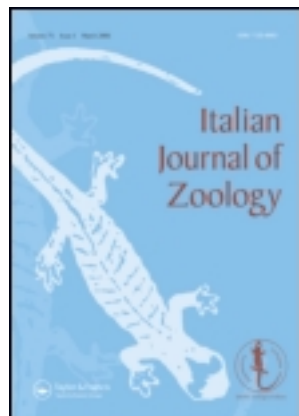


On: 01 May 2012, At: 23:15

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



## Italian Journal of Zoology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tizo20>

### Anti-predator behaviour of the red-legged partridge *Alectoris rufa* (Galliformes: Phasianidae) to simulated terrestrial and aerial predators

R. Binazzi<sup>a</sup>, M. Zaccaroni<sup>a</sup>, A. Nespoli<sup>a</sup>, A. Massolo<sup>b</sup> & F. Dessí-Fulgheri<sup>a</sup>

<sup>a</sup> Department of Evolutionary Biology, University of Firenze, Firenze, Italy

<sup>b</sup> Department of Ecosystem and Public Health, Faculty of Veterinary Medicine, University of Calgary, Calgary, Canada

Available online: 25 Aug 2010

To cite this article: R. Binazzi, M. Zaccaroni, A. Nespoli, A. Massolo & F. Dessí-Fulgheri (2011): Anti-predator behaviour of the red-legged partridge *Alectoris rufa* (Galliformes: Phasianidae) to simulated terrestrial and aerial predators, *Italian Journal of Zoology*, 78:1, 106-112

To link to this article: <http://dx.doi.org/10.1080/11250003.2010.509136>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

## Anti-predator behaviour of the red-legged partridge *Alectoris rufa* (Galliformes: Phasianidae) to simulated terrestrial and aerial predators

R. BINAZZI<sup>1</sup>, M. ZACCARONI<sup>1</sup>, A. NESPOLI<sup>1</sup>, A. MASSOLO<sup>2</sup>, & F. DESSI-FULGHERI<sup>1\*</sup>

<sup>1</sup>Department of Evolutionary Biology, University of Firenze, Firenze, Italy, and <sup>2</sup>Department of Ecosystem and Public Health, Faculty of Veterinary Medicine, University of Calgary, Calgary, Canada

(Received 1 April 2010; accepted 9 July 2010)

### Abstract

This study is intended to investigate the differences in anti-predator behavioural and acoustic response to terrestrial and aerial predators as well as the behavioural differences between sexes in the red-legged partridge. To this aim we observed the response of 114 partridge (57 males and 57 females) to dummy terrestrial and aerial predators, a raptor and a fox. We divided behavioural responses to predators into four mutually exclusive categories: vigilance, freezing, escape and non-anti-predator behaviours. We also recorded and analysed the vocalizations emitted during tests. The animals reacted differently to aerial and terrestrial stimuli. The reactions elicited by the terrestrial predator were ranked as follows: vigilance, escape, non-anti-predator behaviours, and freezing. Those elicited by the aerial predator were ranked as follows: vigilance, freezing, escape and non-anti-predator behaviours. Vigilance and escape were elicited more frequently by the terrestrial predator than by the aerial predator (vigilance:  $p < 0.001$ ; escape:  $p < 0.001$ ). Freezing was the most frequent behaviour following the appearance of the aerial predator ( $p < 0.001$ ). In fact, freezing may represent an effective strategy in an open space, combining camouflage from and detection by the predator. On the other hand, vigilance is an effective behaviour to detect and avoid a terrestrial predator hunting by ambush. We did not find clear-cut differences between sexes. The analysis of vocalizations revealed that the fox and the raptor elicited significantly different calls ( $p = 0.003$ ); the fox evoked significantly more vocalizations than the raptor ( $p < 0.001$ ), differing in addition in frequency parameters. Thus partridges not only discriminate between aerial and terrestrial predators and behave consequently, but are also able to tune alarm calls in relation to the context of predation.

**Keywords:** Predation, vocalizations, *Alectoris rufa*, fox, hawk

### Introduction

Different reactions to different predators or context of predation have been described across a variety of species and range from hiding to alarm signals and escape (Caro 2005; Leavesley & Magrath 2005; Randall et al. 2005; Templeton et al. 2005). Galliformes and other bird species avoid aerial predation by raptors by means of crouching and freezing, while their response to terrestrial predators involves more active reactions such as vigilance and escape (Evans et al. 1993). As regards galliform species in particular, two types of alarm calls elicited by aerial and terrestrial predators respectively were described by Goodwin (1953) on a qualitative basis in the red-legged partridge (*Alectoris rufa*); in other galliforms, a quantitative description was given by

Dessi-Fulgheri et al. (1986) in the grey partridge (*Perdix perdix*), by Collias (1987) in the red junglefowl (*Gallus gallus*), by Gyger et al. (1987) and Evans et al. (1993) in the domestic fowl (*Gallus gallus domesticus*). Anti-predator behaviours were also found to vary according to sex in many bird species: males are generally more vigilant than females in species living in family as well as in foraging groups (jungle babbler *Turdoides striatus*: Gaston 1977; common eider *Somateria mollissima*: Ashcroft 1976), and in monogamous species (mallard *Anas platyrhynchos*: Asplund 1981; magpie *Pica pica*: Buitron 1983; grey partridge *Perdix perdix*: Jenkins 1961 and Beani & Dessi-Fulgheri 1998). In the monogamous galliform white-tailed ptarmigan *Lagopus leucurus*, males spend more time

\*Correspondence: F. Dessi-Fulgheri, Department of Evolutionary Biology, University of Firenze, Via Romana 17, I-50125, Firenze, Italy. Tel: +39 0552288213. Email: [dessi@unifi.it](mailto:dessi@unifi.it)

in vigilance than females (Artiss et al. 1999). In the grey partridge *Perdix perdix*, females spent more time near the males, which were more vigilant during laboratory mate choice experiments (Dahlgren 1990; Beani & Dessi-Fulgheri 1995). Arguably, enhanced vigilance in males of these species may enable females to dedicate more time to feeding (Caro 2005). Our study aimed to investigate the differences in anti-predator behavioural and acoustic response to terrestrial and aerial predators as well as the behavioural differences between sexes in the red-legged partridge, a monogamous species characterized by low sexual dimorphism, in morphology as well as in behaviour (Johnsgard 1988).

## Materials and methods

### Subjects

In December 2006 at the Montepaldi Farm (Florence, Italy), 114 9-month-old red-legged partridges from game farm stock (57 males and 57 females) were housed in 19 outdoor pens (2.4 m × 2.4 m × 2.5 m) in groups of 6 individuals (3 males and 3 females) and provided with food and water ad libitum. Birds were acclimated to the new pens for 1 month and individually marked by means of numbered ponchos. In January 2007, two tests were carried out whereby each of the 19 groups was exposed to aerial and terrestrial dummy predators while in a pen of 2.4 m × 2.4 m × 2.5 m, with the wall screened with plastic weed-mat so as to prevent any visual contact with the outside (Figure 1).

### Test apparatus and procedure

**Experiment 1, aerial predator.** To simulate the aerial predator, we used a black wooden model of raptor with a wingspan of 15 cm. The 'flying' buzzard-like silhouette was pulled by an electric motor at a speed of 1.9 m/s, 3 m above ground, for 3 s. This classical bidimensional dummy simulated a raptor with a wingspan of 100 cm flying at a speed of 45 km/h at 20 m above the ground (Beani & Dessi-Fulgheri 1998).

**Experiment 2, terrestrial predator.** To simulate the terrestrial predator, a stuffed fox *Vulpes vulpes* was presented through a window of 2.20 m × 0.40 m opened through the weed-mat screen at ground level. The fox was fixed on a cart moving along a track parallel to the pen and pulled in front of the window onto and off the stage by means of a string at a speed of 0.5 m/s. During each session the fox was visible for 4.4 s (Zaccaroni et al. 2007). The animals were acclimated to the experimental pen for 30 min before the test session. Each dummy predator was presented only once. We presented the two predators within of 20 min of each other. The order of presentation of the two predator models was randomized.

### Behaviour

Duration of behavioural responses to predators was recorded with a digital video Sony Mini DV DCR-HC40EHandyCam, from the presentation of the stimulus to 100 s after its disappearance, and

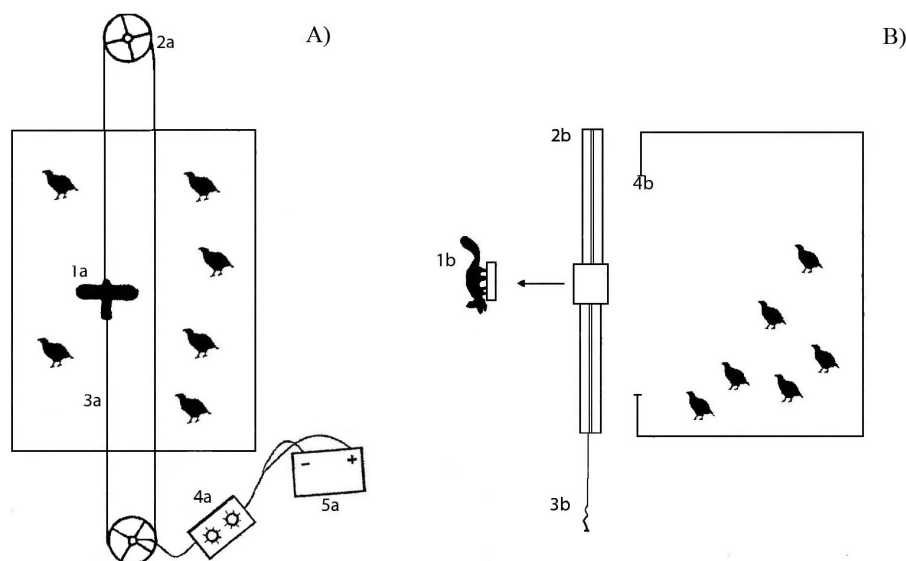


Figure 1. Experimental apparatus to simulate the predators. **A**, aerial predator: (1a) dummy aerial predator; (2a) pulleys on poles and electric motor; (3a) string; (4a) speed control; (5a) battery. **B**, terrestrial predator: (1b) dummy terrestrial predator; (2b) track; (3b) string; (4b) window.

analysed with OBSERVER 3.0 (Noldus Information Technology 2000, Wageningen, Netherlands). Behavioural responses of birds to predators were divided into four mutually exclusive categories. (1) Vigilance: outstretched neck, upright posture, and movements of the head, i.e. scanning from side to side (since birds, unlike mammals, can move their eyes to a small degree only, head movements are good indicators of eye movements, and more easily monitored; see Lazarus 1990). (2) Freezing: the bird remains motionless, sometimes after rapidly squatting down; it includes crouching. (3) Escape: running towards vegetation cover and hiding. (4) Non-anti-predator behaviours: any behaviour not falling into one of the above categories.

#### Vocalizations

We recorded the vocalizations emitted during tests with a digital recorder M-Audio micro track 24/96 (sampling rate 44.1 kHz), supplied with an Aiwa DM-50 microphone. Since the recognition of each individual emitter was not possible, data from different sexes were not differentiated. Accordingly, we considered each group as a statistical unit. Vocalizations elicited by predators were analysed using the interactive sound analysis software Raven Pro 1.3 (Cornell Laboratory of Ornithology; Charif et al. 2003) to generate spectrograms (DFT size: 4096 samples; Hanning window; time step: 10 ms, frequency resolution 10.8 Hz). Aerial and terrestrial alarm calls were characterized by (a) the number of vocalizations for each recording session; (b) the highest frequency of the vocalization, in Hz; (c) the lowest frequency of the vocalization, in Hz; (d) peak (maximum power) frequency within the vocalization, in Hz; and (e) the duration of the vocalization, in seconds.

Experimental procedures followed the European Community Council Directive 86/609/EEC.

#### Statistical analyses

The effects of the stimuli on behaviour and vocalization were analysed using both ANOVA and

MANOVA for repeated measures (before and after; Searle 1982). The multivariate effects were tested using Pillai's trace, while the within-subject effects (behaviour: stimulus and sex; vocalization: stimulus) were tested using the method of Greenhouse and Geisser (1959). To compare the effects of stimuli on individual behavioural responses we used ANOVA and MANOVA with a nested design so as to take the group effect into account. Tamhane post-hoc test for unequal variances was used to check for differences among groups. Statistical analyses were performed using the SYNTAX procedure, implemented in the Statistical Package for Social Sciences 15.01 (SPSS<sup>®</sup> Inc.).

## Results

### Behaviour

*Differences according to the predator.* The animals reacted to both aerial and terrestrial stimuli. The pattern of reactions elicited by the terrestrial predator was characterized by the longer duration of vigilance, followed by escape, non-anti-predator behaviours, and freezing. The reactions elicited by the aerial predator were characterized by the longer duration of vigilance, followed by freezing, while escape and non-anti-predator behaviours were less frequent (Table I).

The comparison between responses to stimuli was performed using ANOVA for repeated measures and revealed a highly significant variation according to the kind of stimulus (Pillai's trace = 0.696,  $F_{4,25} = 14.296$ ,  $p < 0.001$ ). In detail, vigilance and escape (Figure 2) were elicited more frequently by the terrestrial predator than by the aerial predator (vigilance,  $p < 0.001$ ; escape,  $p < 0.001$ ); in contrast, freezing was the most frequent behaviour following the appearance of the aerial predator ( $p < 0.001$ ). No significant difference was found for non anti-predator behaviours ( $p = 0.066$ ).

*Differences according to the sex.* Nested MANOVA in response to the aerial predator revealed an overall significant response (Pillai's trace = 2.251,  $F_{128,252} = 2.535$ ,

Table I. Differential responses to aerial and terrestrial dummy predators by red-legged partridge. Values shown are mean  $\pm$  SE (s) pooling males and females. The results of the one-way ANOVA for repeated measures are reported.

Behaviour	Terrestrial predator Mean $\pm$ SEN = 35	Aerial predator Mean $\pm$ SEN = 33	F	<i>p</i>
Vigilance	90 $\pm$ 1.96	48.14 $\pm$ 5.42	35.026	<0.001
Escape	3.72 $\pm$ 0.54	0.80 $\pm$ 0.24	3.647	<0.001
Freezing	3.06 $\pm$ 2.1	40.86 $\pm$ 6.52	24.453	<0.001
Non anti-predator behaviours	3.21 $\pm$ 0.65	10.18 $\pm$ 2.59	3.647	0.066

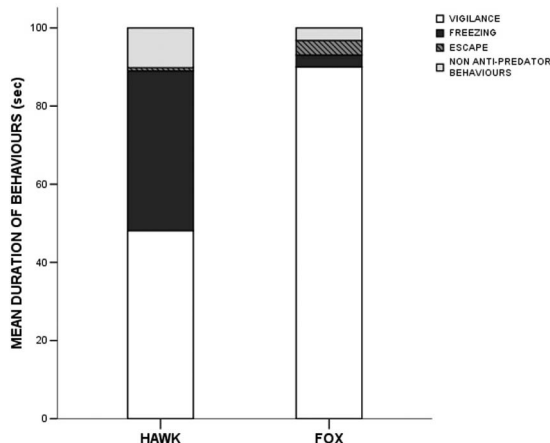


Figure 2. Defensive response by red-legged partridge to different stimuli following a simulated exposure to predators.

$p < 0.001$ ), where females were found to show non anti-predator behaviours significantly more frequently than males ( $p = 0.001$ ; Table II), while duration of freezing ( $p = 0.586$ ), vigilance ( $p = 0.550$ ), and escape ( $p = 0.414$ ; Figure 3A) did not differ between sexes.

In response to the terrestrial predator (Table II and Figure 3B) an overall significant response in marginal means was also detected as well (Pillai's trace = 0.1498,  $F_{102,192} = 1.878$ ,  $p < 0.001$ ), with females reported to spend more time than males in escaping ( $p = 0.001$ ), while vigilance, freezing and non anti-predator behaviours did not differ between sexes (vigilance,  $p = 0.079$ ; freezing,  $p = 0.091$ ; non anti-predator behaviours,  $p = 0.162$ ; Figure 3B).

### Vocalizations

*Differences according to the predator.* The presentation of the dummy fox and raptor elicited alarm calls from all the groups. In particular, ANOVA for repeated measures revealed that the fox and the raptor elicited significantly different calls (Pillai's trace = 0.835,  $F_{5,9} = 9.079$ ,  $p = 0.003$ ), in terms of number and frequency, with the fox eliciting more vocalizations than the raptor ( $p < 0.001$ ; Figure 4A). Moreover, we were able to characterize aerial and terrestrial alarm calls by their acoustic structure (Table III and Figure 4B).

Table II. The results of the ANOVA on the marginal means with nested design are reported. Values shown are means  $\pm$  SE (s). Responses to simulated aerial and terrestrial predator by female and male red-legged partridge.

	Females Mean $\pm$ SE	Males Mean $\pm$ SE		
<i>Aerial predator</i>	<i>N</i> = 56	<i>N</i> = 42	$F_{1,63}$	<i>p</i>
Vigilance	46.59 $\pm$ 3.83	50.01 $\pm$ 4.21	0.362	0.550
Escape	0.68 $\pm$ 0.21	0.94 $\pm$ 0.23	0.676	0.414
Freezing	39.41 $\pm$ 4	42.59 $\pm$ 4.30	0.299	0.586
Non anti-predator behaviours	13.31 $\pm$ 1.34	6.43 $\pm$ 1.48	11.808	<0.001
<i>Terrestrial predator</i>	<i>N</i> = 53	<i>N</i> = 46	$F_{1,64}$	<i>p</i>
Vigilance	87.19 $\pm$ 2.16	93.18 $\pm$ 1	3.185	0.079
Escape	4.95 $\pm$ 0.65	2.58 $\pm$ 0.43	12.120	<0.001
Freezing	3.85 $\pm$ 2.69	0.47 $\pm$ 0.27	2.942	0.091
Non anti-predator behaviours	2.32 $\pm$ 0.72	3.77 $\pm$ 0.96	2.001	0.162

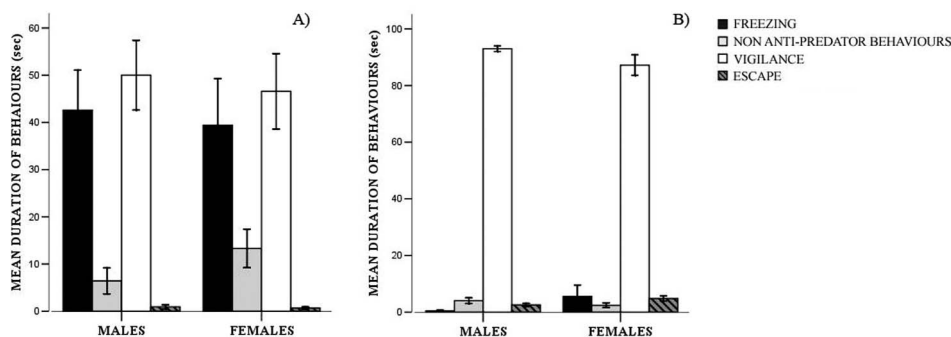


Figure 3. **A**, anti-predator responses to an aerial predator by male and female red-legged partridge. **B**, anti-predator responses to a terrestrial predator by males and females. Values shown are mean (in  $s \pm SE$ ).

Table III. Vocal response by red-legged partridge to the exposure to aerial and terrestrial dummy predators. Values shown are mean  $\pm$  SE. The results of the ANOVA for repeated measures are reported.

	Aerial predator Mean $\pm$ SE N = 15	Terrestrial predator Mean $\pm$ SE N = 14	F	p
No. vocalizations	21.93 $\pm$ 3.41	69 $\pm$ 9.56	27.945	<0.001
Low-freq (Hz)	399.91 $\pm$ 17.94	381.70 $\pm$ 19.30	0.575	0.462
High-freq (Hz)	1359.57 $\pm$ 79.4	2158.75 $\pm$ 19.40	20.311	<0.001
Peak freq (Hz)	653.20 $\pm$ 21.52	727.33 $\pm$ 30.64	4.327	0.058
Duration (s)	0.08 $\pm$ 0.01	0.08 $\pm$ 0.02	0.002	0.964

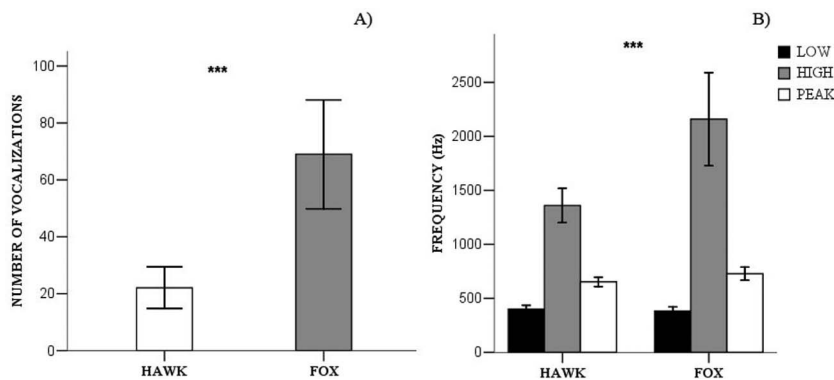


Figure 4. **A**, number of vocalizations by red-legged partridge in response to aerial (hawk) and terrestrial (fox) predators following a simulated exposure to predators. **B**, low, high and max frequency (in Hz) of aerial and terrestrial predators. Values shown are means  $\pm$  SE.

Alarm calls in fox tests reached a significantly higher frequency ( $p = 0.001$ ) and a marginally higher peak frequency ( $p = 0.058$ ), whereas the lowest frequency and the duration of vocalizations did not differ significantly according to the stimuli.

## Discussion

### Behaviour

*Differences according to the predator.* It is proved that terrestrial and aerial predators elicit predator-specific responses in galliform birds, such as *Gallus gallus* (Evans et al. 1993). In our experiment, the presentation of dummy terrestrial and aerial predators elicited clear anti-predator behaviours. The responses to the aerial predator were mainly vigilance and freezing, while escape hardly ever occurred and non-anti-predator behaviours were rare (Table I and Figure 2). The low rate of occurrence of escape could be due to the scarcity of cover and restricted space in our semi-natural conditions. On the other hand, the terrestrial predator elicited vigilance as the most frequent response, while escape was elicited to a lesser extent. In response to an aerial predator, freezing, and subsequently vigilance,

appear to be appropriate (Evans et al. 1993): in fact, they may represent an effective strategy in an open space, combining camouflage from and detection by the predator (Beani & Dessi-Fulgheri 1998; Zaccaroni et al. 2007). On the other hand, vigilance can also be an effective behaviour to detect and avoid a terrestrial predator that mainly hunts by ambush, such as the fox.

*Differences according to the sex.* In our experiment differences between sexes in their response to aerial and terrestrial predators were not pronounced: non-anti-predator behaviours (largely maintenance behaviour) were observed to be adopted more frequently by females following the appearance of the dummy raptor (Table II), while males adopted escape to a lesser extent following the appearance of the dummy fox (Table III and Figure 3). Unlike other studies on galliforms, vigilance was not found to differ significantly between males and females (Table II, III). Vigilance was actually suggested to be important in female grey partridges' mate choice, since females, during the breeding season, prefer males displaying vigilance (Dahlgren 1990; Beani & Dessi-Fulgheri 1995), a testosterone-dependent behaviour (Fusani et al. 1997). Females being close

to vigilant males were observed to increase their foraging time at the expense of vigilance (Dahlgren 1990). We could not find clear-cut differences between sexes. This is probably accounted for by the fact that our animals were tested in groups and, unlike in Dahlgren (1990) and Beani and Dessi-Fulgheri (1998), the tests were conducted before the breeding season. In fact, male red-legged partridges belonging to winter groups are less vigilant than those living in pairs (Alvarez et al. 1986). Similarly, white-tailed ptarmigan males are less vigilant when the proportion of males in the population is higher (Artiss & Martin 1995). Like in grey partridge, differences in vigilance between sexes are less pronounced during non-breeding seasons (Dahlgren 1990). Moreover, sex dimorphism is less conspicuous in this species than in other Galliforms, and the male can brood and give parental care to chicks, and this could account for rather symmetrical roles in vigilance between sexes (Green 1984; Casas et al. 2009).

#### Vocalizations

*Differences according to the predator.* Different vocalizations are emitted in response to aerial and terrestrial predators by many galliformes, including red jungle-fowl (Collias 1987), rock partridge (Menzdorf 1977), red-legged partridge (Goodwin 1953), and domestic fowl (Evans et al. 1993). In our experiment, partridges emitted two different alarm calls in response to aerial or terrestrial predator. The alarm calls following the appearance of the terrestrial predator were significantly more frequent than those following the appearance of the aerial predator (Table III), and the highest frequency was significantly higher (Table III). A similar frequency difference was found in the domestic fowl by Evans et al. (1993). Thus partridges not only discriminate between aerial and terrestrial predators, but also are able to tune alarm calls in relation to the context of predation. Thus they could convey to the audience significant information. The continuous production of terrestrial alarm calls presumably amounts to a tonic communication to conspecifics (Schleidt 1973; Owings et al. 1986) as well as a means to signal to the predator a strategy that may deter it from pursuing the prey (Caro 1986, 1995; Hasson 1991; Holley 1993). On the other hand, the low number of vocalizations in response to aerial predators may help keep the animals concealed. Furthermore, low-frequency communication (Table III) may contribute to hide the source of the sound from the predator and broadcast an alarm message, which can be deciphered by conspecifics (Evans et al. 1993).

#### References

- Alvarez F, Braza F, Pinto R. 1986. Diferencia sexual en la vigilancia antipredatoria en la perdiz roja (*Alectoris rufa*). *Ardeola* 33:11–16.
- Artiss T, Hochenckha WM, Martin K. 1999. Female foraging and male vigilance in white-tailed ptarmigan (*Lagopus leucurus*): Opportunism or behavioural coordination? *Behavioral Ecology and Sociobiology* 46:429–434.
- Artiss T, Martin K. 1995. Male vigilance in white-tailed ptarmigan, *Lagopus leucurus*: mate guarding or predator detection? *Animal Behaviour* 49:1249–1258.
- Ashcroft RE. 1976. A function of the pair bond in the common eider. *Wildfowl* 27:101–105.
- Asplund C. 1981. Time-budgets for breeding Mallards in Northern Sweden. *Wildfowl* 32:55–64.
- Beani L, Dessi-Fulgheri F. 1995. Mate choice in the grey partridge, *Perdix perdix*: Role of physical and behavioural male traits. *Animal Behaviour* 49:347–356.
- Beani L, Dessi-Fulgheri F. 1998. Antipredator behaviour of captive Grey partridges (*Perdix perdix*). *Ethology, Ecology & Evolution* 10:185–196.
- Buitron D. 1983. Variability in the responses of Black-billed Magpies to natural predators. *Behaviour* 87:209–236.
- Caro TM. 1986. The functions of stotting in Thompson's gazelles: Some tests of the predictions. *Animal Behaviour* 34:663–684.
- Caro TM. 1995. Pursuit-deterrence revisited. *Trends in Ecology & Evolution* 10:500–503.
- Caro TM. 2005. Antipredator defenses in birds and mammals. Chicago, IL: The University of Chicago Press.
- Casas F, Mougeot F, Viñuela J. 2009. Double-nesting behaviour and sexual differences in breeding success in wild Red-legged Partridge *Alectoris rufa*. *Ibis* 151:743–751.
- Charif RA, Clark CW, Fristrup KM. 2003. Raven 1.1 user's manual. Cornell Laboratory of Ornithology, Ithaca, NY, USA.
- Collias NE. 1987. The vocal repertoire of the red jungle fowl: A spectrographic classification and the code of communication. *Condor* 89:510–524.
- Dahlgren J. 1990. Females choose vigilant males: An experiment with the monogamous grey partridge, *Perdix perdix*. *Animal Behaviour* 39:646–651.
- Dessi-Fulgheri F, Beani L, Piazza R. 1986. Vocalizations of the Grey partridge, *Perdix perdix* (L.). A spectrographic analysis. *Monitore Zoologico Italiano (N.S.)* 20:441–458.
- Evans CS, Evans L, Marler P. 1993. On the meaning of alarm calls: Functional reference in an avian vocal system. *Animal Behaviour* 46:23–38.
- Fusani L, Beani L, Lupo C, Dessi-Fulgheri F. 1997. The sexually-selected vigilance behaviour of the Grey partridge (*Perdix perdix*) is affected by androgen plasma levels. *Animal Behaviour* 54:1013–1018.
- Gaston AJ. 1977. Social behaviour within groups of jungle hblers (*Turdoides striatus*). *Animal Behaviour* 25:828–848.
- Goodwin D. 1953. Observations on voice and behaviour of the red-legged partridge *Alectoris rufa*. *Ibis* 95:581–614.
- Green RE. 1984. Double nesting in Red-legged Partridge, *Alectoris rufa*. *Ibis* 126:332–346.
- Greenhouse SW, Geisser S. 1959. On methods in the analysis of profile data. *Psychometrika* 24:95–111.
- Gyger M, Marler P, Pickert R. 1987. Semantics of an avian alarm call system: The male domestic fowl, *Gallus domesticus*. *Behaviour* 102:15–40.
- Hasson O. 1991. Pursuit-deterrent signals: communication between prey and predator. *Trends in Ecology & Evolution* 6:325–329.

- Holley AJF. 1993. Do brown hares signal to foxes? *Ethology* 94:21–30.
- Jenkins D. 1961. Social behaviour in the Partridge *Perdix perdix*. *Ibis* 103a:155–188.
- Johnsgard PA. 1988. The quails, partridges, and francolins of the world. Oxford: Oxford University Press.
- Lazarus J. 1990. Looking for trouble. *New Scientist* 125:62–65.
- Leavesley AJ., Magrath RD. 2005. Communicating about danger: Urgency alarm calling in bird. *Animal Behaviour* 70:365–373.
- Menzdorf A. 1977. Contribution to the knowledge of the song of Rock partridge. *Beiträge zur Vogelkunde* 23:85–100.
- Owings DH, Hennessy DF, Leger DW, Gladney AB. 1986. Different functions of ‘alarm’ calling for different time scales: A preliminary report on ground squirrels. *Behaviour* 99:101–116.
- Randall JA, McCowan B, Collins KC, Hooper SL, Rogovin K. 2005. Alarm signals of the great gerbil: Acoustic variation by predator context, sex, age, individual, and family group. *Journal of the Acoustical Society of America* 118:2706–2714.
- Schleidt WM. 1973. Tonic communication: continual effects of discrete signs in animal communication signals. *Journal of Theoretical Biology* 42:359–386.
- Searle SR. 1982. Matrix algebra useful for statistics. New York, NY: John Wiley & Sons.
- Templeton CN, Greene E, Davis K. 2005. Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science* 308:1934–1937.
- Zaccaroni M, Ciuffreda M, Paganin M, Beani L. 2007. Does an early aversive experience to humans modify antipredator behaviour in adult Rock partridge? *Ethology Ecology & Evolution* 19:193–200.