Shoals nest in mixed-species colonies with great black-backed gulls, *Larus marinus*, along rocky shorelines and in loose subcolonies around buildings where nests are relatively isolated from congeners (Savoca, Bonter, Zuckerberg, Dickinson, & Ellis, 2011). To limit the influence of neighbouring birds on individual reactions, we only tested birds nesting in relative isolation in the loose subcolony setting. The alarm call of herring gulls is described as a short staccato ‘yeow’ call that is given in response to a perceived threat (Tinbergen, 1959). The call is given repeatedly such that one burst of alarm calling consists of three or more yeow calls given in quick succession and is effectively used to communicate the presence of a potential threat to conspecifics (Tinbergen, 1959). Recent research shows that the acoustic components of herring gull alarm calls are not affected by body size or sex (Hardouin, Thompson, Stenning, & Reby, 2013); thus, differences in these factors were not of concern in this study.

### Alarm Call Recording

Distance from predator has been used as a measure of threat level in many studies (Baker & Becker, 2002; Leavesley & Magrath, 2005; Welbergen & Davies, 2008), and directness of approach could be a strong indicator of a predator's intent to attack (Stankowich & Blumstein, 2005). To investigate the structure of alarm calls given under varying levels of threat, we recorded yeow calls of incubating herring gulls as a person walked directly towards them, creating a situation of steadily increasing threat level. Humans were major nest predators of gulls in recent history and continue to disturb and harass (often illegally) nesting gulls to this day. As such, the gulls in our study population actively defend their nests against people (Burger & Gochfeld, 1981; MacLean & Bonter, 2013). Thus, this is a suitable system for testing the existence of a risk-based alarm-calling system in a nonpasserine species using the approach of a human as an experimental threat.

All calls were recorded using a Sennheiser ME 67 microphone and Marantz PMD 661 recorder (sampling .WAV files at 48 kHz and 24 bits) mounted on a tripod. The equipment was placed 5–10 m away from a nest with an incubating gull and the bird was then observed from a concealed location. Because amplitude was not a parameter of interest, the distance of recording equipment from the nest could be varied slightly as the rugged terrain required without affecting the consistency of the recordings. One minute after the gull had resumed incubating without any signs of alertness, a researcher (S.S.S.) walked directly towards the nest at a uniform, slow pace of approximately 1.5 m/s from 15 m away to simulate a threat of increasing urgency. Birds typically produced yeow calls throughout the approach. Note that a change in perceived threat level may have been due to the decrease in distance between the researcher and the gull, the increase in duration of exposure to the researcher, or a combination of both. Regardless, this methodology allowed us to record calls given under increasing degrees of perceived threat. In addition, while working in the gull colony on the Isles of Shoals, we (S.S.S., S.A.M. & D.N.B.) have observed that close proximity to a nest (within ~20 m) instigates defensive behaviours whereas extended human activity at greater distances from a nest does not, so we suspect that proximity of the researcher and not duration of exposure was driving the perceived increase in threat.

### Call Analysis

We analysed all recordings in Raven Pro 1.4 (Bioacoustics Research Program, 2011; 16-bit sample format; discrete Fourier transform = 256 samples; frequency resolution = 188 Hz; time resolution = 2.67 ms; frame overlap = 50%). To analyse the difference in call rate depending on threat level, we divided each recording (from the beginning of the first call to the end of the last call) into three sections of equal duration, creating a low-, medium- and high-threat section. We then manually selected each individual call and measured the length of each call and the time between successive calls.

To quantify differences in frequency parameters of calls given under low and high threat, we selected the first and last clear calls of each recording (Fig. 1). All sound below 0.5 kHz was filtered out because it only constituted background noise. Visual inspection of spectrograms suggested variability in the middle third of the yeow calls (Fig. 1), so calls were divided into three sections of equal duration for subsequent analyses. We calculated the centre frequency, the frequency that divides the selection into two frequency intervals of equal energy (Charif, Waack, & Strickman, 2010).

Visual analyses of spectrograms detected discontinuities (frequency jumps) in the fundamental frequency of some call notes (Fig. 1). As such, we (S.S.S.) further blindly scored low-threat and high-threat calls as either ‘continuous’ or ‘discontinuous’ based on whether there was a 0.5 kHz break in the note anywhere except for the first and last 10 ms.

### Playback Experiment

To construct a series of exemplars for use in playback experiments, we selected the first clear call recorded under high-threat and low-threat conditions from each of six gulls recorded in the 2012 nesting season. All calls were recorded using the previously described method. We recorded calls from six birds to create a number of exemplars to reduce potential problems associated with pseudoreplication (Kroodsma, Byers, Goodale, Johnson, & Liu, 2001). We acknowledge, however, that each exemplar was used more than once (2–3 times per exemplar) in our 14 playback experiment trials detailed below.

Each playback consisted of a single call repeated at intervals of 1 s (high call rate) or 3 s (low call rate) for 1 min. These intervals were based on the previous analysis and represented realistic gaps between successive call notes for the low-threat and high-threat calls. This combination of call rate and call type resulted in four playback treatments: (1) high-threat calls at 1 s intervals, (2) high-threat calls at 3 s intervals, (3) low-threat calls at 1 s intervals and (4) low-threat calls at 3 s intervals.

A recording of a song sparrow, *Melospiza melodia*, song was used to quantify the reaction of each focal bird to noise produced by the playback system. Song sparrows are common nesting birds on the Isles of Shoals that are familiar and nonthreatening to the gulls, and their songs have elicited minimal responses in previous playback experiments within our study population (MacLean & Bonter, 2013).

Each playback session began with 3 min of silence to allow the focal bird to return to a calm state after the observer installed the equipment. Each focal bird was then exposed to three consecutive 1 min stimuli, each separated by 4 min of silence (Fig. 2). The playbacks were constructed as Waveform Audio Files using Audacity 2.0.0 (D. M. Mazzoni, Canada, http://audacity.sourceforge.net/). All playbacks were equalized to 60 dB when constructed and the playback system settings were consistent across trials. We tested the amplitude of playbacks with the field playback equipment using a sound pressure level meter (model number 33-2050, Radio Shack Corporation, Fort Worth, TX, U.S.A.), set at C-weighting, fast response (~72.0 dB at 1 m for all playbacks). Each focal bird was videorecorded during the playback sessions using a Camcorder HMX-Q10BP (Samsung Electronic Co.), and subsequent video analysis showed that the periods of silence between each playback were sufficient for the incubating gull to return to a calm state before the next stimulus began. In addition, the videos showed that none of the focal birds left or were otherwise disturbed during the playbacks.

The playbacks were conducted towards the end of the incubation stage when nest defence is at its peak (Tinbergen, 1961). To control for difference in motivation for nest defence, all playbacks were performed during a 2-week period before eggs hatched. Because of this time constraint, playbacks were performed in pairs based on call type (high or low threat). Each playback session consisted of three treatments: a certain call type at 1 s intervals, the same call type at 3 s intervals and the song sparrow vocalization. The playback order within each session was randomized. The order of session type (high-threat call type session or low-threat call type session) was also randomized. At least 24 h elapsed between the two playback sessions. See Fig. 2 for a graphical representation of the playback order for one individual.

To increase the likelihood that the same individual was tested for both treatment pairs, playbacks were conducted at the same

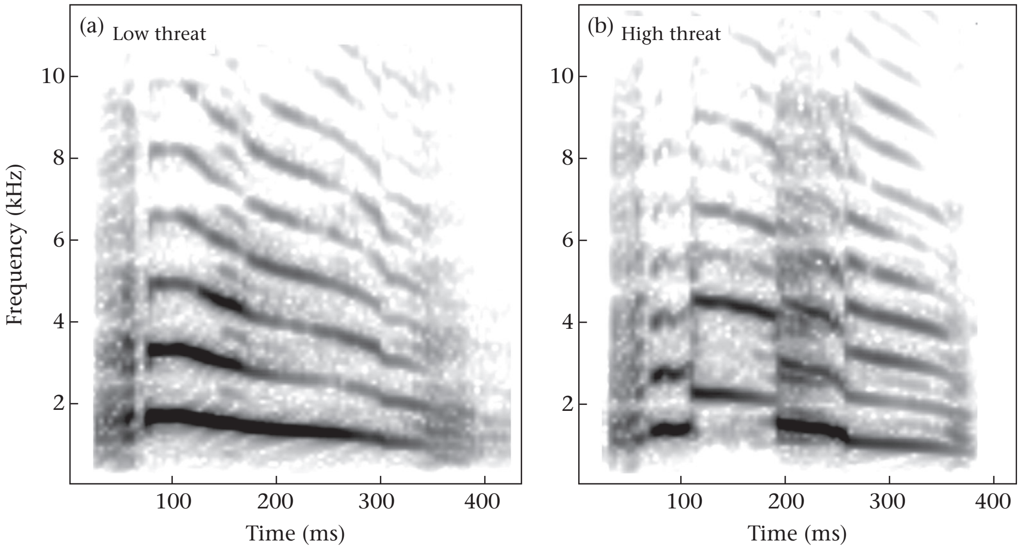

**Figure 1.** Examples of spectrograms of the first and last clear calls of a recording for a call given at (a) low-threat level and (b) high-threat level.

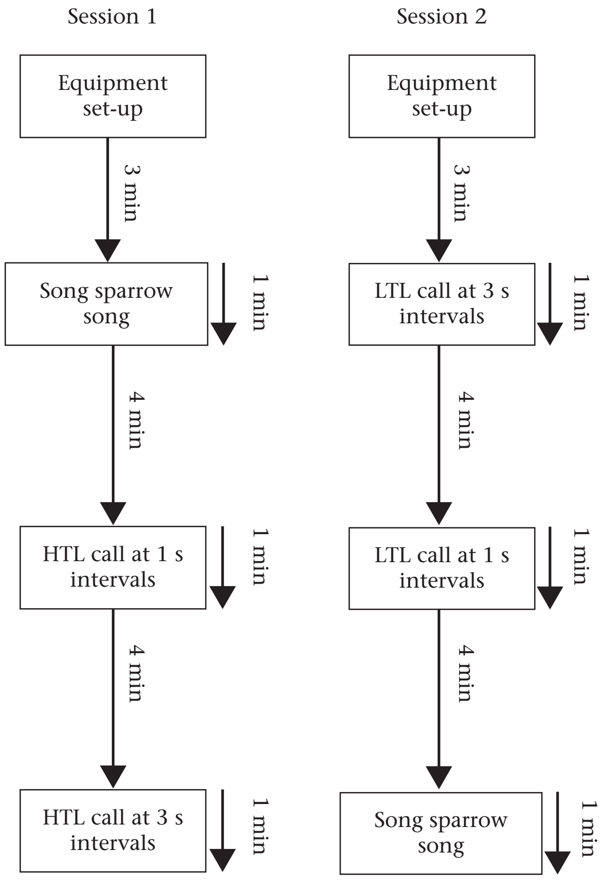

**Figure 2.** Schematic representation of playbacks to one individual herring gull. Order of playbacks was randomized and playback sessions were conducted on different days. LTL: low-threat level; HTL: high-threat level.

time of day (gull pairs have a set incubation rotation; Tinbergen, 1961). In addition, 36% of gulls tested were individually identifiable by field-readable leg bands. All focal birds were exposed to the suite of six playbacks (3/day).

Playbacks were conducted using Panasonic Folding Travel Speakers (RPSPT70) and an iPod (Apple, Inc., 3rd Generation Nano) in WAV format. The speakers were placed 2 m away from the nest, facing the incubating gull, and a video camera was placed 5 m from the nest to record gull responses. As soon as the playback was initiated, the researcher left the vicinity (>20 m) and hid out of view of the incubating gull for the duration of the experiment so that test subjects were only exposed to the auditory threat cues. The playback experiment began with 3 min of silence, giving the incubating gull enough time to return to a calm state after being exposed to the presence of a human being. The response to each auditory stimulus was graded on a scale of 0 to 7 (based on Tinbergen, 1961; MacLean & Bonter, 2013; Table 1) using the video of responses recorded during playback.

### Statistical Analysis

Potential differences in the centre frequency (response variable) of alarm calls were tested using a mixed model in SAS (v.9.2 PROC MIXED, SAS Institute, Cary, NC, U.S.A.). The model tested for differences in the response variable based on threat scenario (categorical: low or high threat), call section (categorical: beginning, middle or ending third of the call), and the interaction between threat scenario and call section. Individual bird identification was included as a random variable because multiple alarm calls were analysed from each individual.

Differences in time between calls and call lengths under various threat scenarios were also tested using separate mixed models with threat scenario as the independent variable and bird identification included as a random variable (PROC MIXED). Differences between levels of categorical variables were calculated using the PDIFF option in LSMEANS. A chi-square analysis (PROC FREQ in SAS) tested for differences in discontinuities between calls recorded under LTL and HTL situations.

Differences in the reactions of gulls to various stimuli presented in the playback experiment were quantified using generalized linear models for categorical response variables (PROC GENMOD), where the response variable was the maximum reaction to the stimuli (ordinal multinomial response variable, cumlogit link). In addition to stimulus type, the order in which each stimulus was presented was included in the full model. Individual was used as a random (repeated) variable in the models because each individual was exposed to all stimuli. We could not test for an exemplar effect in our statistical models because each exemplar was only used in two or three playback trials. We computed log odds ratios using 'estimate' contrasts within GENMOD to compare each pair of stimuli in order to test for differences in the intensity of reaction to the various treatments.

## RESULTS

### Call Analysis

The centre frequency was greater for high-threat calls than for low-threat calls (generalized mixed model: $F_{1,100} = 4.71$, $P = 0.032$). Centre frequency varied among sections of the yeow call with the greatest centre frequency being recorded in the middle third of the call (generalized mixed model: $F_{2,100} = 3.47$, $P = 0.035$). The interaction term demonstrates that the centre frequency of call sections varied differently under different threat scenarios (generalized mixed model: $F_{2,100} = 3.37$, $P = 0.038$; Fig. 3), with the centre frequency peaking in the middle third of the high-threat calls and decreasing in the last third of the low-threat calls. Peak frequency showed a qualitatively similar pattern to centre frequency.

Time between calls was greater in the first third of each recording, when the potential threat was farther from the nest, and decreased as the observer approached (generalized mixed model: $F_{22,53} = 24.61$, $N = 27$, $P < 0.001$), with least squares means indicating a difference in the intercall interval between the low-urgency situation and the two higher-urgency situations (Fig. 4). The average length of calls recorded under various threat scenarios did not differ (generalized mixed model: $F_{2,10} = 0.92$, $P = 0.403$; Fig. 4).

Furthermore, analyses of discontinuities in the yeow calls clearly demonstrated more discontinuous breaks in the vocalizations produced under high-threat level (19 of 21 recordings) than under low-threat level (0 of 21 recordings, chi-square test: $\chi^2_1 = 34.70$, $P < 0.001$).

### Response to Playback

Responses of the gulls were strongly influenced by stimulus type (chi-square test: $\chi^2_4 = 11.87$, $P = 0.018$). Log odds ratio contrasts indicated that the mean response to high-threat calls at high frequency elicited the strongest response, whereas the song of the song sparrow (controlling for the broadcast of any sound from the playback system) elicited the weakest response. High-threat calls at 3 s intervals, low-threat calls at 1 s intervals and low-threat calls at 3 s intervals elicited responses of medium intensity (Fig. 5a).

**Table 1**
Scale used to categorize the maximum response of incubating herring gulls to playback of different yeow call types at varying call rates

| Response level | Behaviour |
|---|---|
| 0 | No response |
| 1 | Increased vigilance (neck outstretched and scanning for threats) followed by relaxation |
| 2 | Increased vigilance (neck outstretched and scanning for threats) throughout playback |
| 3 | Extreme vigilance: neck outstretched, rapid scanning for threats, kek-kek calls |
| 4 | Yeow or long calls |
| 5 | Standing up and off of eggs |
| 6 | Ground-based movement within 3 m of nest |
| 7 | Flying off nest and circling from the air |

Higher response categories often included lower-level reactions.

Playback order did not affect bird responses (chi-square test: $\chi^2_1 = 0.01$, $P = 0.913$).

Because responses to the song sparrow playback were minimal and only intended to gauge the responses of gulls to any sound being broadcast from the speakers, we dropped the sparrow stimulus from further analyses and focused on the primary objective of quantifying the response of gulls to differences in threat level and playback interval. Gulls responded more vigorously to high-threat calls than to low-threat calls (chi-square test: $\chi^2_1 = 4.39$, $P = 0.036$; Fig. 5b) but did not react differently based on call interval ($\chi^2_1 = 0.48$, $P = 0.488$; Fig. 5c). A comparison of artificial playbacks mimicking the scenario typically found in nature (high-threat calls at short intervals versus low-threat calls at long intervals) found that birds responded with marginally more vigour to the high-threat calls at short intervals (chi-square test: $\chi^2_1 = 3.71$, $P = 0.054$; Fig. 5a). Playback order did not influence responses (all $P > 0.291$).

## DISCUSSION

This study is the first to demonstrate the presence of a risk-based alarm-calling system in a nonpasserine species other than domestic fowl (see Karakashian et al., 1988; Manser et al., 2002). This system is similar to those present in many mammal (Manser et al., 2002) and passerine species (Baker & Becker, 2002; Leavesley & Magrath, 2005; Templeton et al., 2005; Welbergen & Davies, 2008), and suggests that risk-based alarm calling is a more widespread phenomenon than has been previously documented. Passerines are traditionally associated with more complex vocal behaviour (Beer, 1980) due to their well-developed syrinx, but this study demonstrates complexity in nonpasserine vocalizations previously considered discrete units lacking gradation (Tinbergen, 1961).

We found that the pattern of frequency modulation in herring gull yeow alarm calls changed with a change in perceived threat level, with higher levels of threat eliciting higher frequencies at the end of the call. This result was similar to that of a study on white-browed scrubwrens, *Sericornis frontalis*, whose aerial trill alarm call showed an increase in minimum frequency with increase in threat urgency (Leavesley & Magrath, 2005). This increase in frequency could be an indication of an extreme state of fear (Morton, 1977).

In addition, we found that significantly more calls given under high-threat scenarios had frequency jumps of 0.5 kHz or more than calls given under low-threat scenarios. Discontinuities such as frequency jumps, biphonation or noise in calls have been shown to elicit stronger responses than continuous calls in mammals such as chimpanzees, *Pan troglodytes* (Riede, Owren, & Arcadi, 2004), yellow-bellied marmots, *Marmota flaviventris* (Blumstein, Richardson, Cooley, Winternitz, & Daniel, 2008), rhesus macaques, *Macaca mulatta* (Fitch, Neubauer, & Herzel, 2002), red deer,

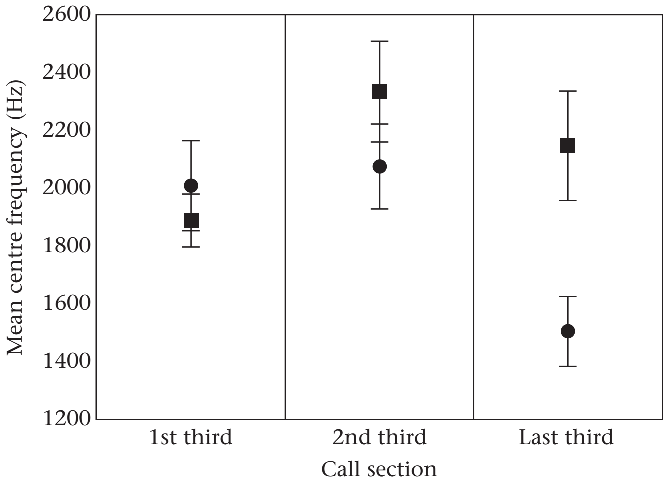

**Figure 3.** Variation in centre frequency across three sections of high-threat level (■) and low-threat level (●) yeow calls. Means and standard errors are reported ($N = 21$ birds).

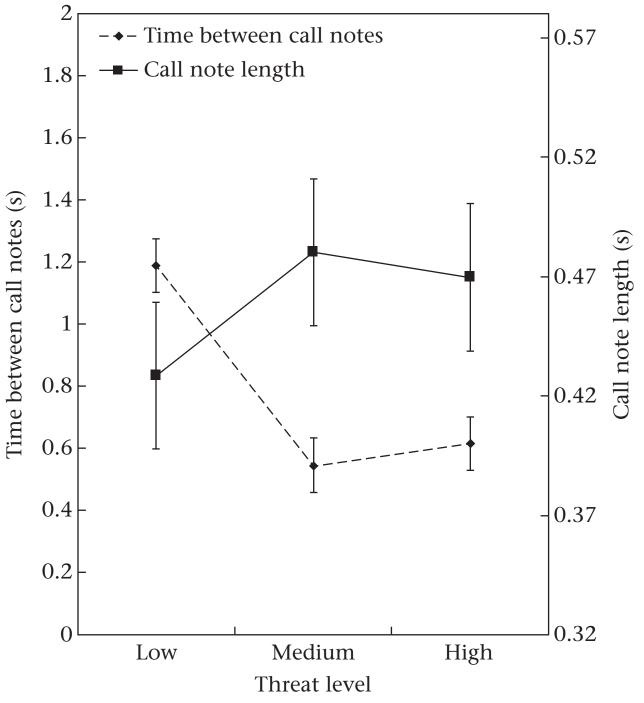

**Figure 4.** Variation in time between calls and call length with change in threat urgency in herring gull yeow calls. Least squares means and standard errors are reported ($N = 27$).

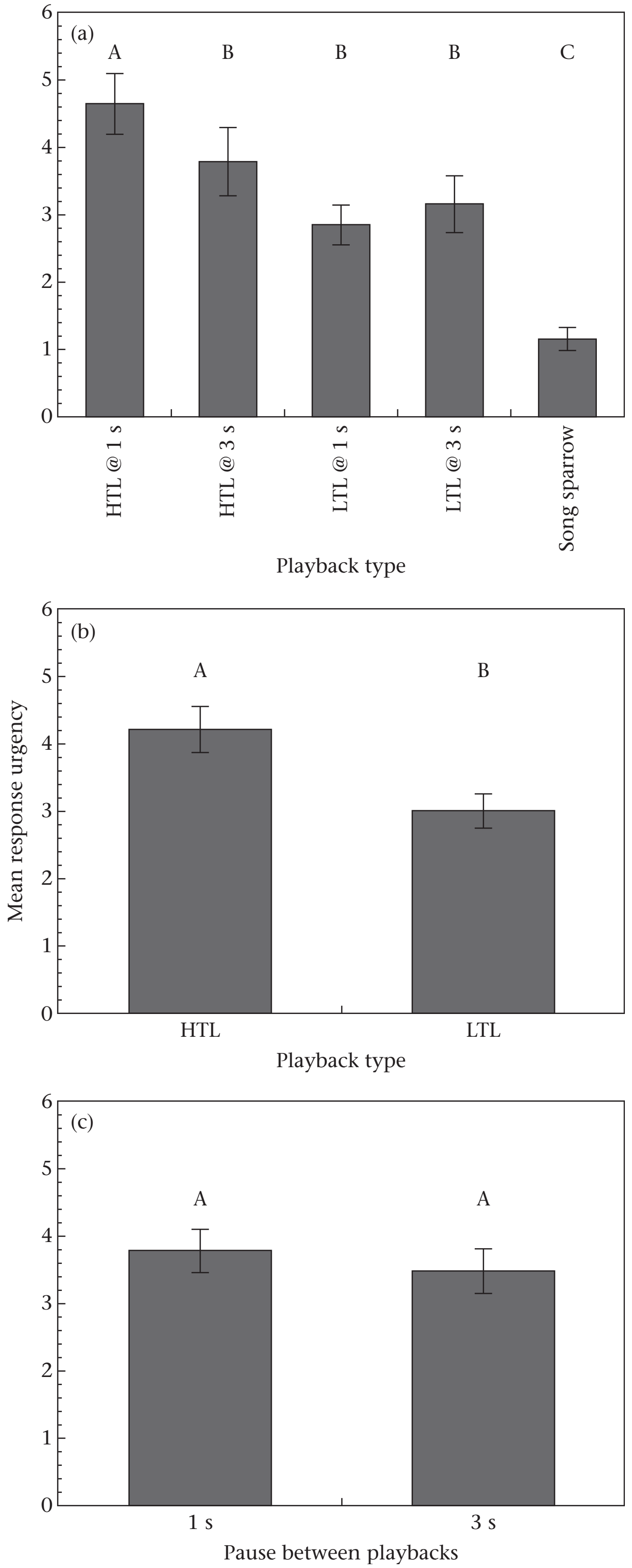

**Figure 5.** (a) Response of 14 herring gulls to five playback treatments including high-threat level (HTL) and low-threat level (LTL) calls at different time intervals as well as a song sparrow (nonthreatening) vocalization. Subsequent analyses restricted the data set to test for differential responses based on threat level alone (b), or to test for differential responses based on playback interval (c). Responses were scored on a scale of increasing intensity (Table 1). Different letters indicate significantly different responses ($P < 0.05$).

*Cervus elaphus* (Reby & Charlton, 2012) and humans, *Homo sapiens* (Facchini, Bellieni, Marchettini, Pulselli, & Tiezzi, 2005; Green, Jones, & Gustafson, 1987) and birds including great-tailed grackles, *Quiscalus mexicanus* (Slaughter, Berlin, Bower, & Blumstein, 2013) and white-throated sparrows, *Zonotrichia albicollis* (Blesdoe & Blumstein, 2014). Such a heightened response may be a result of the unpredictability of discontinuous phenomena that discourages habituation (Fitch et al., 2002). Frequency jumps in herring gull yeow calls given at a high-threat level might similarly elicit a more urgent alarm response in conspecifics.

Herring gulls also increased the rate of alarm calling as the perceived threat level increased. A similar pattern has been observed in mammals such as yellow-bellied marmots (Blumstein & Armitage, 1997), and passerines such as black-capped chickadees (Baker & Becker, 2002) and reed warblers, *Acrocephalus scirpaceus* (Welbergen & Davies, 2008). In both species of passerines, the rate of calling increased with decreasing distance between the simulated predator and the bird (black-capped chickadee: Baker & Becker, 2002), or the nest (reed warblers: Welbergen & Davies, 2008). Thus, our results suggest that call rate is used to communicate urgency in gulls in a manner similar to many passerine alarm calls.

When playback experiments were conducted using this variation in herring gull yeow calls, naïve conspecifics responded most urgently to high-threat call notes played at a high rate. Interestingly, high-threat call notes played at a low rate and low-threat call notes played at a high rate elicited the same level of response as low-threat call notes played at a low rate. This lower level of response, however, was greater than the response to a nonthreatening playback, suggesting that it was a low-urgency alarm response and not simply a reaction to noise generated by the playback system. Future experiments using nonalarm gull calls would be beneficial to establish a baseline nonalarm response to a conspecific call. We are confident, however, that the low-level responses observed to low-threat stimuli are alarm responses because yeow calls are only given in an alarm context. Herring gulls, therefore, seem to use both call type and call rate information to determine urgency of threat. Previous studies on mammals, such as meerkats, *Suricata suricatta* (Manser et al., 2002), and birds, such as tufted titmice, *Baeolophus bicolor* (Sieving et al., 2010) and Japanese great tits (Suzuki, 2014), have shown that different components of calls can be used to communicate different information about predator type and threat urgency. Further experimentation is required to determine whether herring gulls similarly encode information about different aspects of the threat in the two parameters or whether call type and call rate in yeow calls are redundant and reinforcing.

Nest defence is costly and modifying defensive behaviour based on information about urgency of threat can conserve energy (Lima & Dill, 1990). The rate of nest depredation on the Isles of Shoals is high for herring gulls (Ellis & Good, 2006) who actively defend their nests. A risk-based alarm-calling system could be adaptive if the urgency of response elicited is commensurate with the level of threat and energy is not wasted on unnecessary defence behaviours. Various referential and risk-based alarm-calling systems play an adaptive role by eliciting a threat-appropriate response. Black-capped chickadees, for example, adjust the length and intensity of their mobbing response in accordance with the level of threat encoded in conspecific mobbing calls (Templeton et al., 2005), and threat-specific alarm calls determine situation-specific escape responses in other passerines (Griesser, 2008; Suzuki, 2012). Specific information about a potential threat can thus increase the efficiency of antipredator responses and minimize energy expenditure.

Previous studies in other avian systems demonstrate that urgency information can also be communicated between species. For example, white-browed scrubwrens and superb fairy-wrens, *Malurus cyaneus*, two Australian passerines that form mixed-species flocks in the winter, respond to each other's alarm calls (Fallow & Magrath, 2010). Similarly, tufted titmice and Carolina chickadees, *Poecile carolinensis*, that interact in winter foraging flocks in North America respond to specific predator information encoded in each other's alarm calls (Hetrick & Sieving, 2011). Because gulls often nest in congeneric colonies, it would be interesting to test whether variation in the urgency of alarm calls is interpreted not just by conspecifics but also by heterospecifics. A recent study by MacLean and Bonter (2013) showed that great black-backed gulls on the Isles of Shoals respond to herring gull alarm calls, but not as vigorously as they respond to conspecific alarm calls. This might be due to the size difference between the two gull species: great black-backed gulls are larger and thus might be less intimidated by predators that pose a threat to herring gulls. It is unknown whether great black-backed gulls respond more urgently to herring gull calls conveying high-threat level than to herring gull calls conveying low-threat level.

Given the limited genetic differentiation among the white-headed larid gulls (Snell, 1991) and the similarity of vocal and postural signals among many gull species (Tinbergen, 1959), our results likely apply to other members of the Laridae. More generally, the similarity of the system of risk-based alarm calling in herring gulls to those found in other taxa suggests that risk-based alarm communication may be a more widespread phenomenon than previously demonstrated.

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