Report

Referential Calls Signal Predator Behavior in a Group-Living Bird Species

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Summary

Predation is a powerful agent of natural selection, driving the evolution of antipredator calls [1]. These calls have been shown to communicate predator category [2–4] and/or predator distance to conspecifics [5–7]. However, the risk posed by predators depends also on predator behavior [8], and the ability of prey to communicate predator behavior to conspecifics would be a selective advantage reducing their predation risk. I tested this idea in Siberian jays (Perisoreus infaustus), a group-living bird species. Predation by hawks, and to a lesser extent by owls, is substantial and the sole cause of mortality in adult jays [9]. By using field data and predator-exposure experiments, I show here that jays used antipredator calls for hawks depending on predator behavior. A playback experiment demonstrated that these prey-to-prey calls were specific to hawk behavior (perch, prey search, attack) and elicited distinct, situation-specific escape responses. This is the first study to demonstrate that prey signals convey information about predator behavior to conspecifics. Given that antipredator calls in jays aim at protecting kin group members [10, 11], consequently lowering their mortality [9], kin-selected benefits could be an important factor for the evolution of predator-behavior-specific antipredator calls in such systems.

Results

Background

Siberian jays are sedentary birds typical of boreal forests of the northern Palearctic. The species lives in groups consisting of a breeding pair and up to four non-breeders year-round, including retained offspring and/or unrelated immigrants [12, 13]. Predation in jays is substantial and almost the sole cause of mortality [9]. Over 35% of all individuals are killed by predators during their first winter of life, primarily by hawks (goshawk [Accipiter gentilis], sparrowhawk [A. nisus]) and to a lesser extent by owls (hawk owl [Surnia ulula], Tengmalm's owl

[Aegolius funereus], Ural owl [Strix uralensis]) [9, 14]. Siberian jays have evolved a wide range of nepotistic antipredator behaviors [10, 11, 15] as a response to this predation pressure, and these behaviors have been demonstrated to improve the survival prospects of related group members [9].

Calls in Relation to Hawk Behavior

The main predators of Siberian jays, hawks, have a characteristic hunting sequence with three distinctive phases. First, hawks begin by perching on a tree, scanning for prey. They then make search flights to the next perch, where they scan again. Upon detection of a potential prey individual, hawks attack by using vegetation cover to take their quarry by surprise [16, 17]. Field observations suggested that Siberian jays uttered situation-specific calls toward perched, searching, and attacking hawks (Table 1; Figure 1). Jays used alert calls only toward searching hawks (n = 21 encounters), whereas only attack calls were given toward attacking hawks (n = 5 attacks). When encountering perched hawks (n = 3 encounters), jays used a variety of calls while mobbing the hawk, but never uttered attack calls or alert calls. To confirm the situation specificity of the calls, I exposed jay groups congregated at feeders in the wild to perched hawk models, an attacking hawk model and, to control for effects of the experimental setup, a perched, nonnative, jay-sized bird species (blue jay [Cyanocitta cristata]) (Table 1). Jays uttered attack calls only in response to an attacking hawk model, whereas they gave hawk-mobbing calls (perched-hawk calls, ki-ki calls) almost exclusively in the presence of a hawk model. In response to the blue jay model, only one juvenile group member uttered five perched-hawk calls. In the absence of a predator model, jays used a variety of situation unspecific calls, but none of the calls that were specific for hawk behavior.

Test of Predator-Behavior-Signal Hypothesis

To test whether these situation-specific calls convey information about hawk behavior to other group members, I performed a playback experiment with randomly selected dyads of individuals foraging on a feeder (n = 12 groups). Experimental individuals responded with situation-specific behavioral patterns toward the playback of these calls, and these responses matched the behavioral pattern observed during real predator encounters or encounters with predator models (Tables 2 and 3). Upon the playback of alert calls given toward searching hawks, in all cases, both individuals flew immediately to the closest cover, froze, and engaged in passive predator-search behavior (n = 12 groups). This behavioral response accurately matched the behavioral pattern observed during natural encounter with searching hawks. After playback of an attack call, the jays flew immediately to the nearest cover (n = 12 groups) and engaged from there straight away in passive and active predator-search behavior. The response differed from the one of jays exposed to an attacking-hawk model, which

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Table 1. Mean Number of Calls of Siberian Jays during Predator Encounters

Situation	Searching Hawk[a]	Attacking Hawk[c]	Perched Hawk[d]	Perched Blue Jay[d]	No Predator Present[d]
n experiments	21	40	35	15	20
mean group size	3.7	2.0	4.1	4.1	4.0
alert call	1[b]	0	0	0	0
attack call	0	0.85	0	0	0
perched hawk call	0	0	9.73	0.33[e]	0
ki-ki call	0	0	1.18	0	0
other calls	0	0	26.39	9.93	8.14

Mean number of calls of Siberian jays given in response to searching hawks (natural encounters), an attacking-hawk model, perched-hawk models, perched-blue-jay model, and in the absence of a predator.
[a] Counting number of all calls given during encounter length: mean ± standard error (SE) = 5.5 ± 1.91 min.
[b] For calls given toward prey-searching hawks, I only recorded whether alert calls were given or not but did not count the number of calls given.
[c] Counting number of all calls given until birds resumed feeding: mean ± SE = 1.7 ± 0.34 min.
[d] Counting number of all calls given during 4 min.
[e] One juvenile group member gave in response to the blue jay model five perched-hawk calls.

only in four out of 12 experiments engaged in active predator search after the attack. This difference is likely to be attributed to the fact that jays in the playback experiment did not see any attacking hawk and were thus more likely to actively search the hawk. Jays exposed to a mobbing call sequence did not seek cover but directly engaged in passive and active predator search (n = 12 groups), giving calls (n = 8 groups), closely matching the behavior of jay groups in presence of a perched-hawk model. The playback of control vocalizations (pickering, a social vocalization jays utter while foraging) did not cause jays to seek cover, utter alarm calls, or engage in predator search behaviors. Instead, the jays continued to forage on the feeder and cache the collected food in the same manner in which undisturbed jays forage.

Discussion

Numerous studies have investigated antipredator calls in mammals and birds and demonstrated that such calls can convey information to recipients about predator category [2–4], the urgency to respond [5, 6], or both [7]. However, none of these studies considered that predator behavior varies, which could affect the signaling behavior of prey. Most predator species spend only a part of their time hunting prey; they rest, digest, or sleep during the remainder of the day and so vary in the danger that they present to prey. My results suggest that antipredator calls of Siberian jays convey information about predator behavior. The perception of hawk-behavior-specific calls in the playback experiments was sufficient for call recipients to make an appropriate behavioral response, supporting the referential character of these calls [3]. Thus, this is the first study to demonstrate that prey signals convey information about predator behavior to conspecifics. The ability to communicate predator behavior has not previously been demonstrated in any other species, yet this could be a widespread adaptation. Many prey species seem to be able to derive information about the predator's behavior or motivation and modify their behavior accordingly to reduce the
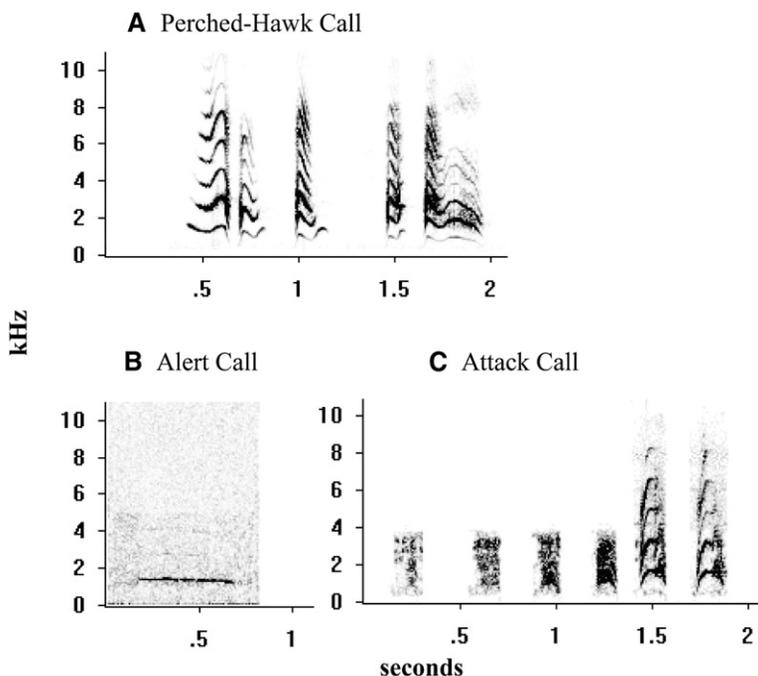

Figure 1. Predator-Behavior-Specific Calls of Siberian Jays

Calls given toward perched hawks (A), searching hawks (B), and attacking hawks (C). Calls were plotted with a 256 point Fourier transformation (Blackman window function).

Table 2. Behavioral Responses of Two Randomly Chosen Focal Individuals towards Predator-Behavior-Specific Calls

Situation[a]	Encounter Type	Forage	Hide	Alarm Calls	Passive Predator Search	Active Predator Search
alert	predator[b]	0	12	1	12	1
alert	playback	0	12	0	12	2
attack	predator[b]	0	12	1	12	4
attack	playback	0	12	0	12	11
mobbing	predator	1	0	12	12	12
mobbing	playback	0	0	8	11	12
control	no predator	12	0	0	0	0
control	playback	12	0	0	0	0

Behavioral responses of two randomly chosen focal individuals (a breeder and a nonbreeder) in 12 groups during predator encounter (predator) in comparison with the response during playback experiments (playback).

[a] Situation: alert, calls given toward prey-searching hawk; attack, calls uttered toward attacking hawk; mobbing, calls given toward sitting hawk; control, control call uttered while foraging.

[b] The behavioral difference when encountering a prey-searching hawk and an attacking hawk was that after an alert call, individuals froze and did not move for up to 4 min and resumed foraging first after 331 ± 115.2 s (mean $\pm$ SE). After an attack call, jays did not freeze and resumed feeding much faster (102 ± 20.5 s).

Table 3. Variables Affecting the Behavioral Responses of Focal Individuals toward Predator Encounters and Playback of the Calls Uttered in the Same Situation

Full Model

	DF	DDFM[a]	F Value	p
type[b]	1	464	0.00	0.96
situation[c]	3	464	13.31	<0.0001
behavior[d]	4	464	16.67	<0.0001
type × behavior	4	464	1.23	0.3
type × situation	3	464	0.84	0.47

Minimal Model

	Effect	SE	p
constant	−0.28	0.28	0.30
situation: alert	0.56	0.29	0.05
situation: attack	0.12	0.28	0.67
situation: control	1.9	0.32	<0.0001
situation: mobbing	0		
behavior: alarm call	1.13	0.34	0.0009
behavior: forage	0.82	0.33	0.01
behavior: hide	−0.33	0.31	0.28
behavior: scan	−1.52	0.34	<0.0001
behavior: search	0		

Tested with a multinomial model (Type III Tests; GLIMMIX module in SAS 9.1). The log likelihood of overall model = 528.01.

[a] Denominator degrees of freedom estimated with the Satterthwaite method.

[b] Type of treatment: playback or predator encounter (both natural encounters and with predator models).

[c] Situation: control (no predator present), alert call (given toward prey searching hawks), attack call (uttered during hawk attacks), or mobbing call (given toward perched hawks).

[d] Behavioral response of the two focal individuals (foraging, hiding, passive, or active predator search). See experimental procedures for detailed definitions.

immediate level of threat [8, 18, 19]. For example, Diana monkeys (*Cercopithecus Diana*) use distinct antipredator strategies toward their main predator, chimpanzees (*Pan troglodytes*), when hunting and when themselves escaping from hunting leopards (*Panthera pardus*), suggesting that Diana monkeys have a causal understanding of their predator's behavior [20]. Moreover, several birds species utter different calls toward flying and perched predators [21, 22], yet none of these studies investigated whether these calls communicate predator behavior to call recipients.

The immediate advantage of predator-behavior-specific calls is highlighted by the different reactions required for jays to survive encounters with attacking, prey-searching, and perched hawks. Although swift escape is essential for a Siberian jay to survive a hawk attack, an encounter with a prey-searching hawk requires the birds to seek cover immediately and remain motionless until the hawk has moved on. Given that predation in Siberian jays is substantial and the sole cause of known mortality, predator-behavior-specific calls can provide the signal recipient with crucial information, improving their survival. The effect of antipredator protection on survival is supported by the fact that antipredator behaviors in jays are nepotistic, reducing in particular the mortality of retained offspring. A link between antipredator calls and improved survival has so far been demonstrated by just a few studies [23, 24], yet in these cases the calls served the function of self-preservation and not protecting others.

Discriminating Predator-Behavior-Specific Calls from Urgency and Risk-Based Calls

Earlier studies showed that animal signals are sensitive to the risk posed by a predator [6, 8, 21]. Although it could be argued that the predator-behavior-specific calls of Siberian jays merely reflect the situation-specific risk but not predator behavior, the calling behavior of jays during hawk encounters suggests that these

calls indeed signal predator behavior. The predator-behavior-specific calls of jays did not depend on the distance or the relative position to a hawk. Jays uttered only alert calls toward a prey-searching hawk independent of the position and distance to the hawk. In the closest encounter, the hawk flew straight over the jays at 10 m distance, whereas in the most distant encounter, the hawk was over 200 m away. Similarly, jays uttered exclusively mobbing calls and unspecific calls when mobbing a hawk both when perched directly below or some meters above the hawk in the same tree or when the hawk was perched over 100 m away from the jays. Although the immediate risk posed by a perched or prey searching hawk decreases with distance to the predator, jay calls did not vary with distance and calls are therefore unlikely to encode the immediate risk or the urgency to respond. Thus, the behavior-specific calls are similar to the predator category specific calls of Diana monkeys [25], which are independent of the spatial position or distance of the predator.

Evolution of Complex Antipredator Call Systems

Prey species have evolved a wide range of strategies to evade the constant but often stochastic threat of predation. Although immobile prey mainly rely on chemical defense or morphological adaptations, such as spines and shells, many mobile animals aggregate together to seek safety in numbers [1]. However, it has been suggested that animals living in kin groups might not benefit from

a selfish herd [26] for two reasons. First, most kin groups are rather small, and group members therefore have a substantial risk of being killed during a predator attack. Second and more importantly, individuals in kin groups are related to each other. Thus, losing a group member often means losing a related individual [26]. Instead, many kin-group-living species seem to use a different strategy and overcome the risk posed by predators with the help of complex antipredation communication systems [2–5, 7, 25], although there are exceptions [21]. Given that antipredator communication in jay groups in particular aims at protection-related group members [10, 11] improving their survival prospects [9], kin selection could indeed be an important agent for the evolution of complex communication [27–30].

Experimental Procedures

Study Site and Species
The data for this study were collected from an individually color-banded population of wild Siberian jays between autumn 1998 and autumn 2004 in Arvidsjaur, about 100 km to the south of the arctic circle in northern Sweden. Field routines and study site, as well as determination of kinship, sex, and age of group members, are described elsewhere [15, 31–33]. All experiments and handling of birds were performed under the license of the responsible ethics board (Umeå Djurförsöksetiska Nämd).

Calls and Behaviors in Relation to Hawk Behavior
To establish the response of jays toward prey-searching, attacking, and perched hawks, I colleted data during all natural predator encounters with hawks during the study period, as well as during model predator encounters. During all natural encounters, I noted the predator species, the distance between of the group to the predator, and the detailed behavioral response of group members. I witnessed only five hawk attacks and three hawk-mobbing events, so I performed experiments with predator models to collect additional data. The response of Siberian jays toward an attacking hawk was collected during attacks with a hawk model (n = 40 experiments; see [10] for detailed description of experimental setup). The response of jays toward perched hawks was collected by exposing groups to mounts of both hawk species that occur at the study site (goshawk [*Accipiter gentilis*], n = 15 experiments; sparrowhawk [*A. nisus*], n = 20 experiments; see [11] for detailed description of experimental setup). For an experiment, I place a model 5 m away from a feeder on the top of a 1 m high pole. Before and after the experiment, the model was hidden with a plastic cover. For different experiments with the same group, I placed the feeder in varied locations within the territory. To control for the effects of the experimental setup, I exposed groups to a blue jay model (n = 15 experiments) using the same setup.

I assessed the base line of calls under undisturbed conditions by recording in 20 groups all vocalizations given by all group members during 30 min while they were foraging on a feeder (I chose situations where no predator was present, including 10 min ahead of the sample period). Each group was exposed once to each model, and the models were presented in random order. Not all groups were exposed to all treatments, depending on annual variation in group size and group composition. I recorded the behavioral response of the birds with a video camera. The vocalizations during the experiments were recorded with a Sony TC-D5M cassette recorder with TDK ICE 1 or UXS ICE 2 tapes connected to a directional microphone (Telinga Pro microphone; diameter of parabolic screen 58 cm). I counted all calls given during the first 4 min of the experiment.

Analyses of Call Structure
Calls were digitalized with Avisoft SAS-lab Pro version 4.23b (Avisoft Bioacoustics [Berlin, Germany]; 16 bit mono, 32 kHz sampling frequency). Because all calls are structurally very different, I counted the number of each call type given by listening to the recordings. To get a measure of reliability of my categorization, I analyzed all

calls of sufficient quality of each call type by using the spectrographic crosscorrelation module in Avisoft 4.23b, with a tolerated frequency deviation of 50 Hz. Calls did not significantly differ from calls of the same call category, wherwas they differed significantly from calls of other categories, supporting my categorization based on acoustic similarity (Table S1 available online).

Playback Experiment
I tested for the information content of the behavior-specific calls with a playback experiment in autumn of 2003. On different days and in random order, 12 groups were exposed to playbacks of calls given toward perched, searching, and attacking hawks and a control treatment (Siberian-jay vocalizations given in the absence of a predator). In all experiments, I let the focal group first forage undisturbed on a feeder for 10 min. Then, I exposed a randomly chosen dyad (a breeder and an extra bird) to the calls. These calls were broadcasted with a Cobalt SP 101 speaker attached with a 15 m standard speaker cable to a Sony TC-D5M cassette recorder. The speaker was concealed in a tree 5 m from the feeder, 1 m above the ground. The behavior of the focal individuals during and 1.5 min after the playback was recorded with a video camera from a distance of 10 m. The video recordings were later analyzed and behaviors were divided into five categories:

> Foraging: At least one individual did not leave the feeder and continued to collect food.
> Hide: At least one left the feeder and flew to a nearby tree, hiding among branches immediately after exposure to the playback stimuli.
> Passive predator search: At least one individual scanned the environment while perched in cover, turning the head at least every third second.
> Active predator search: At least one individual sat in treetops or moved from tree to tree, sat exposed on branches, and scanned the environment.
> Alarm calls: At least one individual uttered calls that are given during predator encounters.

These five behavioral categories are not mutually exclusive, and individuals could easily perform all of them repeatedly within 1.5 min. I scored whether either of the two focal individuals performed these behaviors during 1.5 min after the start of the playback stimulus. To judge whether the response in the playback experiments was appropriate, I sampled the behavior of jay dyads in 12 groups when they were foraging on a feeder during real predator encounters (searching hawks), by using predator models (attacking hawks, perched hawks), and in the absence of a predator. I analyzed the behavioral response of the focal individuals with a multinomial regression (GLIMMIX module in SAS 9.1; SAS institute [Cary, North Carolina]). Encounter type (predator encounter, playback of situation-specific call), treatment (hawk behavior), and behavioral response category were entered as categorical variables in the model. To test for general differences between predator encounters and the playback, I entered the interaction between encounter type and treatment in the model, whereas the difference in behaviors between the treatments was tested for the interaction between encounter type and behavioral response.

In all playback experiments, birds were exposed to calls from to unfamiliar individuals. The mobbing call sequences, calls toward prey-searching hawks, as well as control calls, were unique call sequences. The mobbing call sequence and control sequence of 1.5 min length were recorded in 12 groups each (mean group size 3.8 ± 0.21). The mobbing call sequences were recorded while jays mobbed a perched sparrowhawk model [11]. The control sequences were recorded while jays foraged on a feeder. Because I could record just one alert call of sufficient quality during a natural encounter, I recorded 12 alert calls that I produced by whistling myself in the frequency and length of natural alert calls (frequency = 1.8 kHz, average call length 1.33 ± 0.09 s, 2.3 ± 0.18 calls given). The attack calls were recorded during attack experiments with a wooden goshawk model [10]. Only three of these recordings were of sufficient quality, and each of these calls was thus used in four playback experiments. The stimuli length in the four treatments differed because the playbacks aimed to reflect natural situations. During an attack

[10] or when encountering a searching hawk, jays emit only one short call sequence, whereas they utter calls continuously for several minutes (sometimes more than 100 individual) calls when mobbing a perched hawk [11].

Supplemental Data

Acknowledgments

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