

Antipredator strategies and mimicry in red-necked nightjar *Caprimulgus ruficollis*

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Abstract. Red-necked nightjars *Caprimulgus ruficollis* rely its antipredator behaviour mainly on crypsis. However, under high predation risk, they can also perform a more active antipredator behaviour like defensive displays. Defensive strategies in adults and chicks of this species consist of an initial passive stage and a second, optional active stage, which are used depending on the defensive context. The passive stage, based on crypsis, has a low energetic investment and it is performed when the risk to the bird is low. The active stage, based on defensive displays, has a great energetic cost and it is used when the risk is high. Adults may perform two different Distraction-displays (Broken-wing and False-brooding), while chicks that are prior to fledge apparently perform just a kind of Threat-display (Snake-display). Adults performed Threat-display only when they could not fly, for instance, when they have been captured for banding or are injured, a similar context to that of a chick prior to fledge. The Snake-display is composed of several behavioural elements which are sequentially added to the chick's behavioural pattern during its development. This behaviour could be an example of batesian mimicry.

Key words: Antipredator behaviour, Batesian Mimicry, Defensive displays, *Caprimulgus ruficollis*

Resumen. Estrategias antidepredador y mimetismo en el chotacabras pardo, *Caprimulgus ruficollis*. El comportamiento defensivo del chotacabras pardo, *Caprimulgus ruficollis*, se basa en el uso de la cripsis pero cuando el riesgo asumido es muy alto se hace necesario el uso de una estrategia defensiva más activa como, por ejemplo, el uso de despliegues defensivos, patrones comportamentales en los que el ave finge tener una capacidad física inferior a la real (despliegues de distracción) o una capacidad física superior a la real (despliegues de amenaza). En esta especie, las estrategias defensivas de los adultos y de los pollos consisten en una fase inicial pasiva seguida de una más activa, opcional, que depende del riesgo asociado al contexto defensivo. La fase pasiva, basada en la cripsis, supone un gasto energético bajo y se usa cuando el ave afronta una situación de poco riesgo. La fase activa, basada en el uso de despliegues defensivos, supone un gasto energético mayor y se emplea cuando se afronta un riesgo muy alto. Dentro de esta segunda fase, los adultos pueden emplear dos tipos de despliegues de distracción (ala-rotta y falsa-incubación) mientras que los pollos que aún no pueden volar emplean un despliegue de amenaza (despliegue de serpiente). Los adultos emplean el despliegue de amenaza sólo cuando no pueden volar, ya sea por estar heridos o, por ejemplo cuando son capturados para su anillamiento, contextos similares al de un pollo que aún no puede volar. El despliegue de serpiente está formado por una serie de varias pautas que van añadiéndose secuencialmente durante el desarrollo de los pollos. Muchas de estas pautas e incluso parte de la secuencia total se han descrito en varias especies de caprimúlgidos. El gran parecido que este despliegue tiene con el comportamiento defensivo de una serpiente podría disuadir a algunos depredadores y aumentar las probabilidades de supervivencia de los pollos. El comportamiento defensivo de los pollos de caprimúlgidos podría ser un caso de mimetismo batesiano.

Introduction

Distraction-displays have been described in many bird species (Skutch, 1955; Barash, 1975; Gochfeld, 1984; Miller, 1985; Byrkjedal, 1987; Hobson et al., 1988; Burger et al., 1989) and are frequent in caprimulgids (see Bent, 1940; Schlegel, 1969; Cramp, 1985; Fry et al., 1988; Cleere, 1998). There are two different kinds of defensive displays depending on the message that the bird try to send to the predator: 1) Distraction-displays (also called Injury-feigning): the bird feigns a defensive or physical condition lower than the real one expected by the predator, looking hurt or injured, as occurs in Broken-wing-display, a typical example of this kind of behaviour. Generally it is performed by adults when trying to drive off a predator away from the nest. 2) Threat-displays: in this case, the bird feigns a defensive power and aggressive level higher than the real one. It is used by chicks and young that have not reached the ability to escape.

In red-necked nightjar, *Caprimulgus ruficollis*, egg and chicks protection depend on its cryptic coloration and on parents ability to drive off predators, as occur in other ground nester and cryptic bird species (Ristau, 1991, 1993). In these birds, defensive displays seem to be an alternative defensive system (see Gochfeld, 1984).

Here we describe different antipredator strategies and defensive displays performed by red-necked nightjar under different risk and defensive contexts. Defensive displays of the young seem to be a good example of Batesian mimicry.

Methods

Literature on red-necked nightjar is very scarce, mainly due to its cryptic behaviour, nocturnal habits and a rather restricted breeding range. However, in recent years the information available on this species is increasing (Tomás, 1991; Copete & Gustamante, 1992; Gargallo, 1994; Forero et al., 1995; Cuadrado & Domínguez, 1996; Aragonés 1997a; Aragonés et al., in press). Red-necked nightjar does not construct a nest and eggs are laid on the ground or on the leaf litter. Incubation spans about 16-17 days and young start to be mobiles when they are a few days old. Fledging takes place at 16-18 days old and after 4-5 weeks birds became independent (see Cramp, 1985; Cleere, 1998).

We studied the antipredator behaviour of red-necked nightjar during the breeding season of 1994 and 1995 (early May to September) in two nearby areas (the closest spots between both are only separated by around 750 m) located in Córdoba, Southern Spain. Part of the study area was characterised by a high density of trees (*Quercus rotundifolia*) and bushes (mainly *Q. coccifera*, *Pistacia lentiscus*, *Mirtus communis*, *Chamaerops humilis* and *Crataegus monogyna*), whereas crops (sunflower and wheat) covered the rest of the study area. We intensively explored both areas to locate all breeding pairs by monitoring the singing males and by diurnal and nocturnal observations of individuals. We located 26 nests that were visited each four days from laying to fledging. At each nest, we recorded age of the chicks and defensive response performed by adults and chicks as a response to our presence, a methodology widely employed in this kind of researches (see Burger et al., 1989; Byrkjedal, 1989; Redondo & Carranza, 1989; Westmoreland, 1989; Brunton, 1990; Forbes et al., 1994). Detailed descriptions and

photographs of the different defensive behaviours were also taken. Typical nest predators of red-necked nightjar on this area are *Lacerta lepida*, *Rattus* spp, *Elyomis quercinus*, *Vulpes vulpes* and *Elaphe scalaris*.

The visits were done from dawn to dusk, avoiding the hottest hours of the Mediterranean summer to minimise harms to the nests. We think that the presence of the researcher close to a nest does not have influence on other neighbouring nests since the flushing distance in this species is very short (see Alvarez et al., 1984), specially in the case of adult birds at nest (Aragonés, 1997a).

Results

Some behaviours were displayed by both adults and chicks, while others were exclusive of one age class. Behaviours have been ordered in the sequence of appearance, which is related to risk taking and age, from a basic resting behaviour in which, apparently the bird shows no alertness because the risk of being preyed is very low, to a behaviour involving maximum risk and alertness.

Adult and fledgling behaviour

1. - Motionless (fig. 1): To keep still on the ground keeping a relaxed position with the head up and the eyes closed. Context: This is the resting position, in the nest or out of the nest, when the observer is located at a distance equal or higher than 10 m from the nest.

2. - Flattened-posture (fig. 1, see "Cigar-posture" in Cramp, 1985): To keep still and crouched on the ground with the head extended horizontally downwards and the eyes slightly open. Context: When the distance of the predator to the nest or the resting bird is so close than the risk is very high. The increasing risk is related to distance and it is the factor that makes the bird change its defensive behaviour from Motionless to Flattened-posture. This change is addressed to increase crypsis through shape and shadows dilution against the background (Cott, 1985).

3. - Fly-away: To escape flying. Context: Once the flushing distance is exceeded, while the bird is on the nest or resting out of the nest.

4. - Threat-display: To threat with the bill open, showing the red mouth, and hissing loudly. During this display, the eyes are fully opened while wings and tail are extended and sometimes fluttered against the ground. Context: Only in birds, adults or chicks, captured for banding or measuring, when they are not able to Fly-away.

Adults in the nest

5. - Passing-flights: Approach flights very close over the observer. The conspicuoussness of this flights may be enhanced sometimes with Butterfly-flights (see Cramp, 1985) in which the conspicuous wing and tail bands are shown to the receiver of the message. Context: This behaviour is performed only by adults flushed from the eggs or chicks.

6. - Broken-wing-display (fig. 1): To feign injury through abnormal flights, falls to the ground and spasmodic movements with tail and wings extended over the ground. The head is raised and the opened eyes directed to the observer. The intention is to drive off the predator's attention

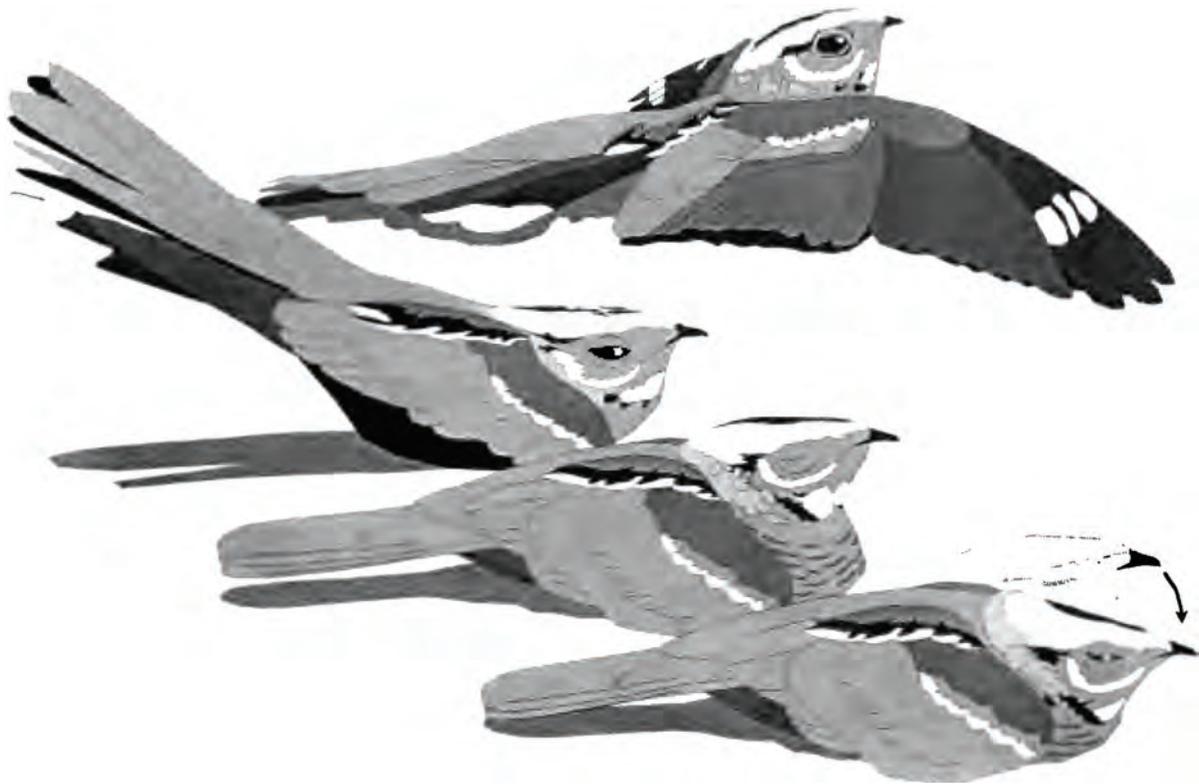


Figure 1. Defensive behaviour of adults. Active measures: Broken-wing (top right) and false-brooding (top left) displays. Passive measures: Motionless (centre) and Flattened-posture (down right).

away from the nest. Context: Performed only by adults flushed from the nest during chick stage.

7. - False-brooding (fig. 1): To land on the ground, after flushed from the nest, and to make movements similar to that of nest accommodation. Following this false accommodation to the nest, the bird closes its eyes and changes its behaviour to Flattened-posture. Context: Performed by adults flushed from the nest during chick stage and sometimes mixed with Broken-wing-display. This behaviour suggests the existence of a nest in a point where there is not a nest and the intention is to drive off the predator away as also occurs in Charadriiformes (Gochfeld, 1984).

Chicks in the nest

8. - Snake-display (fig. 2): This behaviour is a sequence of several behavioural elements, but the sequence is not always complete. In fact this behavioural elements may be found isolated or following the sequence. Context: Performed by the chicks when the hand of the observer is going to touch it or just prior to being touched.

The Snake-display includes the following behavioural elements: a) Threat (see Threat-display). Also included in Snake-display as an element of its behavioural sequence. Early on their development, the chicks do not rise the head and keep the eyes closed but when they grow up, the head is raised while the eyes and the mouth are fully opened. b) Hissing: To produce loudly sounds, which resembles the hissing of a snake. May be performed jointly with Threat. c) Strike: To strike towards the observer from a standing position with mouth fully open, sometimes with the wings extended

vertically. From this position the head may be shot forward and be as rapidly pulled back in readiness for the next strike, in a similar way as snakes do. d) Up-and-down: To rise up and down the body, stretching the neck and legs slowly. When this display is performed, the chicks look similar to a hissing, vibrant and coiling snake ready to strike. (see Cramp, 1985 for Gaping-threat-display in European nightjar, *C. europaeus*)

9. - Run-away (fig. 2): To running away from the observer with the wings occasionally raised vertically over the back. Context: It has been observed only when the bird has performed the Snake-display or one of its behavioural elements.

We recorded the order of appearance of the behavioural elements in 21 nests in which we found three different sequences (fig. 3). Considering the behavioural elements as isolated units, the more frequent were Motionless, Flattened-posture, Threat, Hissing, Strike and Run-away, which were performed in all of the 21 nests. Strike was recorded in 20 of the nests (95.24 %) and last, Up-and-down, performed only in nine of the nests (42.86%). Once the flying ability is reached the defensive behaviour used by chicks was always Fly-away, the most typical defensive strategy of the off-duty adults.

Defensive strategies

The occurrence of the different defensive strategies (Table 1) depended on the defensive context and the age of the performer. We observed defensive situations or observer's approaching (n=377) in which in 98% of cases there was an initial passive or cryptic stage followed by another active or conspicuous stage. The passive/cryptic stage (to keep

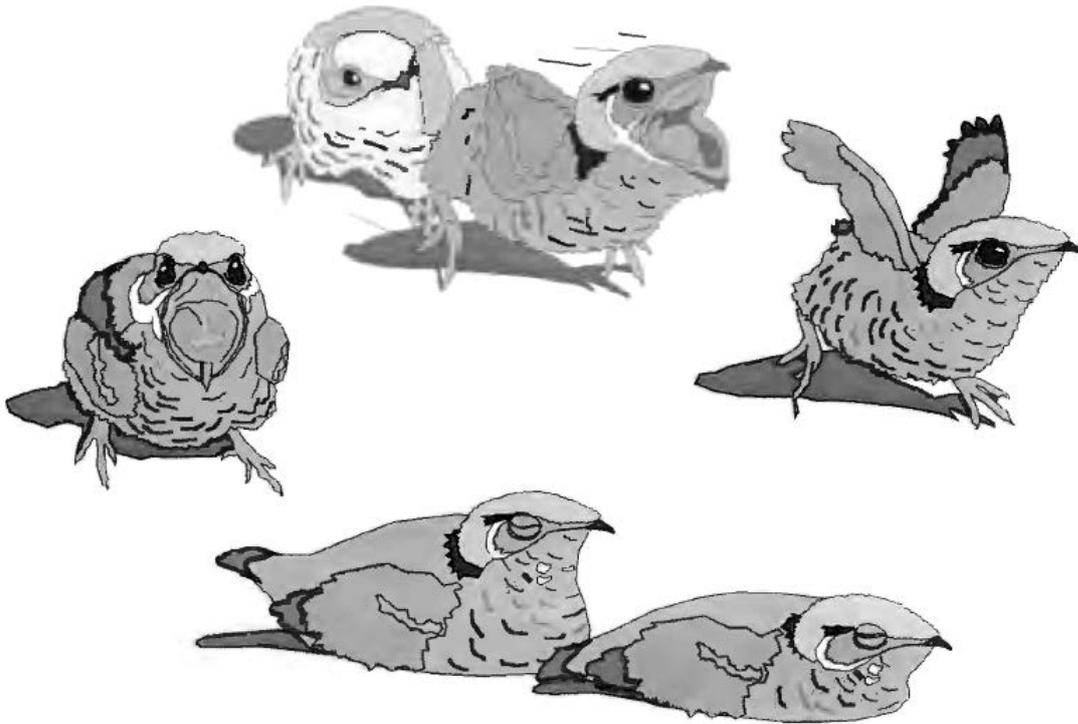


Figure 2. Defensive behaviour of chicks. Active measures: Threat (top left), Strike (top centre) and Run-away (top right). Passive measures: Motionless (down left) and Flattened-posture (down right).

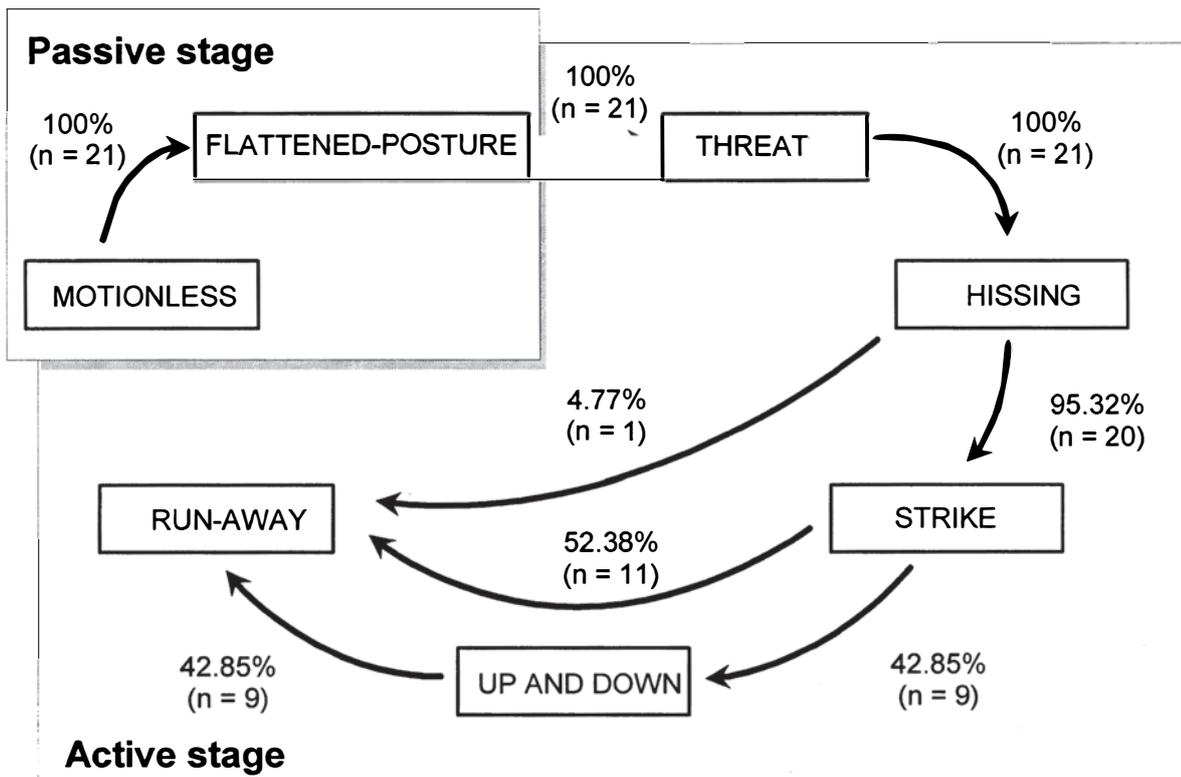


Figure 3. Appearance sequence of defensive behaviour in chicks (n=21 nest). The snake display included the following behaviours: Threat, Hissing, Strike and Up-and-down, the order of appearance of the behavioural elements. When chicks reach flying ability the defensive response was Fly-away in all cases.

Table 1. Defensive strategies following a sequence of age and context. (+) denotes that the bird has the physical ability to perform that behaviour but it was never observed performing it and (-) denotes that the bird does not have physical ability to perform that behaviour, for instance, chicks do not perform the strategy "Crypsis vs Fly-away" since they can not fly.

Defensive strategy	Age and context			
	chicks at nest	fledgings	off-duty adults	Adults at nest
Passive stage 1 vs active stage	n (%)	n (%)	n (%)	n (%)
Crypsis vs Snake-display	86.60 (70)	+	+	+
Crypsis vs Fly-away		100 (25)	100(112)	21.90 (35)
Crypsis vs Passing-flights		+	+	17.40 (28)
Crypsis vs Broken-wing		+	+	60.70 (98)
Crypsis vs none	13.40 (9)	+	+	+
Total	100 (79)	100 (25)	100 (112)	100(161)

¹ Passive stage: in this initial stage the defensive behaviour is always crypsis (Motionless and Flattened-posture).

Motionless and Flattened-posture) is similar for all the contexts and all the individuals while the active/conspicuous stage (defensive displays) could involve different combinations of the behavioural elements: Fly-away, Passing-flights and Broken-wing or False-brooding displays.

Depending on risk taking, adults in nest relied their defensive strategy on passive/cryptic measures when the predation risk was low or on active/conspicuous measures (Broken-wing or False-brooding displays) when the predation risk was high. Off-duty adults performed passive defence when the predation risk was low but when the risk increased they Flew-away. This is the typical defensive strategy out of the breeding season.

The chicks on nest relied its defence on cryptic measures (Motionless and Flattened-posture) if the risk of being preyed was low but they performed and active, conspicuous strategy (Snake-display) when the risk increased. Once the flying ability was reached, the defensive strategy was the same as off-duty adults.

Discussion

The defensive behaviour and the different behavioural elements are very similar to those described for other caprimulgids (Bent, 1940; Cramp, 1985; Fry et al., 1988; Cleere, 1998). All the defensive strategies are a combination of low and high risk behaviours as occurs in other semiprecocious ground nesters (Byrk-jedal, 1989; Brunton, 1990; Aragonés, 1997b). In fact most of caprimulgids perform defensive strategies based on initial passive measures and, if the defensive context requires it, active measured (Cleere, 1998).

If predation risk reaches a high level, adults changed from Motionless to Flattened-posture (see Bent, 1940; Reynolds, 1968; Steyn, 1971; Langley, 1984; Cramp, 1985; Fry et al., 1988; Cleere, 1998). If risk reaches a very high level there are two options, off-duty birds just fly away but adults at nest (and also injured or captured birds) may perform two kind of defensive displays:

1) Threat-display. Our results agree with those found by Sick (1993) who noted that this behaviour is performed only

by adults when handled or when are unable to Fly-away. On the other hand, Cramp (1985) cited an injured red-necked nightjar performing Threat-display but noted that in European nightjar, the performance of Threat-display does not rely on capture, handling or damage. Cleere (1998) cited that Threat-display occurs in many species as a defensive measure both in injured and non-injured birds. Threat-display has been also cited in the common poorwill, *P. nuttallii* (Aldrich, 1935), the lesser nighthawk, *Ch. acutipennis* (Pickwell & Smith, 1938) and the common nighthawk, *Ch. minor* (Gramza, 1967). Recently Cleere (1998) reviewed the published information on caprimulgids and concluded that Threat-display is very common in most of the species and may occur in other, least known species. In the case of the common poorwill, Threat-display may also be addressed to small birds (Orr, 1948).

2) Distraction-display (two types). Broken-wing: Widely described in caprimulgids (Aldrich, 1935; Bent, 1940; Langley, 1984; Cramp, 1985; Marchant, 1987; Fry et al., 1988; Aragonés, 1997a; Cleere, 1998). False-brooding: Ingels & Ribot (1983) and Roth (1985) cited for the blackish nightjar, *C. nigrescens*, a behaviour that would be interpreted as False-brooding. When flushed, blackish nightjars change their defence from Flattened-posture to a more raised position, with eyes fully opened, raising and falling the tail and the posterior part of the body helping to do it with its legs. This behaviour resembles exaggerated nest accommodation movements, and could address predator attention away from the real nest.

The initial defensive response in chicks and fledging is, as occurs in adults, Motionless and Flattened-posture, but if risk increases they may perform a more active defence like Snake-display. Some behavioural elements of the Snake-display have been described in the chicks of several species (Cleere, 1998), though many other could perform the complete sequence. Last, and additionally to Snake-display, the chicks may Run-away from nest and/or acquire Flattened-posture (Lack, 1929; Pickwell & Smith, 1938; Marchant, 1987; Cleere, 1998). The behavioural elements of the Snake-display appears progressively during chick development forming an ordered sequence: Fly-away, Hissing, Strike and

Up-and-down.

Batesian mimicry?

The Snake-display of red-necked nightjar chicks has common elements, both visual and sonographic, with a Threat-display performed by the sympatric ladder snake *Elaphe scalaris*. When threatened, this snake hiss loudly, open its mouth showing the red throat and strike with vibrant, coiling movements (Aragónés, 1997a) in a similar way than nightjar chicks do. However, this is a typical advertising behaviour of many other snakes, some of them poisonous, through the world and nightjar chicks could benefit from the mimicry with the snake advertisement behaviour providing acoustic and visual warning to predators that threaten them.

Acoustic mimicry has been described in the Threat-displays performed by several bird species (Bent, 1940; Sibley, 1955; Coulombe, 1971; Martin, 1973; Burton, 1973; Cramp, 1985; Rowe et al., 1986; Fry et al., 1988). The hissing sounds produced when threatened at the burrow by owlets of the burrowing owl, *Speotyto cunicularia*, closely resembles the hissing of a dangerous rattlesnake, *Crotalus* spp. (Bent, 1940; Ginn, 1973; Martin, 1973; Rowe et al., 1986). In fact, the hissing of both species is similar in its sonographic features (Martin, 1973) and owlets may increase its survival probability by the performance of such an imitation to deter predators. In the case of nightjars, the imitation is enhanced performing coiling and «reptile-like» movements, increasing the effectiveness of the display.

We really do not know the influence of the Snake-display on chick's survival but we have evidences to suspect that nightjar chicks benefit from the performance of such a display. From the point of view of an opportunist predator, there are three kind of snakes: innocuous, poisonous and innocuous that closely resemble the poisonous ones. Therefore whatever their look or size, snakes are risky animals because the probability of misleading is high. In the study area the poisonous snud-nosed viper, *Vipera latastei*, and the innocuous viperine snake, *Natrix maura*, are sympatric species of red-necked nightjar and the second one closely resembles the dangerous viper (see also the North American, innocuous, *Natrix sipedon*, which resembles the poisonous water moccasin, *Agkistrodon piscivorus*). A non-specialised nest predator, which is not able of correct snake discrimination, faces a risky dilemma: to consider innocuous a poisonous snake or to consider poisonous an innocuous one. A mistake in the first case could imply death or serious injuries, while a wrong decision in the second case could imply just the lost of a prey. Obviously is best to do not prey on an uncertain snake than lost a prey. We conclude that nightjar chicks could benefit from this predator's dilemma by performing the Snake-display.

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