Korean J Biol Sci 8: 89-95, 2004

Behavioral Function of the Anomalous Song in the Bush Warbler, *Cettia diphone*

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Key Words:

Cettia diphone
Song function
Alarm
Mobbing
distraction

The bush warblers (*Cettia diphone*) have been recognized to possess two types of songs: a normal song that plays roles in attracting mate and territorial defense, and an anomalous song. The present study suggests that the anomalous song functions as an alarm signal as well as other unknown signals. Field observations and playback experiments on the anomalous song of bush warbler were conducted in order to investigate the contextual information that occurred between sender and receiver. In the field observation, the males frequently emitted anomalous songs to potential predators. The males responded with an anomalous song to stuffed potential predators. The distance from where the anomalous song occurs to the stimulating source varied depending upon the kinds of stimulus. The males of bush warbler possibly show different responses to the anomalous song depending on the level of danger. When the anomalous song was played back to terrestrial males and females, no distinctive behavior was observed. The anomalous song may be sung to defend the territory against predators or to distract invaders from the nest and female because the male and female behaviors were related with the anomalous song and its phonetic characteristics.

Most passerine birds utter vocal signals in the emergence of potential predators. Alarming is a representative example of this kind of vocal signals. The alarm signal diverts the predator's attention to other prey (Greig-Smith, 1981; Hurd, 1996; Charnov and Krebs, 1975), discourages the predator's pursuit (Dawkins, 1976; Sherman, 1977), alerts relatives (Klump and Shalter, 1984; Hoogland, 1983) and reduces re-attacks by the same predator (Trivers, 1971). As the possibility of exposure of the senders transmitting the alarm signals to predator is large, the alarm signals generally show short duration and high frequency to avoid the possible danger (Klump and Shalter, 1984; Klump et al., 1986).

Mobbing is another signal frequently observed in the presence of potential predators (Hurd, 1996). The mobbing signals announce the presence of predators to heterospecifics as well as conspecifics (Marler, 1955; Zimmermann and Curio, 1988). It makes predators confused and compels them out of the territory (Welty, 1982).

The signals caused by predators have quite different patterns and complicated functions compared with those of preys. For example, two types of predator-elicited calls, the sweet and bearbee, are observed in the American goldfinch (*Carduelis tristis*; Knight and Temple, 1986). The signals induce conspecifics to mob, alert chicks in the nest, and distract predators from the nest. The signals may ultimately protect nests, chicks, or other individuals in the caller's territory. In other words, the signals may include predation risk to the sender, and at the same time the signals contain benefits at three levels: group, kin and individual (Smith, 1986).

Bush warblers (*Cettia diphone*) breed in most areas in Korea and Japan from March to August (Lee et al., 2000). The birds are polygamous, potentially due to the lack of pair bonding. Males mainly defend their territory while females build nests, incubate, and breed chicks (Hamao, 1992). The bush warblers have two types of songs: normal and anomalous. The normal songs can be classified into α and β mode songs, which play a role in intersexual selection and intrasexual interactions, respectively (Park and Park, 2000). The anomalous songs, heard only during bush warbler's breeding season, are emitted when a potential predator emerges near the territory this.

We conducted field observations and playback experiments to examine the function of the anomalous song. We measured responses of non-singing male and female to anomalous playback songs.

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Materials and Methods

Study area and population

The study was conducted during the breeding periods from March to July of 2000 and 2002 in three places, Hado, Jeju, and Hakdong, in Gyungnam, Korea.

We observed 19 territorial males in Hado site, which is mainly covered by heavy shrubs and thickets. More than 10 other bird species were observed in the site including great tits (*Parus major*), meadow buntings (*Emberiza cioides*), brown-eared bulbuls (*Hypsipetes amaurotis*) and great egrets (*Egretta alba*). Furthermore, the predators black kites (*Milvus migrans*) and common buzzards (*Buteo buteo*) were frequently observed. In this site, we mainly focused on the conditions under which the anomalous song was emitted and measured the responses of non-singing males.

The playback responses of nesting females were mainly observed in Hakdong. We found 6 nesting females in this site. Black bamboos (*Phyllostachys nigra*) and arrow bamboos (*Sasa japonica*) are main plants in this site. Bush warblers built nests among the stalks of black bamboos. Potential predators, such as black kite and common kestrel (*Falco tinnunculus*), frequently flew over the territories of bush warblers.

Recording and analysis of anomalous song

The normal and anomalous songs of bush warbler were recorded with a digital tape recorder (PDR 1000) and a parabolic microphone (Telinga Pro 4) from 15 males. We measured the frequency and duration of the recorded songs with a Kay 5500 Sonagraph.

Field observation

We collected data on the natural anomalous songs during the first hour of our visit. We recorded anomalous song heard immediately in a camouflaged net located more than 50 m away from the bush warbler's territory and noted what elicited the song. This method was potentially prone to bias, but it helped to investigate the contexts of the anomalous songs in a natural setting.

Experiment inducing the anomalous song

Playback experiments were performed using three types of stimuli: the avian predator, avian non-predator and ground predator to examine the response of the bush warbler males. A taxidermic sparrowhawk and a bull-headed shrike were used as an imitated predator, a taxidermic brown eared bulbul as a non-predator, and one of researchers as a ground predator.

We placed the taxidermic stimuli on the 2.5 m pole and covered it with a piece of opaque cloth. When a territorial male sang on his song post, a researcher, disguised with leaves from plants in the vicinity, removed the opaque cloth and approached him from as far as 30 m with the pole at a speed of 1.5 m/s. The territorial males did not notice the disguised researcher because the males sometimes approached and sang within 2 m from the disguised researcher. Soon after the subject male emitted an anomalous song, the researcher stopped immediately and measured the distance between the taxidermic stimuli and the male with a tape line. If the at subject moved away or did not emit an anomalous song with the researcher approaching within 5 m, we considered it a no-response. For the responses to humans, a researcher approached the subject male and recorded his response. All experiments were conducted once every morning (0600-1000 h) and evening (1500-1800 h).

Playback experiments to males

To test whether an anomalous song is used for communication with other males, we playbacked an anomalous song to the territorial males and recorded their responses. A speaker (JBL-Pro III) was installed at the edge of a male's territory. While a territorial male was singing on his song post, we randomly played back normal or anomalous songs in a camouflaged blind set up about 20 m away from the territory. Whether the males 1) showed no response or 2) approached the broadcasting speaker within 2 m were determined. All experiments were conducted once every morning (0600-1000 h) and evening (1500-1800 h).

Playback experiments to nesting females

We searched for nests on the first day of our visit to the research areas. To control the variables of the chicks' ages, only the nests containing 10-15 d old chicks, identified by the state of their feathers and down were selected for experiments. Normal and anomalous songs of males, who owned the territories that contained the experimental nests, were recorded to be played back. Each contained only one anomalous song with duration of 23.25±1.32 sec.

We monitored the nest with a lipstick camera (Sony MC100), settled about 1.5 m away from the experimental nest, and set up a digital video tape recorder (Sony GVD-900) in a camouflaged blind 20 m away from the nest. After about 1 h, when the female came to within 30 cm of her nest, we played a stimulus song from the speaker (JBL-Pro III) placed 10 m away from the experimental nest. The volume level of the playback song was adjusted to about 90 dB at a distance of 1 m from the speaker.

We determined the behavior of nesting females as 1) feeding, 2) sanitating their nests, 3) leaving immediately,

and 4) just staying. We measured the duration of their staying and returning to their nests with a stopwatch.

The playback experiment was conducted only once for each female so as to exclude any effect of habituation.

Statistical analysis

We used a binomial test to identify whether the males responded to the taxidermic stimulus with the anomalous song. Kruskal-Wallis H was used to analyze the differences in the distances that the anomalous song was first elicited between various stimuli. The Mann-Whitney U-test was performed to examine the female response to the anomalous songs by comparing the returning duration to their nest from off-duty between with and without the playback songs. Chi-square test compared the behaviors of nesting females in response to playback of anomalous song with no-playback (Sokal and Rohlf, 1969).

Results

Structure of the anomalous song

A total of 54 anomalous songs were recorded. The anomalous songs consisted of a first portion (A part), which was made up of short notes, and a frequency fluctuated second portion (B part) (Fig. 1). It often showed that either part A or part B was omitted. The duration varied extremely from 5 s to 80 s (25.37±17.61 s, 54 songs, 15 individuals).

The duration for part A was 3.45 s at minimum and 2.30±0.71 s in average. The main intensity frequency was 1741.0±99.94 Hz (11 indivi. 21 songs). The duration of part B was remarkably diverse (min = 8.54, max = 54.20, 22.55±12.08 s) with the main intensity frequency at 2256.6±175.05 Hz (15 indivi. 54 songs). The anomalous songs were longer in duration and higher in frequency than the normal songs (Table 1).

Field observation of the anomalous song

A total of 99 anomalous songs, elicited by potential predators, were observed (Table 2). The bush warbler sang an anomalous song at the highest rate (47 times, 47.5%) at the emergence of avian predators. The predators that elicited anomalous songs were the black kite (14 times, 29.8%), common buzzard (12 times, 25.5%), common kestrel (8 times, 17.0%), bull-headed shrike (5 times, 10.6%), osprey (*Pandion haliaetus*, 4 times, 8.5%) and the jungle crow (*Corvus macrorhynchos*, 4 times, 8.5%).

Even though there exist many flying avian non-predators, some non-predators, such as the grey heron (*Ardea cinerea*, 4), great egret (4) and the rufous turtle dove (*Streptopelia orientalis*, 1), uncommonly elicited the

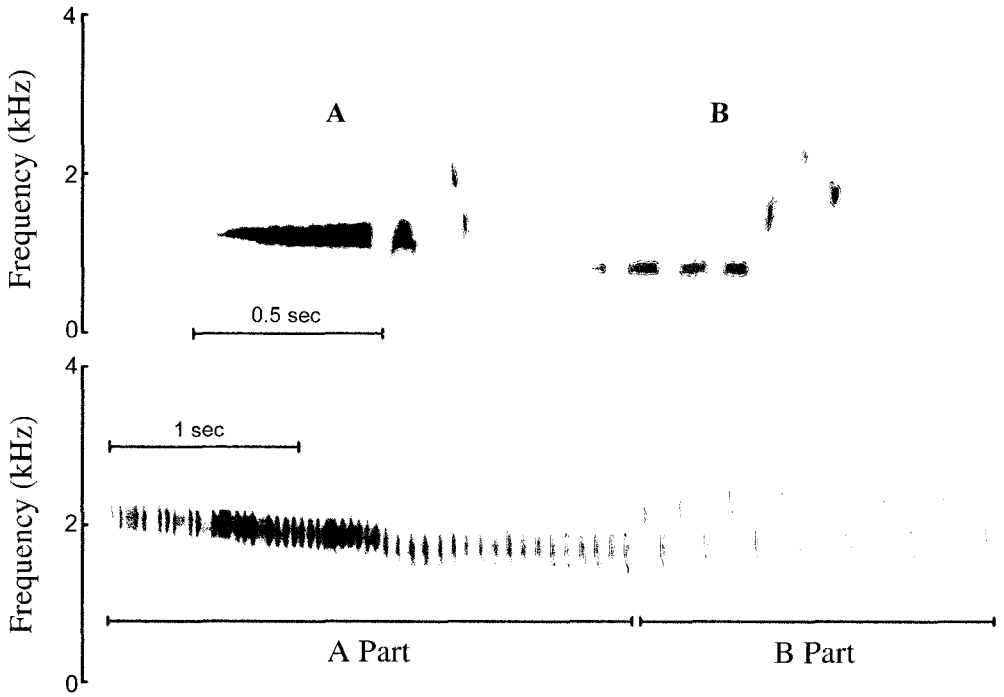

Fig. 1. The structure of song of bush warbler. Upper A, Normal α mode. Upper B, Normal β mode. Lower A and B, Anomalous song.

Table 1. Characteristics of the normal and anomalous songs of male bush warbler

Parameter	Normal song		Anomalous song	
	Alpha song (*n* = 173)	Beta song (*n* = 138)	A part (*n* = 21)	B part (n = 21)
Duration (sec)	1.28±0.35	1.04±0.22	2.30±0.71	22.55±12.08
Dominant frequency (Hz)	1487.5±123.44	876.2±58.34	1741.0±99.94	2256.6±175.05

anomalous songs. Others uncluding, the brown-eared bulbul, meadow bunting, oriental greenfinch (*Carduelis sinica*), great tit, coal tit (*Parus ater*), Japanese white-eye (*Zosterops japonicus*), and the Eurasian woodcock (*Scolopax rusticola*) did not elicit the anomalous song.

Anomalous song behavior of males

While singing their normal songs on the song post, the bush warbler males changed to the anomalous song when they saw potential predators approaching their territory. When the potential predators stayed in the territory for a while, the males left the song post to nearby shrubs where they concealed themselves and continued singing the anomalous song.

The males emitted the anomalous song in the emergence of a stimulus, but never repeated it. Males continued to emit part B of the anomalous song until the stimulus was removed.

The observed anomalous song behavior of males may include two types of stimuli; the aerial stimulus and the ground stimulus. If a black kite glided quickly above the male's territory, the males emitted an anomalous song for as long as if was seen without moving. If the black kite hovered over the territory or made a turning flight, the males moved to nearby shrubs to hide and continued to utter anomalous songs until it flew away.

When a researcher approached the territorial males, they immediately flew down from their song posts and concealed themselves in the nearby shrubs and emitted an anomalous song. When the researcher continued approaching the male's territory, the males moved around the researcher at a distance of 5-10 m and continued part B of the anomalous song.

Table 2. Observed number of anomalous song and its presumed elicitors

Presumed elicitor	Number of observations
Avian predator	47
Avian non-predator	9
Human	12
Unknown	31
Total count	99

Experiment inducing the anomalous song

The territorial males of the bush warbler responded with an anomalous song to the approaching of stuffed potential predators and humans. It showed similar results of the field observation (Fig. 2). Resident males emitted an anomalous song for 16 out of 19 approaches by the unrestigator (binomial test, $p<0.001$) and for 13 out of 19 stuffed sparrowhawk's approach (binomial test, $p<0.05$).

When we used a stuffed bull-headed shrike as a stimulus, resident males responded 11 times out of 19 trials (binomial test, $p=0.152$) with anomalous songs. To the stuffed brown-eared bulbul as a non-predator, males did not respond with an anomalous song significantly (twice in 19 trials, binomial test, $p<0.01$).

In this experiment, the distances from the utterance of anomalous song to the stimulating source significantly differed depending on the stimulating source (Kruskal-Wallis H, $\chi^2=12.660$, $p<0.01$). Males started to emit an anomalous song at 20.29±10.82 m (n=13) against the stimulus of a stuffed sparrowhawk, at 16.82±7.83 m (n=11) against the stuffed bull headed shrike, and at

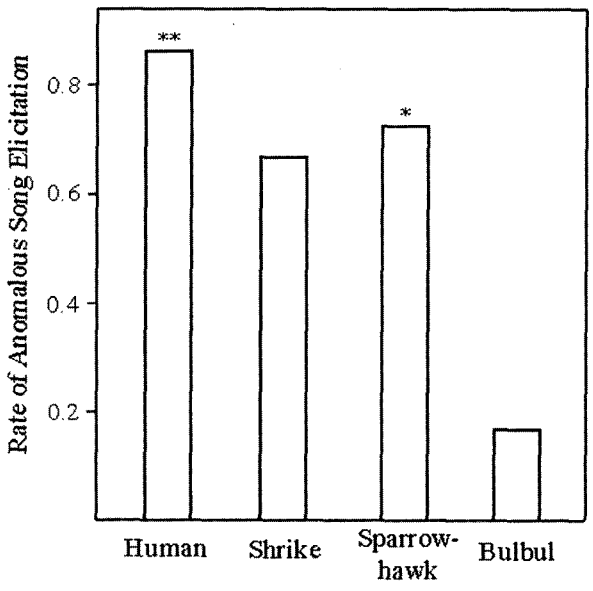

Fig. 2. Rate of anomalous song elicitation to various stimuli. Binomial test, *, $P<0.05$; **, $P<0.001$.

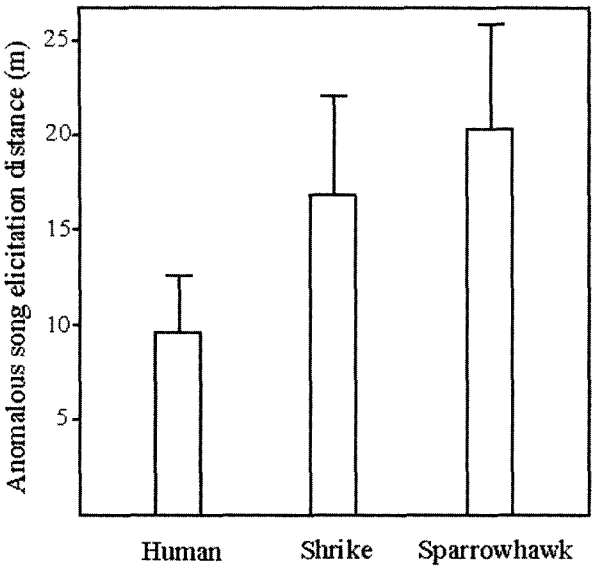

Fig. 3. Distance between various stimuli and bush warbler elicited to sing anomalous song. Kruskal-wallis H, $\chi^2 = 12.660$, $P<0.01$.

9.50±6.26 m (n=16) against human (Fig. 3).

Responses of males to anomalous song playback

Responses of 19 male birds to both anomalous songs and normal songs were successfully recorded. When a normal song was played back, 17 territorial males responded by approaching the speaker. On the other hand, no males responded to the playback of an anomalous song. Territorial males did not move away or approached the speaker, but sang normal songs on their song posts.

Responses of nesting females to anomalous song playback

There was no significant difference between the duration that females stayed in their nest during the anomalous song playback (11.00±5.94 s, n=24) and no-playback (10.68±7.79 s, n=57) (Mann-Whitney U-test, Z=0.75, p=0.455). The behavior and frequency of females in response to the anomalous song playback did not differ from that to the no-playback (Table 3, $\chi^2=2.98$, df=3, p =0.40).

Table 3. Comparison of behaviors of females in the nest between anomalous song playback and no-playback. There is no statistical significance between the two situation (Chi-square test, $\chi^2 = 2.98$, df = 3, $P = 0.40$)

Behavioral types	Without playback (n = 35)	Anomalous song playback (n = 24)
Feeding offsprings	17	13
Sanitating the nest	8	4
Leaving immediately	6	3
Just staying	4	4

The returning duration of the female did not show a difference between the anomalous song playback (259.37±244.52 s, n=16) and the no-playback (299.84 ±237.52 s, n=25) (Mann-Whitney U-test, Z=0.39, p= 0.702).

Discussion

This experiment showed that an anomalous song was brought forth by appearance of any potential predator. It was very difficult to obtain the exact data on the cause of occurrence of an anomalous song in the field observation. Since the area where bush warblers lived was thickly covered with shrubs over 2 m tall, it was difficult to judge the cause of occurrence of an anomalous song. For example, the ground predators, such as wild cats, badgers and raccoons, are highly concealed, and hot easily observed. However, as we consider the data on 68 cases with known causes of anomalous songs observed in the field, it is certain that the birds reacted to any potential predator by singing the anomalous song. This is also supported by the result of the playback experiments using taxidermic stimuli.

The distance between a stimulating source and the point of male's song response varied depending upon the stimulating source, such as stuffed sparrowhawk, stuffed bull-headed shrike and man. However, as the signals of the bush warblers are not relatively varied compared with species showing different vocal signals (Klump and Curio, 1983; Langmore and Mulder, 1992; Blumstein, 1999), the territorial males might determine whether to utter anomalous songs or not depending on the degree of potential threat by the predator. Thus, it is possible to infer that stimuli used in the experiment involve different levels of threat to the bush warbler. The sparrowhawk could be the most significant predator to the bush warbler. Even if the bull-headed shrike also preys on an adult bush warbler, it was easily repulsed by mobbing (personal observations). Human appeared comparatively less threatening to the males, but his direct approach into the territory may be a threat. In addition, the kind of potential predators might determine whether to utter an anomalous song or not, and effective identification of the kind of song would provide a successful reproduction strategy. According to the good gene theory (Ryan, 1997), frequent anomalous songs may act negatively on the sexual selection because it will be a sign of a territory frequently threatened by predators.

Even though the potential predator induced the anomalous song in the male bush warbler, it seems to be hard to deem that the anomalous song is a simple alarm signal due to its phonetic characteristics and singing behavior. Firstly, various durations of the anomalous

song were shown, some, lasting very long (min = 5 s, max=80 s, mean=25.37±17.61 s, n=54). Considering the suggestion that an alarm signal has a short duration so that the sender may not be easily exposed to a predator (Welty, 1982; Klump and Shalter, 1984; Klump et al., 1986), the duration of the anomalous song was not in conformity. The bush warbler continued to sing the anomalous song until the predator disappeared from the subject's territory. In case a predator was hovering or making a turning flight over the territory, the bush warbler continued to sing an anomalous song for a long time; when the predator made a gliding flight over the territory, the bush warbler sang the anomalous song for a short time.

Secondly, any evidence that the anomalous song was used for communication between individuals could not be found. The playback of a normal song made the subject approach the speaker with the anomalous song, while the playback of the anomalous song did not elicite any distinctive behavior, such as approaching the speaker, or stopping singing the song, or moving from place to place. Even in a natural situation where individuals lived in a very dense area, when an individual sang an anomalous song, the neighboring individuals still continued to sing a normal song. In the anomalous song playback experiment on a female bush warbler in a nest, no difference was shown in the behavior from a normal song. These results support the view that the anomalous song is not a simple alarm signal because an alarm signal is a means of communication to make the same species or subspecies safe by providing the information about a predator (Sherman, 1977).

Therefore, considering the phenomena that the anomalous song is different from a general alarm signal in phonetic characteristics, and that other male bush warbler and the female in the nest did not respond to it, the functions of the anomalous song of the bush warbler are suggested as follows: Firstly, it is an active territorial defense means to a predator. A stuffed sparrowhawk caused the males to approach and sing anomalous songs. The male approached the stuffed sparrowhawk and whirled around it by singing the part B continuously. This lasted until the stuffed sparrowhawk was removed. A similar phenomenon was observed where a bull-headed shrike invaded the territory. The bush warbler sang the anomalous song until it retreated out of the territory. The responses of the territorial males suggest that the anomalous song show similar roles of the typical mobbing signal. Although it was not observed that the anomalous song made other conspecifics or heterospecifics assemble, the bush warbler showed vigorous aggression to the potential predator. The repetitive notes have a similar structure to those of the typical mobbing signal, which has a broad frequency band (Catchpole and Slater, 1995). Even if the mobbing behavior does not give direct damage to a predator, it could force the predator to retreat out of the territory (Curio, 1978; Flasskamp, 1994). It has been suggested that this behavior can increase the fitness of the individual's brood or the same family, though it increases the possibility for any individual's position to be exposed to the predator and so to be at the risk of predation (Pettifor, 1990; Pavey and Smyth, 1998). Similarly, the bush warbler seems to protect its spouse and brood by showing an active defense behavior against the predator that invades its territory through singing the anomalous song.

Secondly, the anomalous song of the bush warbler possibly distracts a potential predator. A singing individual induces a predator to have an interest in itself instead of its spouse or brood within its territory. So, the singing individual's position is easily exposed by the anomalous song. This hypothesis can be applied to this study by the two following observations: A potential predator caused the male to change his normal song to the anomalous song on the song post, and this behavior is unusual because the anomalous songs were uttered for a long time mainly into a bush (personal observations). The exposed individual continued to utter the anomalous songs and move from place to place by making a sound. The risk of the individual may not be so high because of the thickly grown shrubs. In addition, the structure of the anomalous song has a broad frequency range, which makes it difficult to find the exact position of the individual (Gill, 1995). Specific response behaviors to a terrestrial potential predator, such as humans, included movements from the song post to the bush, and never going away from the invader, with continuous the anomalous songs and wandering around the invader nearby the neighboring bush.

It is not common to induce a predator as a defense strategy for protecting the same species (Sordahl, 1990), and this has been found in some species: Induction of a predator is made mainly through a behavior called distracting display, such as feigning injury and attempting to lure predators away (Amstrong, 1954; Sordahl, 1990; Pavel et al., 2000). However, a distinctive vocal signal is also accompanied (Hudson and Newborn, 1990). Such inducing behavior is usually made around a nest, suggesting that it has a function to protect the brood in the nest (Weatherhead, 1989; Gill and Sealy, 1996). The male bush warbler is not directly engaged in the nursing behavior, but he seems to indirectly protect the brood by inducing the predator by the anomalous song.

Acknowledgements

We would like to thank to J. G. Oh, K. Y. Kim and S. S. Shin for their special field work, and D. S. Park, H. C. Sung and M. C. Berrington for their thoughtful review and translation. This study received financial support from the Korea Science and Engineering Foundation (R05-2000-000-00114-0). The authors have adhered to the specific national legal requirements for the use of animals in research.

References

Amstrong EA (1954) The ecology of distraction display. *Br J Anim Behav* 11: 121-135.

Blumstein DT (1999) The evolution of functionally referential alarm communication. *Evol Comm* 3: 135-147.

Catchpole CK and Slater PJB (1995) Bird Song. Biological Themes and Variations. Cambridge University Press, London, pp 88-90.

Charnov EL and Krebs JR (1975) The evolution of alarm calls: a truism or manipulation? *Am Nat* 109: 107-112.

Curio E (1978) The adaptive significance of avian mobbing. 1. Teleonomic hypotheses and predictions. *Z Tierpsychol* 48: 175-183.

Dawkins M (1976) The Selfish gene. Oxford University Press, Oxford.

Flasskamp A (1994) The adaptive significance of avian mobbing. 5. An experimental test of the move on hypothesis. *Ethology* 96: 322-333.

Gill FB (1995) Ornithology. WH Freeman, New York, pp 340-342.

Gill SA and Sealy SG (1996) Nest defence by yellow warblers: recognition of a brood parasite and an avian predator. *Behaviour* 133: 263-282.

Greig-Smith PW (1981) The Role of alarm responses in the formation of mixed-species flocks of heathland birds. *Behav Ecol Sociobiol* 8: 7-10.

Hamao S (1992) Lack of pair-bond: a polygynous mating system of the Japanese bush warbler *Cettia diphone*. *Jpn J Ornithol* 40: 51-65.

Hoogland JL (1983) Nepotism and alarm calling in the black-tailed prairie dog, *Cynomus ludovicianus*. *Anim Behav* 31: 472-479.

Hudson PJ and Newborn D (1990) Brood defence in precocial species: variations in the distraction displays of red grouse, *Lagopus lagopus scoticus*. *Anim Behav* 40: 254-261.

Hurd CR (1996) Interspecific attraction to the mobbing calls of black-capped chickadees (*Parus atricapillus*). *Behav Ecol Sociobiol* 38: 287-292.

Klump GM and Curio E (1983) Reactions of blue tits *Parus caeruleus* to hawk models of different sizes. *Bird Behav* 4: 78-81.

Klump GM and Shalter MD (1984) Acoustic behaviour of birds and mammals in the predator context. *Z Tierpsychol* 66: 189-226.

Klump GM, Kretzschmar E, and Curio E (1986) The hearing of an avian predator and its avian prey. *Behav Ecol Sociobiol* 8: 317-323.

Knight RL and Temple SA (1986) Nest defence in the American goldfinch. *Anim Behav* 34: 887-897.

Langmore NE and Mulder RA (1992) A novel context for bird vocalization: predator calls prompt male singing in the kleptogamous superb fairy-wren, *Malurus cyaneus*. *Ethology* 90: 143-153.

Lee WS, Koo TH, and Park JY (2000) A Field Guide to the Birds of Korea. LG Sangrok Foundation, Seoul, pp 234-235.

Marler P (1955) Characteristics of some animal calls. *Nature* 176: 6-8.

Park SR and Park DS (2000) Song type for intrasexual interaction in the bush warbler. *Auk* 117: 228-232.

Pavey CR and Smyth AK (1998) Effects of avian mobbing on roost use and diet of powerful owls, *Ninox Strenua*. *Anim Behav* 55: 313-318.

Pavel V, Weidinger SBK and Kovarik P (2000) Distraction displays in meadow pipit (*Anthus pratensis*) females in central and northern Europe. *Ethology* 106: 1007-1019.

Pettifor RA (1990) The effects of avian mobbing on a potential predator, the European kestrel, *Falco Tinnunculus*. *Anim Behav* 39: 821-827.

Ryan MJ (1997) Sexual selection and mate choice. In: Krebs JR and Davies NB (eds), Behavioural Ecology. An Evolutionary Approach, Cambridge University Press, Oxford, pp 179-202.

Sherman PW (1977) Nepotism and the evolution of alarm calls. *Science* 197: 1246-1253.

Smith RJF (1986) Evolution of alarm signals: role of benefits of retaining group members or territorial neighbors. *Am Nat* 128: 604-610.

Sokal RR and Rohlf FJ (1969) Biometry. WH Freeman and Company, San Francisco, pp 585-601.

Sordahl TA (1990) The risks of avian mobbing and distraction behavior: an anecdotal review. *Wilson Bull* 102: 349-352.

Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46: 35-57.

Weatherhead PJ (1989) Nest defence by song sparrows: methodological and life history consideratons. *Behav Ecol Sociobiol* 25: 129-136.

Welty JC (1982) The Life of Birds. CBS College Publishing, New York, p 227.

Zimmermann U and Curio E (1988) Two conflicting needs affecting predator mobbing by great tits, *Parus major*. *Anim Behav* 36: 926-932.

[Received April 30, 2004; accepted June 4, 2004]