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Risk taking and flushing distance: a way of parental investment in the pauraque (*Nyctidromus albicollis*)

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ABSTRACT: *Risk talking and flushing distance: a way of parental investment in the pauraque* (Nyctidromus albicollis). We studied the antipredator behaviour of a population of pauraque (*Nyctidromus albicollis*), one of the commonest neotropical nightjars, at Parque Nacional de Yasuní (Ecuador) as a mechanism of parental investment. We located two nests and ten diurnal resting-spots during incubation , which were revisited ten and 29 times respectively (mean = 5 visits/nest and 2.9 visits/resting spot). We recorded antipredator response and risk assumed by parents at nest to the approach of a human observer. We considered the response to the observer as a response against a predator. As a control, we compared the response given by adults at nest with the response given by adults at resting spot. Our results show that risk assumed by adults at nest is higher than risk assumed at resting-spot, and suggest an increase in risk assumed by adults at nest along the reproductive season. We think that this increasing risk could be not due to nest revisitation, but to an increase in reproductive value of the nest. Some observations of antipredator behaviour of *N. albicollis* are also described.

KEY-WORDS: Parental investment, risk taking, nest-defense, flushing distance, *Nyctidromus albicollis*.

Introduction

A great number of ground nesting birds base their defence when the approach of a predator takes place on the combination of two alternative strategies to which we will refer to as passive and active. These birds change from a passive to an active strategy when a minimum distance of approach is reached (Aragonés, 1997). The passive strategy consists of two part: 1) staying both still and camouflaged untill risk level is very high, and 2) flush away. The active strategy consist in two parts yet: 1) staying both still and camouflaged untill risk level is very high, and 2) strike-out flight or even make use of defensive displays (Gochfeld, 1984; Byrkjedal, 1989, 1991; Brunton, 1990; Hume, 1996; Piersma, 1996; Aragonés, 1997). Crypsis is one of the most effective anti-predator behaviours (Baker & Parker, 1979; Endler, 1982) and provides an adequate defence at a very low energetic cost. On the other hand, defensive displays imply a higher risk and a greater cost/effort, but the risk can be compensated if the investment which is defended is high enough (i. e. regarding the development of the chicks).

Caprimulgids are a good example of the effectiveness of this kind of defence as they are both highly cryptic and ground nesters. On other species that have been studied up to now, it has been already proved the existence of an alternative defensive behaviour to the cryptic one (Bent,1940; Cramp, 1985; Fry et al., 1988). It has been found that some other species of caprimulgids and charadriiformes use one or another kind of defence depending on the context in which the encounter between the predator and the prey takes place (Brunton, 1990). The individuals that are not attending the nest (off-duty parents) use the pasive strategy, but while attending the nest, adults can use a passive or an active strategy. Regarding other caprimulgids, the use of one alternative or the other depends on the reproductive stage (red-necked nightjar, *Caprimulgus ruficollis*, Aragonés, 1997). During the incubating period, the adults at the nest make use of a passive strategy, in which they fly away or carry out strike-out flights on the predator as an alternative to crypsis, but after hatching, the active strategy is used.

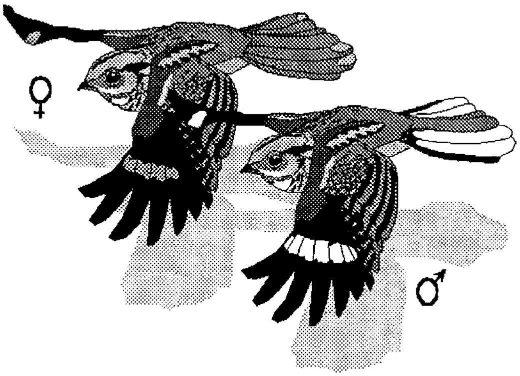

Figure 1. Sexual dimorphism is strong in N. albicollis, with a higher conspicuousness in males, which present a bigger white wing-band and a black-and-white longitudinal desing on the tail that is almost non-existent in females, whereas the wing-band is dun in females. (Line draw, J. Aragonés). [El dimorfismo sexual es muy marcado en *N. albicollis* con una mayor conspicuidad en los machos que presentan una banda alar mayor que las hembras así como un diseño caudal blanquinegro muy patente, que no aparece en las hembras. En las hembras, las bandas alares son más pequeñas y de color parduzco. (Dibujo, J. Aragonés).]

In the pauraque -a neotropical nightjar of about 28-30 cm lenght- as in most of the caprimulgids, the nest defence rely on the cryptic coloration of eggs, chicks and adults. Besides this, predators are kept away from the nests by means of defensive displays from the adults and also the chicks (Aragonés, 1997). *N. albicollis* nests and rests on the ground, which means that the approach of a predator (in this case, a human observer) implies a risk for the adult and for its reproductive investment. This risk is different depending on the context in which the bird is, that is, whether it is at the diurnal resting spot or whether it is at the nest.

Here we study the defensive behaviour of N. albicollis according to sex and the context in which the encounter predator-prey takes place (adults at resting-spot or attending the nest).

Methods

Studied species.

N. albicollis is one of the most extended caprimulgids throughout Central and South America, covering a range that goes from Mexico and southern Texas to Perú and nothern Argentina (Howell & Webb, 1995). This species is very common in tropical lowlands, where it occupies a wide range of habitats that vary from rainforest to semi-arid areas, apart from secondary growth, bushland and edges of open and semi-open areas (Haverschmidt, 1968; Hilty & Brown, 1986; Fjeldsa & Krabbe, 1990; Howell & Webb; 1995). Even though the morphology of this species is that of a forestal bird -short wings and a very long tail-, pauraques feed mainly in clearings or above the top of trees, that is, always choosing open areas. On the contrary, it can be found in dense vegatación areas during the day (Wetmore, 1968; Styles & Skutch, 1989; Aragonés, pers. obs.). This species presents a distinctive sexual dimorphism that can only be noticed when flying, when the wings and tail are open. Males have a broad white wing-band that cross over the five otermost primaries and a very conspicuouss, black-and-white longitudinal design in tail. Females present a less conspicuouss wing-band both in size and colour, furthermore, females do not have in the tail the distinctive tail design (fig. 1). Both males and females have a white gular spot which is, aparently, more conspicuouss in males. The singing of the pauraque, from which different onomatopoeic names are derived - such as cuiejo, buhío, vieja or bruja- can be clearly distinguished and it consists of the continuous repetition of a strong and lightly explosive "cuihoo", sometimes preceded by one or more "chucks": "cuc, cuc, cuc..., cuihooo..." (Hilty & Brown, 1986; Hardy et al., 1989; Howell & Webb, 1995). The word "chuck" has an anglosaxon origin and it is frequently used in papers on caprimulgids to describe the singing (see Bent, 1940; Cramp, 1985). Moreover, it has even been used to name some species, for instance, chuck´s-will-widow, *C. carolinensis*.

Study area.

In September 1995, we carried out a research on *N. albicollis* in Parque Nacional de Yasuní (Amazonia Ecuatoriana), which is located NE of Quito and S of the Napo river. The study area was located in the rainforest at Estación Biológica de Yasuní (EBY) on the bank of the river Tiputini - which is tributary to the Amazonas through the Napo. The mean altitude is below 500 m, and has an annual mean precipitation of about 3500 mm, as well as a temperature that oscillate between 29° and 33° C during daylight hours and between 20° and 24° C at night. The annual variation of temperature is just around four degrees. The area has a typically amazonic vegetation, being abundant the epiphyts (Bromeliaceae, Orchidaceae), palms (Palmaceae), arborescent ferns (Cyatheaceae) and about 2000 tree species (Cecropiaceae, Bombacaceae, etc.). Faunal composition presents the characteristic elements of the Amazon Basin such as arrow-frogs (Dendrobatidae), pirarucú (*Arapaima gigas*), piranhas (Serrasalmidae), jaguar (*Felis onca*), amazonic river dolphin (*Inia geoffreyensis*), harpy eagle (*Hapia harpyja*), macaws (*Ara ararauna*, *A. chloroptera*, *A. macao*), potoos (*Nyctibius grandis*, *N. aethereus*), hummingbirds (Trochilidae) and toucans (*Ramphastos spp*, *Pteroglossus spp*).

In order to look for the nests and the resting-spots of the N. albicollis, we carried out diurnal transects following the paths already delimitted at EBY. We registered the number of detected individuals, sex (whenever this was possible), their exact location and their defensive behaviour. Each time a resting-spot (hereafter resting-spot) or nest was found, we proceeded to a systematic search for a pair or a nearby nest within a radius of around 20-30m.

In order to see if sex of birds coud be determined visually, we carried out a nocturnal test based on playback calls. At night, with the help of a frontal light (PETZL), and a tape recording of *N. albicollis* singing (Hardy et al., 1989), we proceeded to take photographs and determine visually the sex of 12 individuals that approached the tape recording. From the comparison of the results of the visual observations and the photographs (due to problems with the quality of photographs just nine shots were taken into account), a 100 % concordance between both methods was established.

Nest defence and flushing distance.

During the incubating period, the defensive response on adults was measured every time the approach of the observer took place, which is a methodology that has been used by other authors (Simmons, 1955; Burger et al., 1989; Byrkjedal, 1989; Redondo & Carranza, 1989; Westmoreland, 1989; Brunton, 1990; Forbes et al., 1994). In other researches that implied repeated visits or nest revisitation, it has been pointed out that pseudoreplication exists (Westmoreland, 1989). We have opted for assuming the independence of the data coming from the different visits to the same nest, in spite of the statistical problems derived from that (see discussion in Winer,1971; and in Geisser & Greenhouse, 1985).

We took into account the folloing variables: Kind of individual depending on the context: adults attending the nest and adults at the resting-spots, away from the nest. Sex of each individual. Number of visits. Flushing distance (in cm): minimum distance in which an adult alters its cryptic behaviour in the presence of an observer and therefore, it changes to other type of defensive strategy.

Additionally, we registered the frequency of the next behaviours: Strike-out flights, or flights approaching the observer at a short distance (as well as the number of individuals that did it); Flying away from the observer without carrying out any other kind of defence regarding the nest and the diurnal resting-spot; Broken wing display, or injury feigning behaviour which attract the attention of the observer (see Gochfeld, 1984; Ristau, 1993) just to make him move away from the nest.

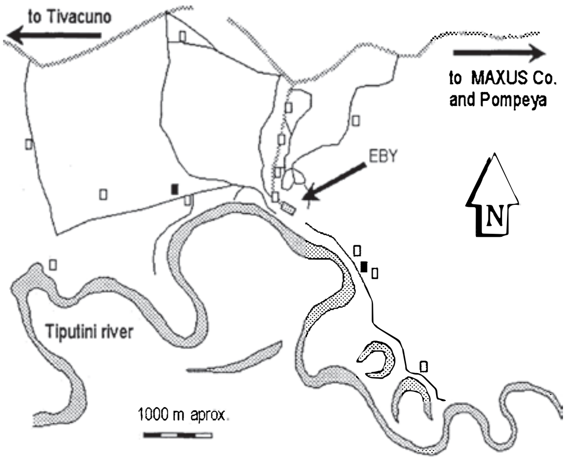

Figure 2: Study area site and location of nests (filled squares) and resting-spots (open squares). The thin lines show the paths of the rainforest and the thick ones represent dirt roads that have not been asphalt-coated. [Area de estudio y localización de los nidos (cuadrados negros) y los posaderos (cuadrados blancos). Las líneas finas representan senderos en la selva, y la línea gruesa de color gris representa carreteras de tierra, sin asfaltar.]

The resting and incubating positions are very similar in all caprimulgids and boths take place on the ground. This similitude makes the behaviour on the diurnal resting-spots an excellent way to control the behaviour of adults attending the nest, in fact, both are only differenciated by the presence or absence of eggs or chicks. Likewise, the differences in behaviour are going to be related to the parental inversion.

The data does not fit a normal distribution so we apply non-parametric statistics: Kruskall-Wallis test for mean comparisons and Spearman correlation to study the effect of the number of visits on the defensive behaviour. All statistiscs are two tailed, with a significance level of < 0.05.

Results

We located ten diurnal resting-spots and two nests (fig. 2). During some of the visits to the nests, as well as during some of the visits to the diurnal resting-spots (Table I), we could observe the bird for a short period of time before flushing. In these cases, the birds changed from a position in which the body is stretched and the head is putting down, giving the impression of being flattened against the ground (see "cigar-posture" in *C. europaeus*, Cramp, 1985). This kind of response seems to be similar in the diurnal resting-spots and in the nests (Table I). As long as the observer did not surpass the minimum flushing distance, the birds kept their eyes almost closed, just with a small aperture. After flushing, and once a minimum distance is surpassed, the eyes were widely open (this has been observed during nine visits to the nests and 11 to the resting-spots). In the case of the nests, adults kept the observer inside their field of vision, sometimes turning their head to control the position and movements of the observer.

Table I. Defensive behaviour of *N. albicollis* observed before and after flushing from the nest or the resting-spot, due to the approach of an observer. At the nest, there is a higher percentage of observations before the flushing than at resting-spot, which indicates a higher risk taken by adults in nests. [Pautas defensivas de N. albicollis observadas antes y después de ser levantado del nido o del posadero debido al acercamiento del observador. En el nido hay un porcentaje mayor de observaciones antes de ser levantados que en el posadero, lo que indica un mayor riesgo asumido por los adultos en nido.]

	nests (n = 2)	resting spots (n = 10)
Visits number (mean), range	10 (5), -	29 (2.9), 1-5
Before flushing observations % (n)	80 (8)	31.3 (9)
Stretching[a] % (n)	87.5 (7)	77.7 (7)
After flushing observations % (n)	100 (10)	100 (29)
Fly away % (n)	20 (2)	100 (10)
Strike-out flights % (n)	30 (3)	0 (10)
Broken wing display % (n)	20 (2)	0 (10)

[a] see "cigar-posture" described in Cramp, 1985.

Flushing distance and nest defence

There are differences regarding the flushing distance between adults at a nest and adults at a diurnal resting-spot (H = 18.63, df = 1, n = 39, P < 0.001). The first ones present a mean flushing distance of 630 cm (sd =129.53, n = 10) whereas adults at a resting-spot fly away a longer distance (mean distance = 889.65 cm, sd = 91.98, n = 29). We could not establish differences with respect to sex, due to the fact that the data of the adults attending the nest did not allow this comparison. However this comparison was possible with adults at resting-spots, showing no differences between male and female flushing distance (H = 0.005, df = 1, n = 29, P = 0.982).

The birds at resting-spots did not vary the flushing distance when the number of visits increased (H = 1.07, df = 4, n = 29, P = 0.898; rs = -0.004, P = 0.979), that is, when the reproductive season advance, as the number of visits and the reproductive season are strongly correlated (Redondo & Carranza, 1989). The adults at the nest showed a tendency to decrease the flushing distance when the number of visits increased (rs = -0.78, P = 0.007), but the differences were not significant (H = 6.25, df = 4, n = 10, P = 0.181).

The adults at the resting-spot just flew away in every case and they never carried out strike-out flights or broken wing displays towards the observer (Table I). In the case of the adults that were in the nests, the flew away only took place in just two visits, whereas the individuals stopped near the observer during the other eight visits, sometimes carrying out strike-out flights (Table I) that were always carried out by one individual only. The broken wing display was only observed in two occasions (at the same nest) and in both cases the adult that did it was a female.

Discussion

During the incubating period, the antipredator behaviour of *N. albicollis* is similar to the one described for the caprimulgids (Bent, 1940; Tomkins, 1942; Gramza, 1967; Alayón, 1985; Cramp, 1985; Fry et al., 1988; Vilella, 1995; Aragonés, 1997), and it is fairly similar to that of other cryptic species that nest on the ground (Gochfeld, 1984; Brunton, 1990; Piersma, 1996). In the occasions that we could observe an individual after flushing from the nest -whether carrying out broken wing displays or not- we could see how the bird turned its head whenever necessary in order to keep visual contact with the observer, as it happens with Chordeiles minor (Gramza, 1967), C. ruficollis (Aragonés, 1997), Charadrius wilsonia and Ch. melodus (Ristau, 1993).

When the approach of a predator (in this case, the observer) takes place, the adults at the nest resist an even shorter proximity than at resting-spot. Due to its cryptic coloration, the flushing distance in caprimulgids does not have to correspond to the distance to which the predator could detect them, at least from a visual point of view. Therefore, when they flush, it is not necessarily because they have been seen by a predator (Aragonés, pers. obs.). The animals that predate on ground-nester birds find nests when they approach enough to smell them or when an adult flies away (Forbes et al., 1994), since it is a higher risk for the adult and the nest to stay in the nest when a potential predator is approaching. On the other hand, if they flush too soon, the risk for the adult is minimum, although the risk for the nest is higher, in fact, some predators learn how to use this sign as a nest searching methods (see Sordhal 1990). When at the nest, keeping a shorter flushing distance tha at the resting-spot is something dangerous for the adult, however, keeping the same flushing distance at nest and at resting-spot is an enormous risk for the nest. This is the reason why the defensive response is highly influenced by the balance between adult's own risk and the danger of the nest. Obviously, the higher the value of the brood is, the greater the compensation they get when taking risks, and the shorter the flushing distance can be.

As reproductive season goes by, the risk taken by adults at nest increase, which can be due to both the increasing brood value or to the effect of the revisitation (Knight & Temple 1986a, b, and c). If the effect of resivisitation has as a result a shorter flushing distance, we would expect to find a similar effect at the resting-spots, however, this is not the case. The adults that are at the resting-spot keep a constant flushing distance along time and they are not affected by the number of visits, which means that they are not affected by the time of the reproductive season of the reproductive season. This fact makes us think that the higher risk taken by the adults at nests -whenever the number of visits increase or the reproductive season advances- is due to the fact that the value of the investment is continuously increasing and this compensates for the higher risk to defend it. Even if the adults risked less at the resting-spots than at the nests, in the second case did not deffend the nest intensely using other kinds of defense such as the broken wing display or the strikes, as both kinds of behaviour were observed in few occasions. This can be due to the small number of nests that have been controlled or to he fact that the investment during the period of incubation is so low that it does not compensate for other risks such as strikes-out flights and broken wing displays. If we compare this defensive response with the one carried out by *C. ruficollis* - which is very similar to the one described here (Aragonés, 1997)- we can observe that this species do not make use of the broken wing display during the incubating period and that strike-out flights are more intense just before hatching. In *C. ruficollis* there is an increase in risk taking by adults regarding increase of brood value, which agreed with pattern of risk taking by *N. albicollis*.

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Resumen

En el Parque Nacional de Yasuní (Ecuador) estudiamos el comportamiento defensivo y el riesgo asumido en la defensa por los adultos de pauraque (*Nyctidromus albicollis*) como una forma de inversión parental. Durante la fase de incubación encontramos dos nidos y diez posaderos diurnos, que fueron revisitados en diez y 29 ocasiones respectivamente (una media de 5 visitas/nido y 2.9 visitas/posadero). Se registró el comportamiento defensivo y el riesgo asumido por los adultos en el nido ante la aproximación de un observador humano, considerando la respuesta obtenida como una respuesta antidepredatoria. Como control, comparamos esta respuesta con la dad por los adultos en los posaderos. Nuestros resultados indican que se asume un mayor riesgo en el nido que en el posadero, y sugieren que a medida que avanza la estación reproductora existe un incremento en el riesgo asumido. Pensamos que este incremento no es debido a un efecto de la revisitación, sino a un incremento en el valor de la inversión que se defiende. Adicionalmente, se describen algunas observaciones sobre el comportamiento antidepredador de *N. albicollis*.

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