



Original article

Nest-climatic factors affect the abundance of biting flies and their effects on nestling condition

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ARTICLE INFO

Article history:

Received in revised form

21 June 2010

Accepted 5 July 2010

Available online 30 August 2010

Keywords:

Biting midge *Culicoides*

Black flies

Ficedula hypoleuca

Host–parasite interactions

Temperature

Vectors

ABSTRACT

The first step in the establishment of a host–biting fly relationship is host location. While a number of studies highlight the role of host emitted products as important cues affecting host location by biting flies, the role of host temperature is far from clear. We investigated the role of different nest microclimatic variables affecting the interaction between pied flycatchers and two biting flies: black flies and biting midges. Biting midge abundances increased with temperature inside the nest, supporting the potential importance of nest temperature as a cue used by insects to localize their hosts. The possibility that biting fly infestations were associated to ecological conditions in the vicinity of the nests is also discussed. Furthermore, we found a negative association between nestling weight (including tarsus length as a covariate in the analyses) and the interaction between the abundance of biting midges and the presence/absence of black flies in nests. The potential negative effect of these ectoparasites on nestling weight (condition index) and potential differences in the bird phenotypic/genetic quality associated with nest site choice and parasite infestations are considered.

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1. Introduction

Location of the hosts by biting flies is a complex and active behavioural task that enhances the probability of contact of haematophagous insects with their hosts (Sutcliffe, 1986). This behaviour could be divided into three phases: (i) appetitive searching, (ii) activation and orientation and (iii) attraction (Lehane, 2005), although the definition of these phases could vary between authors (Kettle, 1995). In addition to vision and smell, other stimuli including heat and humidity become available to the insect in close proximity to their hosts and are also involved in the biting flies' host-seeking behaviour (Gatehouse and Lewis, 1973).

Biting insects may respond to the heat emitted by the host or to the thermal gradient between insects and hosts (Lehane, 2005). There are clear evidences for the role of thermoreceptors of blood-sucking arthropods in responses to thermal stimuli related to the presence of their hosts (Howlett, 1910; Nigam and Ward, 1991; Guerenstein and Lazzari, 2009). However, the importance of host temperature or humidity on host location is far from clear for the

vast majority of blood-sucking insects, in contrast to the well-known role of chemical cues (Guerenstein and Lazzari, 2009). In the case of biting flies attacking wild birds the difficulties for sampling insects in avian nests (but see two recent descriptions of easy sampling methods by Tomás et al., 2008a; Votýpka et al., 2009) do the research on these factors even more complicated.

Biting midges (genus *Culicoides*, Diptera: Ceratopogonidae) and black flies (Diptera: Simuliidae) are two of the main haematophagous insects attacking birds under natural conditions (Kettle, 1995; Malmqvist et al., 2004; Martínez-de la Puente et al., 2009a, 2009b; Votýpka et al., 2009). Among these insects only females feed on animal blood, affecting hosts directly by draining resources and causing physical harassment and indirectly as vectors of multiple pathogens (Bennett, 1961; Valkiūnas, 2005). In spite of the few studies on the effects of biting fly attacks on wild birds, there are clear evidences supporting the role of biting flies increasing mortality in immature birds (Hunter et al., 1997; Smith et al., 1998). These adverse effects on nestlings may be due to the direct impact of insect attacks but also by their effects affecting parental decisions, including nest desertion or reduction of parental provisioning rate (Bukaciński and Bukacińska, 2000).

Here, we investigated the effects of two microclimatic factors, nest temperature and humidity, potentially affecting the relationship between biting flies and avian hosts. To that end, we studied the interaction between pied flycatchers *Ficedula hypoleuca* and two

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different haematophagous insect groups, biting midges and black flies, after controlling for the potential effect of other variables such as brood size and hatching date (see Martínez-de la Puente et al., 2009b). Also, we investigated the potential negative effect of biting flies on nestling condition after controlling for the confounding effect of rearing conditions (Dawson et al., 2005b; Pérez et al., 2008).

2. Methods

2.1. Host population

This study was conducted during the spring of 2008 in a population of pied flycatchers *F. hypoleuca* breeding in nest-boxes in a Pyrenean oak *Quercus pyrenaica* forest located in Valsaín (Central Spain, 40°53'74 N, 4°01' W, 1200 m.a.s.l.). All nest-boxes were hung from branches at about 4 m above the ground, thus, avoiding potential height differences in avian exposure to insect attacks (Fallis and Smith, 1964). Periodical visits in the course of the breeding season allowed us to record hatching date and brood size of birds at each nest.

2.2. Nestling measurements

At the age of 12 days, nestlings were weighed with a Pesola spring balance to the nearest 0.1 g and tarsus length was measured with a digital calliper to the nearest 0.01 mm. The average of nestling body mass and tarsus length per brood was calculated. Mass and tarsus length were not significantly correlated (Simple regression: $F_{1,44} = 2.55$; $p = 0.12$). Nestling mass was corrected by size by using tarsus length as a covariate in further analyses (see Biard et al., 2005; Suárez et al., 2005; Shapiro et al., 2006 for a similar procedure).

2.3. Insect collection

In order to capture biting flies visiting nest-boxes, we put inside and close to the roof of each nest-box a plastic Petri dish (8.5 cm diameter; 56.7 cm²) with a thinly spread layer of body gel–oil (Johnson's[®] baby chamomilla, Johnson & Johnson, Dusseldorf, Germany) when nestlings were 9 days old (see Tomás et al., 2008a for a validation and a thorough description of the method of insect capture). Petri dishes were collected 3 days later. Although daily changes of Petri dishes could provide data on daily variation in biting fly activity, this possibility was discarded to reduce avian disturbance during bird reproduction that could induce nest desertion. According to a previous study, nest-boxes without broods attract almost no biting flies (Tomás et al., 2008a). A stereoscopic microscope (Motic K700; 46.5× magnification) was used to quantify the abundance of black flies and biting midges collected at the bottom of each Petri dish.

2.4. Rearing conditions in the nests and weather data collection

A HOBO data logger (Onset Computer Corporation, Pocasset, Massachusetts, USA) with a flexible sensor was placed in each nest-box to record nest temperature (°C) and nest absolute humidity (gm/M3) with a frequency of 2 min during the 3-day period of insect capture. Data loggers were inserted between the nest-material and the inner wall of the nest-box, close to the chicks but avoiding any contact with them. The average of nest temperature and nest humidity for the 3 days of sampling was calculated.

The Spanish National Meteorological Institute provided daily maximum and minimum temperature data from the closest meteorological station located in Segovia, approximately 9 km from the study area. In previous studies, data from this meteorological station have been used to find clear effects of weather on several factors related to avian biology and bird–haematophagous insect interactions

carried out in the same area (Sanz et al., 2003; Lobato et al., 2006; Martínez-de la Puente et al., 2009b). Environmental temperature was then estimated by calculating the averages of the maximum and minimum temperatures respectively for each insect sampling period. Furthermore, the temperature gradient between the nest and the environment was estimated in two different ways. In the case of biting midges, the temperature gradient was measured as the difference between temperature in the nest and the minimum environmental temperature because most of the biting midges are considered crepuscular or nocturnal (Lehane, 2005) with a pronounced burst of activity at sunset during spring, summer and autumn (Kettle et al., 1998). However, in the case of black flies, the temperature gradient between the nest and the maximum environmental temperature was calculated because, contrary to biting midges, most adult black flies are essentially diurnal, usually showing a maximum activity in the early morning and afternoon (Lehane, 2005; McCreadie et al., 1985; Grillet et al., 2005). Although there are some reports of nocturnal black fly activity, the level of activity detected in these cases is low (McCreadie et al., 1985) and there are not evidences of black flies attacking avian hosts after dark (Bennett, 1960).

2.5. Statistical analysis

Statistical analyses were conducted using Statistica (version 6.0, StatSoft, Inc. 2001). In order to investigate the variables affecting the temperature in avian nests, the Akaike's second-order Information Criterion (AICc) was used for ranking the fit of models to the data (Burnham and Anderson, 1998) including hatching date, brood size and maximum and minimum external temperatures as continuous variables. The same procedure was employed to test for the effect of brood size, hatching date, nest temperature, nest humidity and the temperature gradient (the difference between the nest temperature and the environmental minimum temperature) on the abundance of biting midges. We also used AICc to identify the ranking of models to the presence/absence of black flies in avian nests, including brood size, hatching date, nest temperature, nest humidity and the temperature gradient (the difference between the nest temperature and the environmental maximum temperature) on the abundance of biting midges. We considered that models with a difference in AICc ($\Delta AICc$) of less than two units ($\Delta AICc < 2$) were similarly supported by the data. In order to quantify the relative importance of individual variables we calculated variable weights by summing the Akaike weights for each model containing the variable of interest (Johnson and Omland, 2004). All models obtained in the analyses (including those with a difference in AICc higher than two units) were considered to get variable weights.

Finally, to investigate the variables affecting nestling mass, we included in a General Regression Model (GRM, lineal models) the presence/absence of black flies as a factor and hatching date, brood size, nest temperature, nest humidity, tarsus length, biting midge abundance and the interaction between the presence/absence of black flies and biting midge abundance as covariates. This analysis allows us to identify the role of biting midges and black flies as well as their potential joint effect in affecting nestling body mass after control for body size (including tarsus length as a covariate in our analyses). The abundance of biting midges was logarithmically ($\log_{10}(x + 1)$) transformed to normalize its distribution. Residuals of the model were tested for normality.

In this study, we include 21 control and 25 unmanipulated nests from several experiments carried out in the pied flycatcher population with known nest temperature and humidity. Nests treated as control were sprayed with water 3 times during the incubation period. Unmanipulated nests were visited in the same way as controls but they were not sprayed with any product. As expected, this treatment conducted during the incubation period did not modify significantly

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