Effects of feather lice on flight behavior of male Barn Swallows (Hirundo rustica)

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ABSTRACT.-Parasites may affect host behavior in a number of ways, including their locomotory performance. We investigated whether the number of holes produced by the feather louse (Myrsidea rustica) affected flight behavior in adult male Barn Swallows (Hirundo rustica) by video-taping flight performance of individuals during escape and level flight. Percentage of time spent flapping during foraging flight was positively related to number of holes, but not to other flight parameters such as wingbeat frequency. These results suggest indirect effects of feather lice on host performance that must be considered together with effects of thermoregulation and feather breakage. This is the first report of an effect of parasite load on flight behavior.

RESUMEN.-Los parasitos pueden afectar el comportamiento de sus hospederos de diferentes maneras entre las que se incluye la locomocion. Investigamos si el numero de agujeros en el plumaje producidos por el piojo de pluma Myrsidea rustica afecta el comportamiento de vuelo de machos adultos de Hirundo rustica durante el escape y la alimentation. El numero de agujeros producidos por los piojos estuvo relacionado positivamente con el porcentaje de tiempo empleado en vuelo batido, pero no se encontro ninguna relacion con otros parametros de vuelo tales como la frecuencia de batido de las alas. Estos resultados sugieren la existencia de efectos indirectos de los piojos de pluma sobre sus hospederos que deben considerarse junto con sus efec

tos sobre la termorregulacion y el plumaje. Esta es la primera vez que se encuentra un efecto de un parasito sobre el comportamiento de vuelo.

Parasites have numerous effects on behavior, life history, and ecology of their hosts (e.g. Price 1980, Clayton and Moore 1997). Many studies have shown that parasites can change host behavior and thereby influence host fitness (Price 1980, Dobson 1988, Poinar 1991). However, most studies of host-parasite interactions have focused on life-history components such as reproductive success, quality of offspring or survival (see review in Moller 1997), sexual selection (Hamilton and Zuk 1982, Read 1988, Clayton 1991), dispersal (Brown and Brown 1992), and habitat selection (Emlen 1986, Chapman and George 1991). All those effects of parasites on host fitness are mediated by behavioral mechanisms that cause differences in performance. However, only very few studies have investigated the direct effect of parasites on locomotor performance of hosts, and those studies have exclusively been done on reptiles (Daniels 1985, Oppliger et al. 1996). This lack of information is all the more surprising given the importance of locomotion in efficient foraging and successful escape from predators (Webb 1986, Barbosa and Moreno 1999). As far as we know, effects of parasites on flight performance in birds have never been studied, although flight performance is one of the main ecological factors affecting bird life (Norberg 1990).

The feather louse (Myrsidea rustica) is abundant on adult and nestling Barn Swallows (Hirundo rustica; Moller 1994). This feather louse produces small holes in feathers causing damage to the plumage (Clayton 1991, Kose and Moller 1999). Feather lice have no effect on reproductive success of their hosts due to their vertical transmission and hence low level of virulence (Clayton and Tompkins 1995, Tompkins et al. 1996). However, feather lice have been found to indirectly affect thermoregulation and feather quality of avian hosts (Booth et al. 1993, Kose and Moller 1999). Although it has been suggested that parasites potentially may affect flight performance of avian hosts (Moller 1994), that possibility has not yet been tested.

The aim of this paper is to investigate whether the number of holes produced by the Myrsidea rustica affected flight behavior in adult male Barn Swallows. The Barn Swallow is a good model to test those relationships because it spends a large amount of time in flight while foraging.

Methods.-The study was carried out during the breeding season in 1997 in a colony of Barn Swallows located in the surroundings of

Badajoz (38 deg 50'N, 6 deg 59'W), Spain, where colonies are located in rural buildings. Barn Swallows were captured in mist nets and we measured a number of morphological characters including length of outermost tail feathers, wingspan, and body mass.

During spring 1997, we filmed 25 male Barn Swallows released by hand (see Jones 1986 for a similar approach). Birds were previously captured and color-marked with color rings to provide easy identification. Several aspects of flight behavior were measured: (a) time taken to reach level flight (escape flight); (b) wingbeat frequency during escape flight until level flight was reached; (c) wingbeat frequency during level flight (foraging flight); and (d) percentage of total time flapping during foraging flight.

Timing of different kinds of flight mode (flapping and gliding) and wingbeat frequency was carried out in a magnetoscope using the frame by frame utility. Wingbeat frequency was determined by counting number of wingbeat cycles and measuring time taken (see Pennycuick 1990, Warrick 1998). Flight parameters (see below) were similar to those published by other authors (20% gliding flight; Turner 1980; 8.18 Hz wingbeat frequency; Warrick 1998), indicating reliability of our measurements of flight behavior. Moreover, when birds reached level flight, they immediately began to forage indicating that measurements during level flight were a reliable measure of foraging flights.

Myridisea rustica were counted on the basis of the number of holes in tail feathers. Estimated number of holes produced by lice in the tail is strongly positively related to the total load of lice obtained from extraction with chloroform vapor, indicating that holes in feathers provide a reliable estimate of Mallophaga abundance (Moller 1991).

Results.-The raw data of flight of male Barn Swallows are as follows: time to take-off (x(overscore) = 5.39 s, SE = 0.27), wingbeat frequency during take-off (x(overscore) = 8.06 Hz, SE = 0.20), wingbeat frequency during level flight (x(overscore) = 6.51 Hz, SE = 0.16), percentage of time flapping (x(overscore) = 88.2, SE = 1.82), and percentage of time gliding (x(overscore) = 11.8, SE = 1.82). Feather lice were present on 13 (52%) of the birds sampled with a mean number of holes = 9.6, SE = 1.58.

No significant relationship was found between number of holes produced by lice and the morphological variables measured (wingspan, F = 0.17, df = 1 and 23, r^sup 2^ = 0.007, P = 0.68; tail length, F = 2.68, df =land 23, r^sup 2^ = 0.10, P = 0.11).

Results showed a positive and significant relationship between percentage of time in flapping flight and number of holes produced by lice (F = 5.35, df = 1 and 23, r^sup 2^ = 0.17, P = 0.03,). Other flight variables did not show any significant relationship with number of holes (time to take-off, F = 0.01, df = 1 and 23, r^sup 2^ = 0.0004, P = 0.91; wingbeat frequency at take-off, F = 0.06, df = 1 and 23, r^sup 2^ = 0.0025, P = 0.79; wingbeat frequency at level flight, F = 0.003, df = 1 and 23, r^sup 2^ = 0.0001, P = 0.95). As flight behavior could also be affected by variation in morphology among individuals (A. Barbosa unpubl. data), we performed a stepwise multiple regression analysis between percentage of time flapping and morphological variables (tail, wingspan, and body mass) and number of holes produced by lice. We found that only body mass and number of holes showed significant positive relationships with percentage of time flapping flight (partial correlation, body mass, r = 0.67, P

Discussion.-As far as we know, this is the first study investigating the relationship between parasites and flight performance in birds. Our results showed that individuals with high number of holes produced by lice spent a higher proportion of time in flapping flight during level flight, but no significant relationship was found between number of holes and wingbeat frequency or with flight behavior during escape flight. These results suggest that holes produced by lice did not produce mechanical constraints to flight. Variation in flight behaviour could be due to indirect effects.

The main effect of feather lice on their bird hosts is feather damage (Clayton 1991). Feather damage caused by Mallophaga can cause feather breakage (Kose and Moller 1999), which also may affect flight. However, none of the birds in our sample suffered from feather breakage when filmed, and effects of Mallophaga on flight behavior through breakage can therefore be excluded as an explanation for our results.

Another effect of feather damage is increase of thermoregulation costs (Clayton 1991, Booth et al. 1993). Booth et al. (1993) found that

Rock Doves (Columba livia) with high parasite loads suffered a reduction in body mass, and they suggested that fat reserves were used to cope with elevated metabolic rates of individuals with high parasite loads. If that were also the case in Barn Swallows, individuals with a high parasite load would have to increase their foraging efficiency through an increase in flapping flight to balance the extra metabolic cost due to Mallophaga. Barn Swallows forage on the wing, selecting large actively flying Diptera, which constitute their optimal diet (Turner 1982). Barn Swallows use flapping flight to capture such optimal prey (Turner 1980), whereas gliding is used mainly to save energy during flight, as in other birds (Norberg 1990).

On the other hand, lice load could indicate a poor condition of birds due to other factors (Potti and Merino 1995). In such cases birds could also increase foraging efficiency by trying to increase their condition. Changes in foraging behavior to increase foraging efficiency have been reported in parasitized fishes, even to the point of increasing predation risk (Milinski 1993).

Our study recorded a novel indirect effect of feather lice on their hosts, because abundance of feather lice estimated by the number of holes produced was related to flight behavior. This does not preclude direct effects of Mallophaga on the flight behavior of hosts through feather breakage, although that possibility remains to be tested.

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