Mobbing calls signal predator category in a kin group-living bird species

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Many prey species gather together to approach and harass their predators despite the associated risks. While mobbing, prey usually utter calls and previous experiments have demonstrated that mobbing calls can convey information about risk to conspecifics. However, the risk posed by predators also differs between predator categories. The ability to communicate predator category would be adaptive because it would allow other mobbers to adjust their risk taking. I tested this idea in Siberian jays *Perisoreus infaustus*, a group-living bird species, by exposing jay groups to mounts of three hawk and three owl species of varying risks. Groups immediately approached to mob the mount and uttered up to 14 different call types. Jays gave more calls when mobbing a more dangerous predator and when in the presence of kin. Five call types were predator-category-specific and jays uttered two hawk-specific and three owl-specific call types. Thus, this is one of the first studies to demonstrate that mobbing calls can simultaneously encode information about both predator category and the risk posed by a predator. Since antipredator calls of Siberian jays are known to specifically aim at reducing the risk to relatives, kin-based sociality could be an important factor in facilitating the evolution of predator-category-specific mobbing calls.

Keywords: *Perisoreus infaustus*; family group; referential calls; semantic calls; *Accipiter*

1. INTRODUCTION

Predation is an important evolutionary force shaping life histories and behavioural decisions of prey. Since encounters with a predator put the life of prey at risk, prey often rely on morphological adaptations, such as cryptic coloration, to reduce the likelihood of being detected (Caro 2005). Alternatively, many prey have evolved behavioural strategies, such as grouping together or warning call systems, to reduce predation risk (Caro 2005). However, predators are not hunting all the time and spend a substantial amount of their time resting. Many species of prey gather to approach and inspect or even harass resting predators (Owings & Coss 1977; Pavey & Smyth 1998; Caro 2005), although these behaviours are not risk-free because prey can be taken by the predator (Dugatkin & Godin 1992).

While mobbing can be costly, approaching predators has been suggested to be beneficial for at least two reasons. First, predators are sensitive to disturbance and move on as a reaction to mobbing prey (Kruuk 1964; Pavey & Smyth 1998), and laboratory experiments demonstrated the distressing effect of mobbing calls on predators (Shalter 1978). Second, mobbing calls can inform other group members and convey information about the risk posed by the predator or level of urgency to conspecifics (Naguib *et al.* 1999; Manser 2001; Templeton *et al.* 2005; Graw & Manser 2007). Field observations and experiments have shown that prey utter different calls, or alter the number of times calls are given, when

approaching different predator categories (Naguib *et al.* 1999; Zuberbühler 2000, 2001; Manser 2001; Graw & Manser 2007). In meerkats *Suricata suricatta*, mobbing calls vary depending on predator category as well as risk and conspecifics adjust their predator inspection behaviour accordingly (Manser *et al.* 2001). However, it remains unclear so far if mobbing calls, not only in meerkats but also in other species, denote the risk posed by the predator and predator category. The ability to communicate predator category and the risk posed by the predator to conspecifics would be adaptive since it would allow prey to adjust their mobbing and escape behaviour to the specific risk posed by different predators.

Here, I investigate the information content of mobbing calls in a group-living bird species, the Siberian jay *Perisoreus infaustus*. Jays live on year-round territories in groups with varying composition (Ekman *et al.* 2001; Griesser *et al.* 2006). Beside the breeding pair, groups can contain up to five non-breeders from different cohorts and origin. These non-breeders are retained offspring that queue on the parental territory for a nearby breeding opening and/or immigrants (Ekman *et al.* 2002; Griesser *et al.* 2008). The two main predator categories of jays, *Accipiter* hawks and owls, differ in their frequency of killing jays, and hawks are responsible for 80 per cent of the kills (Griesser *et al.* 2006). Given that hawks hunt during the day when jays are active, hawks pose a higher risk to jays than owls, which mainly hunt between dusk and dawn.

When encountering a predator, the behavioural response of the jays depends on the behaviour of the predator (Griesser 2008). If encountering an attacking or prey-searching predator, jays seek immediate cover. When encountering a perched predator, however, jays approach and swoop over these predators while uttering

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a variety of mobbing calls. Predators quickly respond to the mobbing behaviour and move on (Griesser & Ekman 2005). The response of Siberian jays towards predators depends also on group composition. Jay breeders are nepotistic in their antipredator behaviour and specifically protect their retained offspring from prey-searching, perched and attacking predators (Griesser & Ekman 2004, 2005; Griesser 2008). This protection has been demonstrated to boost the survival of retained offspring compared with immigrant group members (Griesser et al. 2006).

Based on this background of the Siberian jay mobbing system, I tested three non-exclusive hypotheses regarding the function of mobbing calls by exposing jay groups to three hawk and three owl mounts of varying risk. (i) Mobbing calls of jays could encode information about risk (see below). Jays could mob less dangerous predators more intensely and give more mobbing calls. Alternatively, jays could increase the mobbing intensity when mobbing a more dangerous predator. In either case, calling investment would allow other group members to acquire information on the risk posed by a predator. (ii) Mobbing calls could convey information about predator category and call types would thus vary between owls and hawks. (iii) Mobbing calls could serve as a signal to protect kin and jays living in family groups would be expected to mob predators more intensely and give more calls. This hypothesis is based on earlier observations that showed that antipredator calls of Siberian jays are nepotistic and aim at protecting kin group members (Griesser & Ekman 2004, 2005; Griesser 2008).

2. MATERIAL AND METHODS

Data for this study were collected in an individually colour-ringed population of Siberian jays in Arvidsjaur, Northern Sweden. This population has been monitored from 1989 onwards and the number of studied groups has increased from 3 to over 40. In these groups, basic data on reproduction and group composition have been regularly collected (see Griesser et al. 2006, 2007, 2008, for detailed description of the study site and methods). Since Siberian jays are monomorphic, a small blood sample was taken from each individual for molecular determination of the sex, using the method described by Griffiths et al. (1998). All experiments, handling of birds and blood sampling were performed under the licence of the ethics board in Umeå.

(a) Assessment of group composition and relatedness

The relatedness among group members was assessed using two different methods. In most groups, reproduction was followed and nestlings in successful broods were ringed before or directly after fledging ($n = 192$ broods). In groups where reproduction was not followed, relatedness of unbanded group members was assessed on the basis of behavioural interactions of group members on a feeder ($n = 47$ instances). Parents tolerate their offspring when foraging together, while they aggressively chase unrelated individuals off a feeder. This behavioural proxy has been demonstrated to be a reliable assessment of kinship when compared with individuals of known relatedness (Ekman et al. 1994; Griesser 2003).

(b) Predator exposure experiments

I exposed jay groups foraging on a feeder in the autumns of 1999–2003 to mounts of three diurnal raptor species (goshawk female *Accipiter gentilis*, ca 55 cm body length; sparrowhawk female *Accipiter nisus*, ca 35 cm; hobby male *Falco subbuteo*, ca 30 cm) and three owl species (Ural owl *Strix uralensi*, ca 60 cm; hawk owl *Surnia ulula*, ca 36 cm; pygmy owl *Glaucidium passerinum*, ca 16 cm) that occur at the study site. Goshawks are the largest and most powerful raptors preying upon jays, and jay-sized birds (70–100 g, 28–30 cm body length) are the main prey item of goshawks in Scandinavia (Cramp 1980). Sparrowhawks sometimes kill jay-sized birds (approx. 15% of their diet), but mainly hunt smaller bird species (Cramp 1980). Hobbies prey primarily upon small birds and large insects that are substantially smaller than Siberian jays and only rarely kill jay-sized birds (Cramp 1980). Thus, I classified the goshawk as the most dangerous hawk, the sparrowhawk as the intermediately dangerous hawk and the hobby as the least dangerous hawk. Hawk owls are agile hunters that primarily hunt voles or hares during the breeding season, while birds up to the size of jays are the main prey item (ca 90%) in Lapland outside the breeding season (Cramp 1985; see also Duncan & Duncan 1998). Despite hawk owls being smaller than Ural owls, they pose a higher risk to jays since their diet outside the breeding season mainly contains birds. Moreover, hawk owls are very agile and diurnal hunters increasing the actual risk they pose to jays. Ural owls are the largest of the three owl species and hunt on small mammals and up to pigeon-sized birds. Birds can make up 10–25% of their prey items outside the breeding season (Cramp 1985). Pygmy owls are about half the size of a Siberian jay and the main prey items are voles and small passerines such as *Parus* tits, but they have rarely been reported hunting birds up to jay size (Cramp 1985). Thus, I categorized pygmy owls as the least dangerous owl species.

I used data available from an earlier experiment with perched sparrowhawk and Ural owl mounts ($n = 15$ experiments each; Griesser & Ekman 2005) and supplemented these data with two different-sized hawk and owl species ($n = 15$ experiments for each predator species) in a total of 44 groups in 36 territories (table 1; table 1 in the electronic supplementary material). Groups where all group members had changed between years were categorized as a different group even when living in the same territory. A group did not receive the same treatment more than once and not all groups were exposed to all treatments depending on annual variation in group size and group composition (mean number of experiments per group $\pm$ SE = 2.84 $\pm$ 0.23). Groups were exposed in random order to the predators within the two data collection blocks (sparrowhawk and Ural owl: years 1999–2000; all other mounts: year 2003). Given that this design could affect the response of the experimental individuals, I included the order in which a group received the treatments and year as random factors into the statistical analysis (see below).

For each experiment, I exposed a group to a perched predator mount. The predator was placed 5 m away from a feeder on the top of a 1 m high pole and hidden under a plastic cover before the experiment. When all group members were present and jays had fed undisturbed for approximately 15 min, I removed the plastic bag and exposed the feeding jays to the mount. For different experiments with the same group, I placed the feeder in varied locations within the territory. I recorded the behavioural response of the jays with a

Table 1. Number of experiments of the different treatments.

species	goshawk	sparrowhawk	hobby	hawk owl	Ural owl	pygmy owl	blue jay	control
predator class	hawk	hawk	hawk	owl	owl	owl	—	—
risk	high	medium	low	high	medium	low	—	—
experiments (n)	15	15	15	15	15	15	15	20
family groups	9	8	8	11	8	7	7	10
non-family groups	6	7	7	4	7	8	8	10
mean group size	4.3	4.0	4.3	4.1	4.1	4.2	4.1	4.0

video camera. The vocalizations during the experiments were recorded with a Sony TC-D5M cassette recorder using 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. I controlled for the effect of the experimental set-up on calling behaviour by exposing 15 jay groups to a blue jay (*Cyanocitta cristata*), a non-native, jay-sized species. To assess the baseline of calls under undisturbed conditions, I recorded from 20 groups all vocalizations given by all group members during 30 min while foraging on a feeder (choosing situations where no predator was present, including 10 min ahead of the sample period).

(c) Analyses of calls

Calls were digitalized using AVISOFT SAS-lab Pro version 4.23b (Avisoft Bioacoustics, Berlin, Germany; 16 bit mono, 32 kHz sampling frequency). Since all calls are structurally very different (see figure 1), I counted the number of each call type given by listening to the recordings. This categorization was initially confirmed with the help of spectrograms, and later on for calls which were difficult to categorize (short and long croaks; see below). To get a measure of reliability of my categorization, I analysed all calls of sufficient quality of each call type using the spectrographic cross-correlation module in AVISOFT, with a tolerated frequency deviation of 50 Hz. Calls were significantly more similar to other calls within the same call category than with other calls, supporting my categorization based on acoustic similarity. The statistics of the call structure analyses is given in tables 2 in the electronic supplementary material.

(d) Statistical analysis

I analysed the number of calls given towards perched predator mounts using a multinomial regression (GLIMMIX module in SAS 9.1; SAS institute, Cary, NC). Given that I was interested in testing whether a call type is specific for a predator category, I analysed only the eight specific call types that were uttered in the presence of a predator mount (table 2). I added all explanatory terms of interest and possible interactions in the model, and subsequently used a backward removal procedure to drop all terms that did not influence the explanatory power of the model. Call type, predator category (owl, hawk) and kinship were entered as class variables. Groups were categorized as family groups with retained offspring or non-family groups with immigrants. Groups that contained both retained offspring and immigrants ($n = 13$) were categorized as family groups since breeders in the Siberian jays adjust their antipredator behaviour only with respect to the presence or absence of retained offspring (Griesser 2003; Griesser & Ekman 2004,

2005). Group size and the risk posed by the predator species relative to the risk of other mounts within the same predator category (low, medium, high) were entered as quantitative variables in the model. To control for the effect of the order of exposure to the different mounts within each group, group identity and year effects, I entered these variables as random effects into the model. The effect of predator category on the number of specific calls was clarified with the help of contrasts of least squares means (also called adjusted means), which are the predicted population margins (Littell et al. 1996).

3. RESULTS

Immediately after exposure to a predator mount, group members interrupted foraging, flew up to nearby trees, called and swooped over the predator mount. Siberian jays used both predator-category-specific calls and nonspecific calls (i.e. calls that also were uttered in absence of a predator; table 2). Jays uttered 'perched hawk calls' and 'ki-ki calls' almost exclusively in the presence of a hawk mount, while they used 'croaks' and 'gargles' mainly towards an owl mount (figure 1, tables 2 and 3; figures 1 in the electronic supplementary material). Moreover, the calling behaviour was influenced by risk and kinship. Jays gave more calls towards more dangerous predators independent of predator category and jays living in family groups gave more calls (mean number of calls $+$ SE $= 14.1 + 1.69$) than jays living in non-family groups ($4.7 + 0.93$; table 3). This increase in the number of calls given towards more dangerous predators differed between family groups, which increased the number of calls given parallel to the risk (table 3; low risk: $6.9 + 1.31$; medium risk: $15.2 + 3.32$; high risk: $21.5 + 3.11$), and non-family groups, which only increased the number of calls in high-risk situations (low risk: $3.1 + 0.74$; medium risk: $1.9 + 0.73$; high risk: $12.5 + 2.06$).

4. DISCUSSION

Mobbing experiments with different hawk and owl mounts revealed that Siberian jays have a large repertoire of mobbing calls, which convey both information about predator category and risk posed by the predator. Jays used two different rules to adjust their calling behaviour: they altered the calling rate and they used different calls. For riskier situations, jays increased the calling rate. This applied both to the risk posed by the predator (more calls towards more dangerous predators) and the risk for relatives in the group (more calls given in family groups). Meerkats and black-capped chickadees *Poecile atricapilla* also communicate risks posed by predators towards
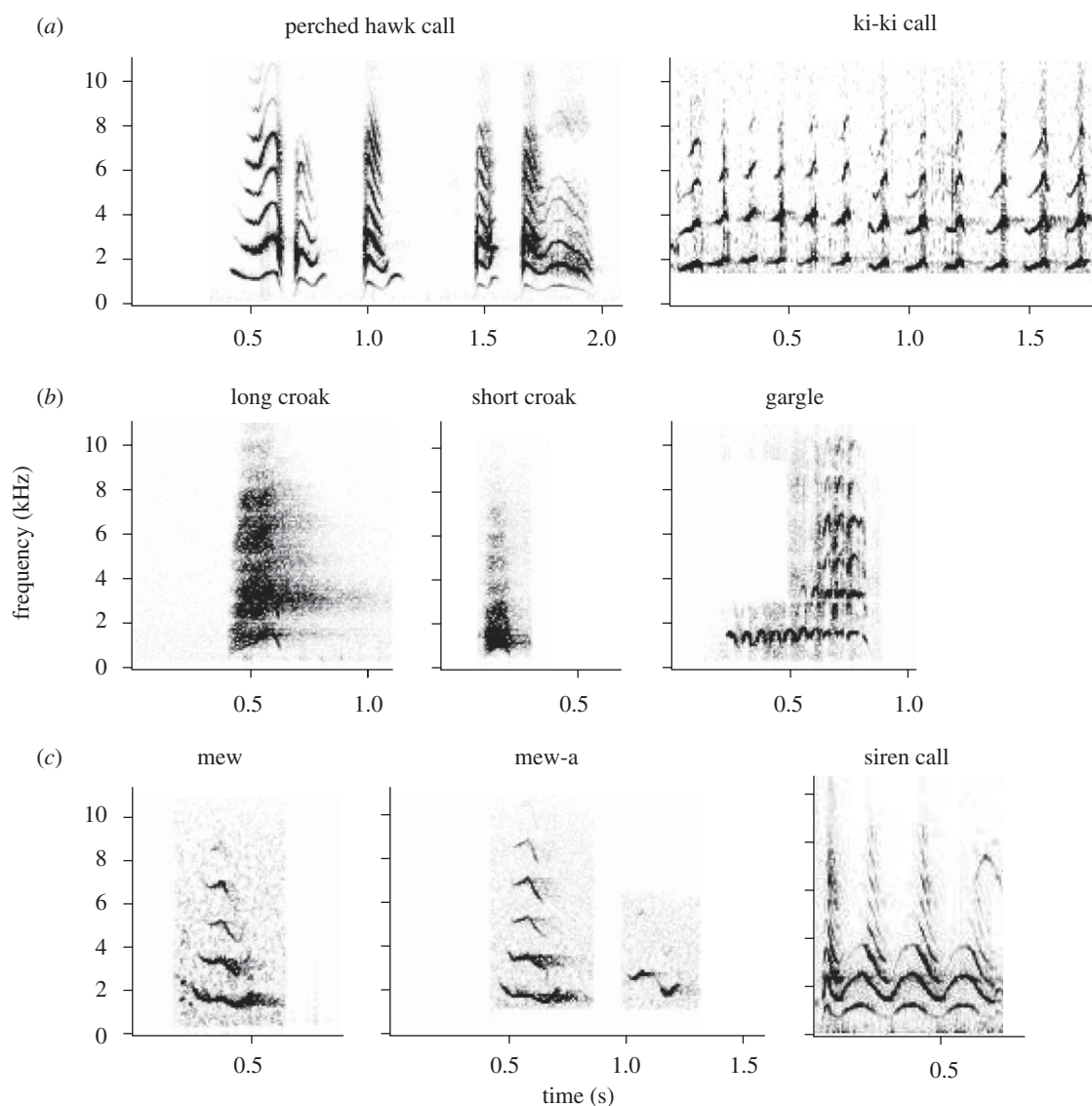
Figure 1. Predator-category-specific mobbing calls of Siberian jays: (*a*) hawk-specific calls, (*b*) owl-specific calls and (*c*) nonspecific antipredator calls. Calls were plotted using a 256-point Fourier transformation (Blackman window function) with the software SYRINX.

conspecifics by increasing the calling rate (Manser 2001; Templeton *et al*. 2005). However, when exposed to different predator categories (hawks, owls), jays used predator-category-specific calls, similar to the way meer-kat mobbing calls encode information about predator category (Manser *et al*. 2001; Graw & Manser 2007). Given that these calls are uttered to a predator category independent of the risk posed by the predator, different predator categories could require different calls to be repelled efficiently. Alternatively, these mobbing signals could referentially encode information about predator category to conspecifics. Since other prey species are able to efficiently repel predators using the same call type (Shalter 1978; Templeton *et al*. 2005), it is unlikely that jays require different calls to repel different predator categories. Rather, differences in calls depending on pred-ator categories have most probably evolved to convey information about predator category to other group members.

Siberian jays approach and mob predators indepen-dent of the presence of other group members (Griesser & Ekman 2005). Thus, the mobbing calls in such a situation

seem to be directed at the predator, with the aim of repel-ling the predator (Pavey & Smyth 1998). This idea is supported by observations of natural encounters with perched predators. In all cases, the predators quickly moved on after jays started to utter mobbing calls (*n* = 7 encounters; M. Griesser 2008, unpublished data), confirming findings from laboratory experiments that demonstrated a distressing effect of mobbing calls on pre-dators (Shalter 1978; Flasskamp 1994). Alternatively, jay calls could also be directed to other group members, in particular family members, but without further exper-iments it is not possible to tell whether these calls are given to family members, the predator or both.

Although mobbing behaviour is very widespread among birds and mammals (Caro 2005), only a handful of studies have looked at the information that these sig-nals contain. Mobbing calls have been shown to provide conspecifics with information about the nature of danger through either changing the number of times calls are given (Naguib *et al*. 1999; Templeton *et al*. 2005) or by using referential predator-category-specific calls when encountering predators (Seyfarth *et al*. 1980;

Table 2. Mean number of calls given towards perched predator mounts during 4 min. Specific calls are rarely given in the absence of a predator, whereas nonspecific calls are only given in absence of a predator. Perched hawk calls are significantly more often given towards a hawk, while short and long croaks and gargles are significantly more often uttered towards an owl (see table 3 for statistics).

species	goshawk	sparrowhawk	hobby	hawk owl	ural owl	pygmy owl	blue jay	control
specific calls								
perched hawk call	12.3	6.3	4.7	0.6	0	0.7	0.3	0
ki-ki call	1.9	0.3	0.1	0	0	0	0	0
long croak	0.1	0	0.1	6.2	6.7	0.4	0	0
short croak	2.7	0	1.0	6.7	2.5	1.6	0.3	0
gargle	0.7	0	0	1.3	0.3	0	0	0
mew-a	0.5	0.5	0.3	0.5	0.3	0.1	0	0
mew	1.8	0	1.2	1.9	0.9	0.3	0	0
siren call	0.5	0	0	0.1	0	0	0	0
nonspecific calls								
dyy call	3.2	9.9	3.8	4.5	5.6	1.3	0.7	0.2
ki call	4.1	4.7	0.7	1.2	1.5	0	0	0.1
babbling	0.3	1.8	0.4	0	4.0	0	0	0.4
y call	12.8	1.9	4.9	16.3	9.9	7.9	1.6	0.6
submissive call	0.1	0.3	0.1	0.1	0.6	2.1	1.4	2.7
pickering	1.6	0	1.3	2.7	0	3.9	5.9	4.2
other calls	0.9	0	0	0.1	0	2.1	0	0.1
all calls	43.5	25.7	18.6	42.2	32.3	20.4	10.2	8.3

Table 3. Effect of predator category, kinship and danger posed by predator on the number of calls given towards perched hawk and owl mounts as well as contrasts for predator-specific calls. Multinomial model (type III tests). Group identity, year and order of exposure were entered as random variables into the model.

effect	Num DF	Den DF	*F*-value	*p*-value	
call type	7	667	9.85	<0.0001	
predator category	1	667	0.00	0.97	
kinship	1	667	16.29	<0.0001	
risk posed by predator	2	667	24.06	<0.0001	
call type × predator category	7	667	11.75	<0.0001	
kinship × danger	2	667	3.41	0.03	
contrasts for call type × predator category					
perched hawk call	1	667	41.85	<0.0001	hawk > owl
ki-ki call	1	667	0.00	0.97	
long croak	1	667	25.20	<0.0001	owl > hawk
short croak	1	667	14.94	0.0001	owl > hawk
gargle	1	667	5.97	0.01	owl > hawk
mew	1	667	0.26	0.61	
mew-a	1	667	0.09	0.76	
siren call	1	667	1.77	0.18	

Zuberbühler 2000, 2001). The graded calling system of the Siberian jay, which combines information about risk and predator category, resembles the calling system of meerkats where mobbing calls convey both information about predator category and the level of urgency to conspecifics (Manser 2001; Graw & Manser 2007). Both meerkats and jays possess an extensive repertoire of structurally very different calls when mobbing predators. In almost all model systems where alarm calling is well investigated, prey use only one specific type of call for a certain situation or predator category (Seyfarth *et al.* 1980; Macedonia & Evans 1993; Zuberbühler *et al.* 1997; Zuberbühler 2000; Templeton *et al.* 2005). This raises the question of what the benefit of such a large variety of mobbing calls could be. The different call types uttered in the same situation could reflect subtle differences in the

perceived risk, or they might indicate differences in the motivational state of the individuals themselves (Graw & Manser 2007). It is intriguing in this context to point out the structural similarity of the 'ki-ki' calls given towards perched hawks, which closely matches the calls uttered by *Accipiter* hawks. This could facilitate recognition of prey category for conspecifics (see also Graw & Manser 2007); however, the confirmation of this idea would require a playback experiment.

To conclude, the results presented here support the idea that mobbing calls can encode information about predator category (Manser 2001; Manser *et al.* 2001). Such predator-category-specific mobbing calls could be widespread, but so far it remains unclear whether calls in other species specify differences in escape strategy or indeed reflect predator category independent of escape

strategy or level of urgency. Siberian jays not only possess the ability to communicate predator category when encountering a perched predator, but they can also convey information about predator behaviour to conspecifics (Griesser 2008). The efficiency of these warning calls is demonstrated by the fact that antipredator signals of jays aim at protecting kin group members, which have a much higher survival rate than unrelated group members (Griesser *et al.* 2006). Kin-based sociality therefore could be an important factor to facilitate the evolution of predator-category-specific mobbing calls.

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