Animal Behaviour xxx (2013) 1–7

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Communication about predator type by a bird using discrete, graded and combinatorial variation in alarm calls

Toshitaka N. Suzuki [a,b,*]

[a] Department of Evolutionary Studies of Biosystems, The Graduate University for Advanced Studies, Kanagawa, Japan
[b] Department of Life Science, Rikkyo University, Tokyo, Japan

ARTICLE INFO

Article history:
Received 5 January 2013
Initial acceptance 14 February 2013
Final acceptance 11 September 2013
Available online xxx
MS. number: 13-00024R

Keywords:
acoustic communication
alarm call
discrete alarm call
graded alarm call
great tit
mobbing
note combination
Parus major minor

Many animals use variation in their alarm calls to warn conspecifics about different predatory threats. Information about predators can be encoded by producing discrete types of alarm calls and/or through graded variation in a single call type (i.e. calling rate or note repetitions). Another way to encode predator information is to combine different types of calls or notes into longer structured sequences. However, few studies have examined how individuals use discrete, graded and combinatorial variation in alarm calls to denote specific risks. I investigated the acoustic structure and information content of alarm calls in Japanese great tits, *Parus major minor*, by exposing their nests to three predator species (snakes, crows and martens) and a nonpredator species (doves). Great tits produced acoustically discrete alarm calls for the different nest predators: 'jar' calls for snakes and 'chicka' calls for crows and martens. The adults further discriminated between crows and martens by altering the calling rate and note number of the 'chicka' calls. A total of 175 types of note combinations were observed in the 'chicka' calls, and the tits used these combination types differently for the crows and martens. These results provide the first demonstration that birds can encode information about predator type by using production specificity, graded features and note combinations of discrete alarm calls. Previous studies have shown that parent and nestling Japanese great tits can respond in different, adaptive ways to discrete alarm calls. However, further playback studies are required to determine whether and how conspecifics can extract predator information from graded and combinatorial variation in alarm calls.

Animals often live in environments with multiple predator types, and many produce alarm calls in response to a wide variety of predators (Caro, 2005). Previous studies have shown that variation in the acoustic structure of alarm calls enables animals to convey information about the risk type or threat level of predators (Gill & Bierema, 2013; Zuberbühler, 2009). For example, vervet monkeys, *Chlorocebus aethiops*, produce acoustically discrete alarm calls for eagles, leopards and snakes, and thereby provide information about the predator type to receivers (Seyfarth, Cheney, & Marler, 1980). A single type of alarm call may also show graded variation in the number of notes per call (Fallow & Magrath, 2010; Leavesley & Magrath, 2005; Templeton, Greene, & Davis, 2005), calling rate (Colombelli-Négrel, Robertson, & Kleindorfer, 2010; Fasanella & Fernández, 2009; Griesser, 2009; Naguib et al., 1999) or length of call (Ellis, 2008; Le Roux, Jackson, & Cherry, 2001; Manser, 2001; Wilson & Evans, 2012; Yorzinski & Vehrencamp, 2009). Such graded variation in alarm calls may encode a variety of information about predator attributes such as predator type, distance, size and behaviour (Manser, 2009).

Another way to encode threat information is to combine different types of calls or notes into longer structured sequences. For example, putty-nosed monkeys, *Cercopithecus nictitans martini*, combine acoustically discrete calls into a fixed sequence depending on the type of predators that they encountered (Arnold & Zuberbühler, 2006a, 2008). Similarly, Campbell's monkeys, *Cercopithecus campbelli*, produce combinations of different call types in a variety of contexts, and the use of call combinations is associated with the perceived threat type (e.g. predator type; Ouattara, Lemasson, & Zuberbühler, 2009). Combinations of different call or note types have also been documented for threat communication in other animal taxa such as rodents (e.g. Blumstein, 1999; Swan & Hare, 2008) and birds (e.g. Griesser, 2009; Templeton et al., 2005). Nevertheless, the manner in which nonprimate animals provide specific information about predators by using signal combinations, in addition to discrete and graded variation in alarm calls, remains unclear.

Japanese great tits, *Parus major minor*, produce at least two discrete types of alarm calls ('jar' and 'chicka' calls; Fig. 1) when encountering and mobbing nest predators (Suzuki, 2011). 'Jar' calls

* Correspondence and present address: T. N. Suzuki, Department of Evolutionary Studies of Biosystems, The Graduate University for Advanced Studies, Hayama, Miura-gun, Kanagawa 240-0193, Japan.
E-mail address: toshi.n.suzuki@gmail.com.

0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.10.009

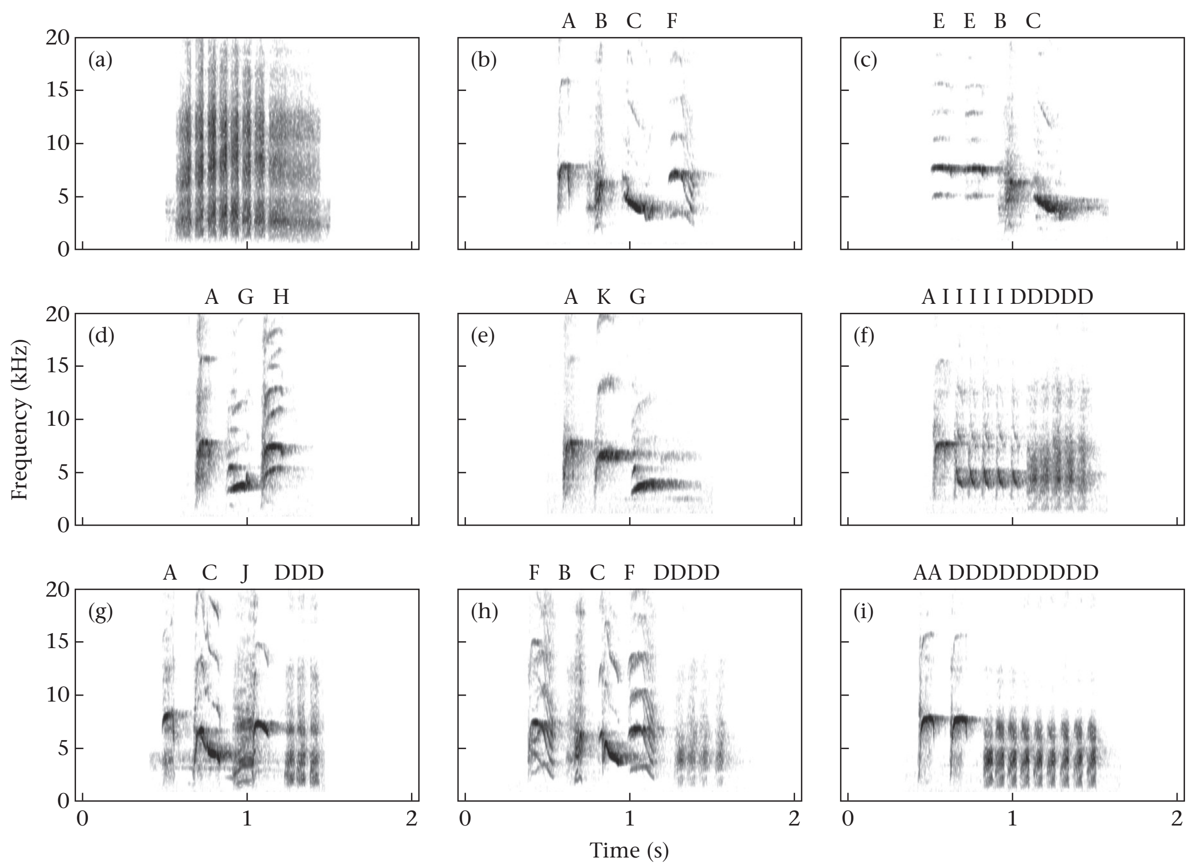

Figure 1. Spectrographic illustration of Japanese great tit mobbing calls: (a) 'jar' call and (b–i) 'chicka' calls. 'Jar' calls are strings of a single type of broadband note. 'Chicka' calls vary in the number and presence of each of the note types (A–K).

are strings of single broadband notes that vary in duration (Fig. 1a). By contrast, 'chicka' calls are combinatorial calls, which can vary in the number and combination of different note types (Fig. 1b–i). Pilot observations suggested that great tits produce 'jar' calls specifically in response to snakes and 'chicka' calls for a variety of predators such as avian and mammalian nest predators (Suzuki, 2011; Suzuki & Ueda, 2013). Although great tits may use the same call type for avian and mammalian predators, they might subtly alter their calling rate and note repetitions of 'chicka' calls to signal different predator types, as has been shown in other avian species (Griesser, 2009; Sieving, Hetrick, & Avery, 2010). Moreover, like some nonhuman primates (e.g. Arnold & Zuberbühler, 2006a, 2008; Ouattara et al., 2009), Japanese great tits might use different note combinations of 'chicka' calls for different predator types, because the presence and absence of note types in 'chicka' calls are highly variable (Fig. 1b–i).

In the present study, I investigated the acoustic structure and information content of alarm calls in Japanese great tits in a nest defence context. Previous studies have confirmed the following three species as nest predators of Japanese great tits: Japanese rat snakes, *Elaphe climacophora*, jungle crows, *Corvus macrorhynchos*, and Japanese martens, *Martes melampus* (Barnett, Sugita, & Suzuki, in press; Suzuki & Ueda, 2013). The risk of predation may differ between these three predators. Snakes may pose the greatest threat to offspring as they can invade nest cavities and young nestlings cannot avoid their attacks (Suzuki & Ueda, 2013). Martens pose a greater threat than crows since the martens can take nestlings from outside the entrances by using their forelimbs (Barnett et al., in press), while crows can only snatch nestlings from outside the nest entrances with their bills. Such differences in predatory threats may provide a selective force for the evolution of different predator-searching behaviours in adult tits (Suzuki, 2012), and also different predator avoidance behaviours in nestlings (Suzuki, 2011). Therefore, it would be advantageous for adults to be able to signal predator type to defend their offspring (see Gill & Bierema 2013; Magrath, Haff, Horn, & Leonard, 2010).

I tested alarm call responses of Japanese great tits by exposing their nests to the three nest predator species and a nonpredatory species. I then analysed the acoustic features of the calls to examine how predator type affects the use of discrete alarm calls ('jar' and 'chicka' calls) as well as graded and combinatorial variation in a single call type ('chicka' calls).

METHODS

Study Site and Subjects

The study was conducted on a population of Japanese great tits in a mixed forest in Karuizawa, Nagano, Japan (36°21–22′N, 138°35–36′E). Data were collected from 24 pairs of great tits, using nestboxes for their first broods of the season. The nestboxes were attached to tree trunks 1.8 m from the ground. Experiments were carried out between 29 May and 13 June 2010, when the nestlings were 5–8 days old. The study was conducted with the permission of the Forestry Agency and the Ministry of the Environment of Japan.