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The influence of environmental conditions on immune responses, morphology and recapture probability of nestling house martins (*Delichon urbica*)

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Abstract Nestling birds produced later in the season are hypothesized to be of poor quality with a low probability of survival and recruitment. In a Spanish population of house martins (*Delichon urbica*), we first compared reproductive success, immune responses and morphological traits between the first and the second broods. Second, we investigated the effects of an ectoparasite treatment and breeding date on the recapture rate the following year. Due probably to a reverse situation in weather conditions during the experiment, with more rain during rearing of the first brood, nestlings reared during the second brood were in better condition and had stronger immune responses compared with nestlings from the first brood. Contrary to other findings on house martins, we found a similar recapture rate for chicks reared during the first and the second brood. Furthermore, ectoparasitic house martin bugs had no significant effect on the recapture rate. Recaptured birds had similar morphology but higher immunoglobulin levels when nestlings compared with non-recaptured birds. This result implies that a measure of immune function is a better predictor of survival than body condition per se.

Keywords Hirundine · Ectoparasites · Immunoglobulins · Survival · Weather conditions

Introduction

Late breeding birds commonly fledge fewer chicks than early ones because of their smaller clutch size, but they also produce a smaller proportion of recruits than early breeding individuals (e.g. Verhulst and Tinbergen 1991; Møller 1994a; Brown and Brown 1996). The two major factors invoked to explain the seasonal decline in reproductive success are deterioration of environmental conditions for reproduction, mainly due to a decline in food availability, and/or poor quality parents breeding late thereby acquiring poor territories late during the season. Experimental studies in which clutches were experimentally delayed or advanced provide some support for one or both of these hypotheses (Verhulst and Tinbergen 1991; Brinkhof et al. 1993; Wiggins et al. 1994). However, considerable residual variation related to breeding date remains to be explained (Verhulst and Tinbergen 1991; Wiggins et al. 1994). Whatever the reasons for the seasonal decline in reproductive success, chicks hatched later in the season usually exhibit a lower body condition compared with early hatched chicks. Furthermore, small size or body weight is often associated with low survival prospects (Perrins 1965; Owen and Black 1989; Tinbergen and Boerlijst 1990; Magrath 1991; Lindén et al. 1992; Brinkhof et al. 1997).

Among unknown factors related to breeding date, parasites could play an important role (Brown and Brown 1999). Ectoparasites are well known to decrease the breeding success of their hosts (review in Lehmann 1993; Møller 1997). The magnitude of the impact of ectoparasites may also depend on environmental factors such as weather conditions influencing host performance (de Lope et al. 1993; Johnson and Albrecht 1993; Merino and Potti 1996), since temperature has been shown to influence growth and activity of ectoparasites (Marshall

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1981). For example, *Carnus hemapterus* infesting barn owls (*Tyto alba*) showed increased fecundity as the season progressed (Roulin 1999). Weather conditions could, for example, explain why house martins (*Delichon urbica*) experimentally infested during their first clutch with an haematophagous ectoparasite, the house martin bug (*Oeciacus hirundinis*), had lower reproductive success during the second clutch as compared to fumigated nests (de Lope et al. 1993).

Food availability during the breeding season will determine chick nutrition, an important factor determining immune function (Chandra and Newberne 1977; Gerschwin et al. 1985; Lochmiller et al. 1993). Thus, immunocompetence is positively correlated with body condition in free living bird populations (Saino et al. 1997a; Sorci et al. 1997; Christe et al. 1998; Brinkhof et al. 1999). This may also explain why aspects of immunocompetence correlate negatively with hatching date in the barn swallow (*Hirundo rustica*) and the magpie (*Pica pica*) (Saino et al. 1997a; Sorci et al. 1997). Indeed, the negative relationship between survival and hatching date could be mediated by immunocompetence.

Previous experiments on house martins and house martin bugs in the same population were limited to: (1) the effect of house martin bugs on phenotypic traits, energetics and seasonal reproductive success of house martins; (2) the effect of body condition and immunocompetence on survival during the brood care period of nestlings experimentally infested with house martin bugs; and (3) genetic variation in immune response and morphology determined using a cross-fostering experiment. First, it has been demonstrated that the experimental manipulation of parasite loads resulted in an increase in host metabolism and a reduction in reproductive success and body condition particularly during the second brood (de Lope et al. 1993; Møller et al. 1994; de Lope et al. 1998). Second, it has been shown that house martin nestlings with low condition and immunocompetence were more likely to die before fledging (Christe et al. 1998). Third, we found significant environmental variance, but no significant additive genetic variance in immune response parameters (Christe et al. 2000).

In the present study, we first investigated the effect of breeding date on immune responses and morphological characters by comparing estimates obtained during the first and the second broods. Second, we estimated the effect of both ectoparasite treatment and season (first and second brood) and their possible interaction on first year local recaptures by comparing values obtained for nestlings recaptured 1 year later with those that were not recaptured.

Materials and methods

Study organism and study site

The house martin is an aerial insectivorous hirundine with a strong colonial nesting habit. When returning from their winter quarters, adults may either build a new nest or use an old one. A second brood is raised in the same nest. The house martin bug (*Oeciacus hirundinis*, Hemiptera, Cimicidae) is the most important haematophagous ectoparasite found in the study site (de Lope et al. 1993).

The field study took place in Badajoz, Extremadura, Spain, during the breeding season of 1996 in a colony of approximately 600 nests located at the university campus (RUCAB). After a 4-year period of drought in this warm part of Spain, it rained during 42 days in April-May 1996, thereby reversing the common seasonal pattern of prey availability during the breeding season.

Manipulation of loads of nest parasites and nestling measurement

Before egg laying we experimentally removed nest ectoparasites by spraying all nests with a pyrethrin solution (0.91%). When clutches were completed, we experimentally infested 50 randomly chosen nests with 50 house martin bugs. Fifty other nests were fumigated every second day throughout the breeding season until the second clutch fledged. This treatment reduced significantly the number of house martin bugs and fleas present in the nests (Christe et al. 2000).

When nestlings were 15 days old they were ringed with an individually numbered aluminum ring, their tarsus length measured to the nearest 0.01 mm with a digital calliper and their wing length measured to the nearest millimetre with a ruler. Nestlings were weighed with a precision of 0.1 g on a Pesola spring balance. At this time, we collected a small blood sample in a microcapillary tube from the brachial vein. One drop of blood was used for a blood smear for subsequent leucocyte counts and detection of eventual blood parasites. However, none of the blood smears examined (n=343) showed infestation with blood parasites. Microcapillary tubes were centrifuged for 10 min at 14,000 rpm in order to estimate the haematocrit value, which is the proportion of total blood volume occupied by erythrocytes after centrifugation. When nestlings are 15 days old their body mass peaks and tarsus length reaches its final size in the study area (Pajuelo et al. 1992).

Measures of immunocompetence and immune responses

T-cell response

Immunocompetence was assessed by the intensity of the T-lymphocyte response, a cell-mediated in vivo immune response, to the injection of 15-day-old nestlings with 0.625 mg phytohaemagglutinin (PHA-P; Sigma, St. Louis, Mo.) in 0.125 ml phosphate-buffered saline (PBS) in the middle of the wing web (patagium). In the other wing we injected a similar volume of PBS as a control. Twenty-four hours later the thickness of the wing web at the inoculation sites was measured with a digital calliper to the nearest 0.01 mm. The change in thickness in the wing where PHA-P was injected minus the change in the control wing was used as a measure of immunocompetence. This method has been shown to be a reliable indicator of immunocompetence (Lochmiller et al. 1993) without imposing high stress levels in nestling house martins (Merino et al. 1999). All nestlings were measured 3 times. We then computed the means and used these values for calculations.

Immunoglobulin assay

Immunoglobulins were assayed by densitometric analysis after electrophoretic separation of plasma proteins on agarose gels (Paragon SPE kit; Beckman). Densitometric analysis was performed with a computer image analysis procedure (Gelanalyst; Eidosoft). The relative titre of immunoglobulins was expressed as the ratio between the area of the densitometric profile corresponding to the immunoglobulin region and the total area of the densitometric profile. The total area of the densitometric profile is proportional to the actual total protein content because all the samples were diluted in the same way. As shown in a previous study, within-blood-sample repeatability of immunoglobulin titres was high [for more details, see Saino and Møller (1996)].

Leucocyte count

Blood smears were air dried, fixed in absolute methanol and stained by the May-Grunwald-Giemsa staining method. Leucocytes and red blood cells were counted at ×1,000 magnification. In each smear we counted the number of leucocytes per 10,000 red blood cells ("no. of leucocytes"). To obtain the total number of leucocytes circulating in the blood, we used the number of leucocytes per 10,000 red blood cells multiplied with the haematocrit value (hereafter "absolute counts") following the method described by Dufva and Allander (1995).

Statistical analyses

For comparisons of phenotypic traits between first and second clutches we computed the mean nest value for each trait. Paired *t*-tests were performed and only broods reared by the same two adults (determined by captures) were used in these analyses. Individual values were used for comparisons of immune responses and phenotypic traits between recaptured and non-recaptured birds.

All statistical analyses were performed using Systat (Wilkinson 1992). Percentages were square-root arcsine transformed before analyses. All P-values reported are two-tailed.

Results

Immunocompetence and phenotypic traits of nestlings in the first clutch

We tested for phenotypic correlates of immune response of nestling house martins in order to identify environmental determinants. There was no significant relationship between T-cell response and hatching date in the first brood ($F=0.27$; $df=1{,}65$; $r^2=0.004$; $P=0.61$). T-cell response estimated from the wing web index increased with average nestling body mass [linear regression; $F=15.92$; $df=1{,}65$; $r^2=0.197$; $P<0.001$; slope (SE)=0.057 (0.014)]. The relationship between T-cell response and body condition (body mass corrected for structural body size) was significantly positive [Fig. 1; linear regression; $F=11.25$; $df=1{,}65$; $r^2=0.148$; $P<0.001$; slope (SE)=0.049 (0.014)]. In contrast, there was no significant relationship between T-cell response and tarsus length ($F=1.53$, $df=1{,}65$, $r^2=0.023$, $P=0.45$).

Fledging success was positively correlated with mean within-brood T-cell response, defined as the percentage of hatchlings that fledged [$F=23.03$; $df=1{,}65$; $r^2=0.262$; $P<0.001$; slope (SE)=0.464 (0.097)]. Mean within-brood concentration of immunoglobulins did not correlate significantly with fledging success ($F=0.69$, $df=1$, 74, $r^2=0.009$, $P=0.41$).

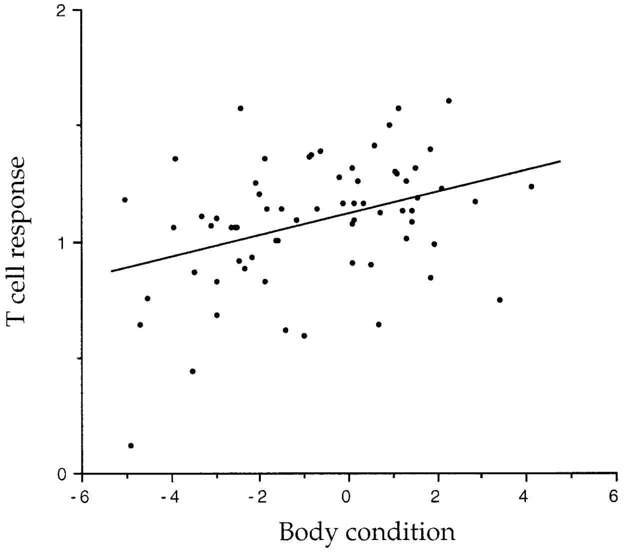

Fig. 1 Mean T-cell response per house martin nestling to an injection with the antigenic phytohaemagglutinin for first broods in relation to mean body condition measured as the residuals from a regression of body mass on tarsus length. The regression line is given by the equation: T-cell response=1.122+0.049 (0.015) body condition

Effect of date on clutch size and immune response in the second brood

For the second clutch there was a decrease in clutch size as the season progressed [linear regression; $F=18.17$; $df=1{,}67$; $r^2=0.213$; $P<0.001$; slope (SE)=–0.042 (0.009)]. There was a weakly negative relationship between T-cell response and hatching date in second broods [$F=6.23$; $df=1$, 60; $r^2=0.094$; $P=0.015$; slope (SE)=–0.029 (0.019)]. For immunoglobulins the relationship was not significant ($F=0.004$, $df=1$, 60, $P=0.96$).

Comparison of first and second brood

Compared to the first clutch, the second clutch size was significantly smaller [first clutch 4.55 (0.08), second clutch 3.93 (0.09), $t=5.48$, $df=41$, $P<0.001$]. Hatching success, defined as the percentage of eggs that hatched, was slightly higher in the second brood than in the first brood [first brood 0.86 (0.03), second brood 0.93 (0.03), $t=2.70$, $df=41$, $P=0.05$]. The number of fledglings was greater during the first compared to the second brood [first brood 3.52 (0.14), second brood 3.07 (0.16), $t=2.27$, $df=41$, $P=0.028$]. There was no significant difference in fledging success between the first and second brood [first brood 0.92 (0.03), second brood 0.84 (0.03), $t=1.38$, $df=41$, $P=0.173$].

Compared to first-brood chicks, nestlings from second broods were in better body condition (Table 1). The mean within-brood T-cell response was also larger for the second brood than the first brood, and this also applied to immunoglobulins (Table 1). The absolute number of leucocytes and leucocyte densities were not significantly different between the two broods (Table 1).

The change in the T-cell response from the first to second brood differed between sprayed and parasite-infested broods, with nestlings from sprayed broods showing a larger increase in T-cells than nestlings from parasite-infested broods (Mann-Whitney U-test, $U=164$, $n=31$, $P=0.05$).

Table 1 Body condition, wing length and immune parameters during rearing of the first and second brood of nestling house martins by the same parents. Values are means (SE)

	First brood	Second brood	*t*	*df*	*P*
Body condition	1.58 (0.03)	1.80 (0.03)	–4.44	36	<0.001
Wing length	48.9 (0.8)	50.6 (0.9)	–0.76	29	0.455
T-cell response	2.98 (0.11)	3.56 (0.14)	–2.45	30	0.020
Immunoglobulins	0.127 (0.006)	0.156 (0.006)	–3.72	36	<0.001
Absolute no. leucocytes	6515 (415)	7117 (770)	–0.03	10	0.973
Leucocytes/10^4 erythrocytes	156 (10)	180 (9)	–1.13	12	0.279

Recapture rate

A total of 35 birds ringed as nestlings in 1996 were recaptured in 1997. The return rate of first-clutch chicks was 6.7% (20/300) and 7.3% (15/205) for second-clutch chicks. Natal philopatry was strongly male biased, a common pattern found in avian studies (review in Clarke et al. 1997). Of the 35 birds recaptured in 1997, 30 were males and five were females (binomial test, $P<0.001$). Brood size at fledging influenced the probability of being recaptured. Chicks from large broods had a higher probability of being recaptured (ANCOVA recaptured vs. non-recaptured; $F=12.2$; $df=1, 142$; $P<0.001$; first vs. second brood; $F=13.07$; $df=1, 142$; $P<0.001$).

Treatment during the nestling phase had no significant effect on recapture rate the following year, neither in the first ($X_2=3.0$, $P=0.083$) nor in the second brood ($X_2=0.40$, $P=0.505$). Morphological characters, body condition and immune responses at day 15 were not different between birds recaptured compared to birds that were not recaptured in 1997 (all $P>0.10$) except for immunoglobulin levels. Recaptured house martins had higher immunoglobulin levels compared with non-recaptured birds (ANCOVA recaptured vs. non-recaptured; $F=7.146$; $df=1, 524$; $P=0.008$; first vs. second clutch; $F=30.49$; $df=1, 524$; $P<0.001$).

Because birds recaptured were strongly male biased we performed the same analyses as above by comparing only the males recaptured with the nestlings not recaptured, but it did not change the conclusions.

Discussion

Previous experimental manipulation of intensities of house martin bugs of the same house martin population showed severe negative effects on seasonal reproductive success (de Lope et al. 1993). Environmental conditions affecting the reproduction of insectivorous birds generally deteriorate as the season progresses (Lack 1966; Bryant 1975). The stronger effect of parasites observed during the rearing of the second clutch was mainly due to the combination of an increase in parasite number with a simultaneous decrease in prey availability (de Lope et al. 1993). Surprisingly, in the present study, we found higher body condition and immune response of offspring from the second clutch as compared to the first one. As an example, in 1995, mean body mass of nestling house martins in the same colony was 19.1±0.5 g during the first and 16.5±0.7 g during the second brood, which is the usual pattern observed (de Lope et al. 1998). In contrast, we found the reverse situation in 1996 with a mean body mass of only 17.6±0.3 g during the first and 20.2±0.3 g during the second brood. This difference between years certainly reflects the adverse meteorological conditions during rearing of the first clutch in 1996, with an exceptionally rainy spring for this part of Europe, resulting in reduced body condition and immune response in first as compared to second broods. Rainfall certainly delayed the emergence of insects, which became very abundant during the rearing of the second brood. House martins are exclusively aerial feeders and are therefore very sensitive to weather conditions (Bryant 1975).

The effects of weather on the activity and timing of development of parasite populations may also differ among ectoparasite species (Merino and Potti 1996). For example, the number of adult fleas or their larvae did not vary significantly during the great tits' breeding season (Heeb et al. 2000). In contrast, fecundity of *Carnus hemapterus* infesting barn owls (*Tyto alba*) showed a seasonal increase (Roulin 1999), as did the abundance of the mite *Ornithonyssus bursa* infesting barn swallow nests (Møller 1994b).

Studies on the house martin have reported the probability of first-year survivorship declining from 9.1 to 3.8% (Rheinwald and Gutscher 1969) and from 11.9 to 6.2% (von Gunten 1963) when comparing recapture rates from first and second clutches. The probability of recruitment decreases also for nestling barn swallows and cliff swallows *Petrochelidon pyrrhonota* reared late in the breeding season (Møller 1994a; Brown and Brown 1996). We can envisage three explanations for the difference in recapture rate between early- and late-hatched chicks. First, late-hatched nestlings may experience a lower survival rate during migration. Second, birds may differ in dispersal distance between first and second broods (Rheinwald and Gutscher 1969). Third, competition between early and late young may affect the probability of recruitment and/or survival. This latter hypothesis may particularly apply to non-migrant bird species that have to acquire a high-quality territory (e.g. great tits, Verhulst and Tinbergen 1991; Lindén et al. 1992). It is unlikely that this hypothesis applies to the migratory and colonial house martin. In the present study, we found no evidence of a difference in the proportion of birds that returned to their natal site between the first (6.7%) and the second brood (7.3%). This result gives no support for the hypothesis of a larger natal dispersal distance for birds raised later in the season. However, there was no difference in body mass between birds recaptured and not recaptured 1 year later. Hirundine nestlings typically decrease in body mass during the last part of their nestling period (Ricklefs 1968), and body mass at 15 days may not reflect fledging mass, since house martin nestlings fledge when 22–30 days old. However, on a sample of post-fledging chicks captured 50 days (±0.8) after first measuring their body mass, we found a weakly significant positive relationship between initial mass and post-fledging mass (r=0.353, n=31, P=0.05). Even if the correlation is weak, this result indicates that body mass at 15 days to some extent reflects post-fledging mass. A similar result has been obtained for cliff swallows (Brown and Brown 1996).

Another problem in the present study could have been the method used to estimate recapture rate. As the colony under study contained several hundred nests (520 nests), we cannot be sure, despite an intensive capture effort, that we caught all surviving nestlings. However, a study in a smaller colony near the present colony site (ca. 15 km) revealed a mean first year return rate of 6.1% (de Lope and da Silva 1988); a percentage very close to the one recorded in the present study. Unfortunately, these birds were previously ringed as fledglings with no knowledge of whether they were reared during the first or the second brood.

A positive correlation between immunocompetence and survival has been reported for very few free-living organisms (Saino et al. 1997b; Soler et al. 1999; González et al. 1999). Here we have shown that a T-cell mediated immune response is correlated with body condition and survival in offspring, while immunoglobulin levels predict subsequent post-fledging survival. As body condition was not significantly different between recaptured and non-recaptured birds, this implies that a measure of immune function is a better predictor of survival than body condition per se. Immunoglobulins comprise a diverse class of serum proteins involved in the humoral immune response. We can envisage at least two different explanations for the high level of immunoglobulins in survivors:

1. Females that allocate large amounts of immunoglobulins to their eggs will produce offspring with a head start in anti-parasite defense (Kissling et al. 1954; Reeves et al. 1954; Sooter et al. 1954; Brambell 1970; Kowalczyk et al. 1985), and such offspring may have a high probability of survival.
2. Offspring that for genetic reasons are better able to produce large amounts of immunoglobulins may be better able to survive the negative effects of parasitism by not only house martin bugs, but also by other kinds of parasites, and hence enjoy increased probability of survival.

In a cross-fostering experiment (Christe et al. 2000), we found little evidence of additive genetic variation for immunoglobulin titres, suggesting that the second explanation is unlikely.

In conclusion, our findings support the predictions that immune function in nestling birds is strongly affected by environmental conditions, and that immune function predicts survival. Nestlings reared during the second brood were in better body condition because of unusual weather patterns. These results suggest that environmental conditions are the main factor determining the seasonal decline in reproductive success observed in numerous bird studies.

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