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Blood parasites, reproduction and sexual selection in the red-backed shrike (*Lanius collurio*)

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We investigated the occurrence of blood parasites on the red-backed shrike *Lanius collurio* during a three-year study in southern Czech Republic. Selected traits of shrike body morphology, male plumage and reproduction were studied with respect to the presence and intensity of haematozoan infection in blood samples collected from 172 breeding adults. *Haemoproteus lanii* was found to be the most common parasite (72.7%), the prevalence of other parasites (i.e., haemoproteids *Plasmodium* sp. (cf. *relictum*) and *Leucocytozoon* sp., kinetoplastid *Trypanosoma* sp. and microfilariae *Aproctella stoddardi*) being markedly lower. Incidence of parasitemia did not differ between sexes in any of the parasite species considered. However, females infected by *Haemoproteus lanii* initiated egg-laying later in the season than uninfected females. Among males, infected individuals had significantly longer wings and larger melanin-based tail colour patterns (a secondary sexual trait) than uninfected individuals. Moreover, mating was assortative with respect to infection status.

Introduction

Blood parasites transmitted by haematophagous arthropods are widespread, and are suggested to have a negative impact on their avian hosts. Unfortunately, the available data are mostly based on laboratory studies using domestic birds. In contrast, in natural populations, blood parasites are frequently considered to be of low pathogenicity (Atkinson & van Riper 1991). Parasites will inevitably compete for energy and nutrients with the host, however, which consequently must resolve trade-offs between the amount of energy invested in reproductive effort and any immunological battle against parasites (*see* Møller 1997).

Parasite loads can correlate negatively, positively, or not at all, with reproductive output in birds. First, a negative relationship (i.e. parasite presence associated with reduced reproductive investment — "*parasite influence hypothesis*") implies that the energetic resources available for

current reproduction may be limited by an existing parasitaemia (Atkinson & van Riper 1991, Goater & Holmes 1997, Møller 1997). Second, a *false* negative relationship (i.e. parasite presence associated with low reproduction with no causal relationship exists between reproductive effort and prevalence of blood parasites) is predicted by the "*individual optimization hypothesis*". The reproductive effort of each female should match her individual investment capacity, i.e. low-quality females invest less in both reproduction and parasite resistance which results in a negative non-causal correlation between reproductive investment and parasitemia (Pettifor *et al*. 1988). Third, a positive relationship where investment in eggs is expected to be positively correlated with subsequent parasite load in females, because the more energy invested in reproduction, the less is available for parasite resistance (Gustafsson *et al*. 1994, Sheldon & Verhulst 1996).

In addition to these considerations, parasites may also play an important role in sexual selection by affecting the expression of male secondary sexual traits (Hamilton & Zuk 1982). The Hamilton-Zuk hypothesis (HZH) predicts that extravagant traits, such as plumage brightness and song, are more developed in males of more parasitized species. This is because selection for parasite resistance should be greater in species where parasites play an important role in determining individual fitness. Therefore, male sexually selected traits may be indicators of good health due to resistance to parasites. At the intraspecific level, HZH predicts a negative relationship between the presence and/or quantity of parasites and sexual ornaments, as only the healthiest individuals will be able to pay the costs of fully developed sexually selected traits. The hypothesis also predicts a negative relationship between host fitness and parasite load. Hamilton and Poulin (1997) reanalysed an extensive set of 200 publications with regard to HZH, and they found a significant over-all negative correlation between parasites presence and male showiness.

Avian blood parasites are a very suitable model for testing hypotheses relating to sexual selection and underlying physiological mechanisms of reproductive costs (Ots & Hõrak 1998). However, to date, tests of all three hypotheses above have mainly been limited life-history or sexual selection context, but few studies have considered both factors together (cf. Atkinson & van Riper 1991, Møller 1997).

We investigated simultaneously the relations between body condition, morphology, breeding time, male secondary sexual traits and prevalence and intensity of blood parasite infection in the red-backed shrike. In particular, we were interested to explore the relationship between parasitaemia and timing of breeding, as this trait is linked with many others such as clutch size, brood size, survival and number of recruits (reviews in Svensson 1995, Nilsson 1999). In addition, the relationship between parasitaemia and expression of a male secondary sexual trait (SST) was investigated to see whether males differing in their expression of the SST differed also in their infection status as predicted by HZH.

Materials and methods

The red-backed shrike is a small, socially monogamous passerine bird with conspicuous sexual dichromatism, widely distributed throughout Europe. Males are conspicuous having black facial mask and black-and-white tail pattern, while females lack these features. The species is a long-distance migrant with wintering grounds in southern and south-eastern Africa. Breeding begins in early May and continues to the end of July. Only one brood per season is reared and one to three replacement clutches may follow a first unsuccessful breeding attempt (Cramp & Perrins 1993).

Our 15 km^2 study area was located in South Bohemia north-east of the town of Písek (49°19´N, 14°15´E). Different aspects of the breeding ecology of the red-backed shrike have been studied in this area over the period 1989–1999. The mean population density was 3.5 pairs/km^2. Samples of blood parasites were collected 1997–1999. In total, 98 adult males and 74 adult females were trapped during different stages of their breeding cycle using standard mist nets or bowl traps with a mealworm inserted as lures. For more details about the study area and the local red-backed shrike population, *see* Šimek (2001).

Blood collection and parasite detection

Data on blood parasites were obtained by analysing blood smears. Blood samples were obtained by puncturing the tarsal vein; blood smears were made and air-dried immediately in the field. The smears were fixed in absolute methanol (10 min), air-dried and subsequently stained with Giemsa's solution (Sigma) for 30 min. The slides were examined with a light microscope at 200× magnification for 5 min. During this time 50 microscopic fields on each smear were examined for leucocytozoids, trypanosomes and microfilariae. Each smear was examined another 10 min at 1000× magnification (equivalent to the observation of 100 microscopic fields; approximately 10 000 erythrocytes) for detection of *Haemoproteus* and *Plasmodium*. When no parasites were detected after this time, the smear was considered negative. Parasite scores were blind in the sense that the observer (J.V.) was given the ring number and no other information about the birds from which samples were taken.

Haemoproteus lanii was identified by its pigment granules and characteristic halteridial shape, medium to large size, partial surrounding of the erythrocyte nucleus and entirety of parasite outline (Bennett & Peirce 1988, Bennett *et al*. 1990). *Haemoproteus* is known to be a very pleomorphic haemoproteid; therefore, it was assumed that all *Haemoproteus* specimens belonged to the same species. *Plasmodium* sp. (cf. *relictum*) was identified by its dark pigment granules and spherical or ellipsoid shaped gametocytes (Bennett *et al*. 1993a). The exact identification of particular species of *Plasmodium* and *Trypanosoma* is quite difficult without subsequent experimental transmission studies. In the red-backed shrike undetermined species of *Leucocytozoon* have been reported only twice (Böing 1925, Eide *et al*. 1969). In addition, the fact that we found this parasite in only two individuals, and that the parasitaemia was extremely low, made exact species determination difficult. Determination of microfilariae (*Aproctella stoddardi*) was according to the size and characteristic shape of the anterior and posterior ends.

Abundant presence of *Haemoproteus* parasites allowed rough quantification in three categories (low, medium and high parasitemia, respectively). However, very few birds fell into the two last categories (below 10% of all records). Hence, as in many other studies (e.g. Korpimäki *et al*. 1993, Sanz *et al*. 2002), we decided to divide the data into only two groups: infected and non-infected individuals.

With respect to the low number of shrikes infected by other parasite species, only birds infected by the most common parasite (*Haemoproteus lanii*) were taken into account for the subsequent analyses (*see* also remarks on shrike blood parasites in Shurulinkov and Golemansky (2002)).

Measurement of morphometric traits

For each individual, we measured length of right wing (maximum length; with an accuracy of 0.5 mm) with a metric ruler, length of right tarsus (with an accuracy of 0.05 mm) with callipers, and body mass (± 0.1 g) with a spring balance. We estimated body condition index as body mass divided by tarsus length raised to the power of three to obtain similar dimensionality for the two variables. Because of a significant decrease in the female body mass during the breeding cycle (Takagi 2002, J. Šimek, unpubl.), body mass of each female was adjusted by regression analysis to that at the time the first egg was laid.

As a potentially important male secondary sexual trait we quantified variation in the tail pattern. In shrikes, the tail is presented during courtship to female and it plays an important function in pair formation (Lefranc & Worfolk 1997, Harris & Franklin 2000). We measured two tail pattern parameters: size of black patch and asymmetry of the tail pattern. The size of the black terminal tail patch was measured on the three outermost tail feathers. Asymmetry of tail patches is expressed as relative value of the difference between size of black terminal patch on left and right halves of the tail.

The red-backed shrikes were sexed and aged according to Svensson (1992). However, as more detailed ageing is complicated, the birds in subsequent analyses were classified into two categories: 2 years old and older.

Measurements of reproduction

Only the reproductive parameters of first (non-replacement) breeding attempts were included in the analyses. Timing of breeding was established as a relative value separately for all three years and 0 was the median value for the breeding population in a given year. Nests were classified as successful if at least one fledgling left the nest.

Length and width of each egg was measured with dial calliper (to the nearest 0.1 mm) and egg volume was calculated using the Hoyt's (1979) equation: volume = length × breadth^2 × 0.51. We measured reproductive output using clutch volume, which was the summed volume of all eggs.

As the breeding biology of the red-backed shrikes has been studied since 1989 in the study area, this enabled us to quantify territory attractiveness for each established territory. We used the following territory attractiveness index: TA = $\sum 1/n$, where n is the number of breeding pairs in the study area in a given year, and the index is summed over all years, when a given territory was occupied.

All morphological parameters and reproductive measurements were made by one person (J.S.).

Statistical analyses

For birds that had been sampled in two or three years, we randomly picked one observation to be included in the analyses to avoid pseudo-replication. Thus, each bird entered the analyses only once.

Statistics were performed with SPSS for Windows (Norusis 1993), and all tests are two-tailed. Bonferroni corrections were applied to adjust the p values for the increased probability of obtaining statistical significance from multiple testing (Rice 1989). Data are presented as means ± SD. Data from three years were pooled for analyses because of small sample sizes and because there was no evidence for significant among-year heterogeneity in parasite prevalence (Chi-square test: $\chi^2 < 7.18$, df = 2, $p > 0.14$).

Results

Blood parasite prevalence

In the blood smears of 172 adult red-backed shrikes, the following five species of blood parasites were identified: apicomplexan *Haemoproteus lanii* de Mello, 1936, *Plasmodium* sp. (cf. *relictum* Celli & Sanfelice (1891)) and *Leucocy-*

Table 1. Prevalence of blood parasites in adult red-backed shrikes during three breeding seasons ("+" denote parasite presence, "–" parasite absence and "% (+)" prevalence of a given parasite).

Parasite species	Presence	Males			Females			Males Σ	Females Σ
		1997	1998	1999	1997	1998	1999		
Haemoproteus lanii	+	9	31	31	10	24	20	71	54
	–	8	9	10	5	7	8	27	20
	% (+)	52.9	77.5	75.6	66.7	77.4	71.4	72.5	73.0
Plasmodium sp. (cf. *relictum*)	+	0	4	2	0	0	2	6	2
	–	17	36	39	15	31	26	2	72
	% (+)	0	11.1	5.1	0	0	7.7	6.5	2.8
Leucocytozoon sp.	+	0	0	0	1	1	0	0	2
	–	17	40	41	14	30	28	98	72
	% (+)	0	0	0	7.1	3.3	0	0	2.8
Trypanosoma sp.	+	0	4	2	1	3	3	6	7
	–	17	36	39	14	28	25	92	67
	% (+)	0	11.1	5.1	7.1	10.7	12.0	6.5	10.4
Aproctella stoddardi	+	0	3	0	0	4	1	3	5
	–	17	37	41	15	27	27	95	69
	% (+)	0	7.5	0	0	12.9	3.6	3.1	6.8

tozoon sp., trypanosome *Trypanosoma* sp. and microfilariae *Aproctella stoddardi* Cram, 1937.

The majority (72.7%) of the 172 examined individuals were infected by *Haemoproteus*. *Trypanosoma* sp. was found in 13 individuals (7.6%), *Plasmodium* occurred in eight individuals (4.7%), *Aproctella* in eight individuals (4.7%) and *Leucocytozoon* was found only in two females (1.2%; Table 1). In total, 73.8% of adult red-backed shrikes examined were infected by at least one haematozoan parasite. The rate of parasitism did not differ between the sexes in any of the investigated parasites (Chi-square test: *Haemoproteus*: $\chi^2 = 0.01$, df = 1, $p = 0.93$; *Plasmodium*: $\chi^2 = 1.11$, df = 1, $p = 0.29$; *Trypanosoma*: $\chi^2 = 0.67$, df =1, $p = 0.61$; *Aproctella*: $\chi^2 = 1.3$, df =1, $p = 0.25$; $n = 172$). Incidence of blood parasite infection was similar to both sexes ($\chi^2 = 0.01$, df = 1, $p = 0.93$) and age (for females: $\chi^2 = 1.05$, df = 1, $p = 0.31$; for males: $\chi^2 = 1.98$, df = 1, $p = 0.16$).

Haemoproteus infection *vs.* morphometric traits

No significant relationship between incidence of *Haemoproteus* parasitism and wing length or body condition was found in females (Table 2). In males, parasitized birds had significantly longer wings than uninfected birds ($p < 0.003$; Table 2). Furthermore, the average size of the black tail patch of parasitized males was significantly larger than that of uninfected males ($p = 0.01$; Table 2). However, we found no difference in asymmetry of the tail pattern between infected and uninfected males (Table 2).

Haemoproteus infection *vs.* reproduction

Uninfected females breed significantly earlier than females infected with blood parasites (Table 2), but there was no relationship between incidence of parasitemia and time of breeding in males (Table 2). Uninfected males did not occupy territories of higher attractiveness than infected males ($p = 0.10$). This was also true of females ($p = 0.25$).

Assortative mating for *Haemoproteus* loads

There was a significant assortative mating with respect to incidence of parasitemia: uninfected females were mated to uninfected males more often than expected by chance ($\chi^2 = 5.7$, df = 1, $n = 49$, $p = 0.017$).

Discussion

This study revealed a negative correlation between blood parasite infection by *Haemopro-*

Table 2. Mean (± SD) morphometric and reproductive traits of red-backed shrikes in relation to *Haemoproteus* parasitism. Sample size in parenthesis. *t* = test value of *t*-test, *U* = test value of Mann-Whitney *U*-test.

	Uninfected	Infected	Test
Males			
Wing length (mm)	92.8 ± 2.0 (27)	94.2 ± 2.0 (71)	$t = -3.06$, $p < 0.003$*
Body condition	1.17 ± 0.06 (26)	1.18 ± 0.06 (68)	$t = -0.94$, $p = 0.35$
Tail patch (mm^2)	10.46 ± 1.27 (18)	11.89 ± 2.33 (47)	$t = -2.46$, $p = 0.02$*
Tail asymmetry (mm)	0.37 ± 0.19 (18)	0.34 ± 0.26 (46)	$U = 341$, $p = 0.28$
Territory quality	12.9 ± 7.1 (21)	10.1 ± 6.5 (58)	$t = 1.64$, $p = 0.10$
Timing of breeding	13.5 ± 8.8 (10)	10.6 ± 0.0(24)	$U = 92$, $p = 0.28$
Females			
Wing length (mm)	92.2 ± 2.4 (20)	93.1 ± 2.4 (54)	$t = -1.39$, $p = 0.17$
Body condition	1.51 ± 0.17 (18)	1.46 + 0.19 (54)	$t = 0.91$, $p = 0.37$
Clutch volume (cm^3)	16.24 ± 2.57 (8)	15.43 ± 1.50 (79)	$t = 0.84$, $p = 0.41$
Timing of breeding	6.3 ± 5.94 (9)	11.7 ± 8.0 (25)	$U = 58.5$, $p = 0.04$*

* significant at $p < 0.05$ using a sequential Bonferroni.

teus lanii and timing of breeding in red-backed shrike females. We also found a positive relationship between parasitism and wing length, and the size of the black tail patch in males, a secondary sexual trait. Moreover, we found evidence of assortative pairing with respect to infection. We will discuss each of these findings in turn.

Parasite detection and prevalence

There are only a few studies on blood parasite prevalence in shrikes (for central Europe, *see* Böing 1925, Kučera 1981a, 1981b). The previous studies contained data collected from different areas and mostly from non-breeding birds. The genera *Haemoproteus* and *Plasmodium* were found in 44% and 5%, respectively, out of 41 adult red-backed shrikes investigated (Kučera 1981a, 1981b). Our data showed that *Haemoproteus lanii* was a common parasite with a high prevalence (73%). Böing (1925) and Eide *et al*. (1969) reported undescribed species of *Leucocytozoon* in red-backed shrikes. In our study, we found only two infected birds. Accordingly, our data fit well with previous reports, and do so using a study population appropriate for answering questions relating to sexual selection.

Correlation between blood parasites, body condition and reproductive success

Infected females initiated breeding later than uninfected females. A similar result was reported by Allander and Bennett (1995) for great tits in Sweden. Interestingly, Ots and Hõrak (1996) reported no relationship between infection and breeding time for great tits in Estonia, and Merilä and Andersson (1999) found no relationship in blue tits. Early breeding is often positively correlated with reproductive success, but it can be also costly (Nilsson 1999). Therefore, the nutritional state of females may influence timing of breeding. Protozoan blood parasites may compete for energy by consuming a variety of host metabolites, as well as haemoglobin, but also by affecting tissues like the liver, spleen, lungs, heart or brain (Bennett *et al*. 1993b, Fargallo & Merino 1999, Figuerola *et al*. 1999) thus influencing timing of laying. Timing of breeding is an important life-history character that affects many other reproductive traits such as clutch size, brood size, survival and number of recruits (reviews in Svensson 1995, Nilsson 1999). However, our findings do not support the hypothesis on negative influence of blood parasites on breeding traits in birds.

We found a positive relationship between male wing length and incidence of parasitism. A possible explanation of the wing-parasite relationship could be a different migration distance to geographically distinct wintering grounds. Individuals of different wing length wintering in separate regions might encounter a differing probability of infection. However, the presence of blood parasites (*Haemoproteus* and *Plasmodium*) in red-backed shrike fledglings (authors' unpubl. data) suggests that these haemoproteids are autochthonous to the breeding area. A more plausible explanation is age differences between infected and non-infected birds. Although age differences in parasite prevalence were non-significant, power of this test was probably low. In the red-backed shrike, older males have longer wings than younger ones (Jakober & Stauber 1989) and a correlation between parasitism and wing length can be an effect of older birds having longer exposure time for infections.

Evidence of parasite-mediated sexual selection

We found that uninfected males had smaller black tail patches than infected males, and a small tail patch can be indicative of a higher individual quality. During male advertising and courtship, the tail is partly spread and is waved slightly from side to side in front of the female. Females could use the black and white pattern on the tail as an indicator of male quality (Harris & Franklin 2000).

Melanin may be important as a quality feature because it strengthens feathers. Møller *et al*. (1996) suggested that ectoparasite load reduces the size of melanin-based breast badge in house sparrows *Passer domesticus*, whereas in house finches *Carpodacus mexicanus* Hill

and Brawner (1998) did not find a correlation between experimental coccidial infection and melanin-based plumage colours. However, in an experiment with breeding great tits *Parus major*, Fitze and Richner (2002) demonstrated that the size of the melanin-based breast stripe of adults depends on parasite infestation. They concluded that the trait can serve as an honest signal of previous parasite exposure. However, our findings are opposite to predictions, since we found that uninfected birds had smaller black patches than those infected by blood parasites. Absence of melanin weakens keratin and hence white patches in feathers, such as that on the tail of the shrike. Therefore, tail whiteness may indicate male quality and serve as a handicap (Fitzpatrick 1998a, 1998b) and small black patch on shrike tail could be viewed as an honest signal of quality (*sensu* Zahavi 1977). Accordingly, our results provide empirical evidence for Fitzpatrick's (1998a) suggestion, although the possible age dependency in tail patterning remains an alternative explanation.

Another potential explanation is that age-differences correspond with different tail patterns. However, there is no published evidence of the effect of age on the characteristics of importance presented here, and our data are insufficient to address this possibility. Fulin (1994) suggested that white-black tail pattern is age independent in the red-backed shrike. As such, we can predict that sexual traits in this species are really mediated by blood parasites.

Finally, we note that contrary to earlier predictions (Møller & Thornhill 1998), no relationship between tail asymmetry and prevalence of blood parasites was found. This suggests that asymmetry in tail patterns is not indicative of parasitaemia in red-backed shrikes.

Parasite-mediated assortative mating

We found a bias in pair formation related to parasite status suggestive of assortative. However, since the blood samples were collected after pair-formation, this evidence is suggestive at best. Two possible scenarios may explain assortative pair-formation in red-backed shrikes. First, if time of arrival is independent of parasitism, both uninfected and infected females will compete for males. If uninfected females are in better condition than infected ones, they will more frequently be winners of such competition, and consequently mate with high quality males. Similarly, uninfected males with smaller black terminal tail patches may have superior parasite resistance. As a result, uninfected females choosing preferred mates, may select males with smaller tail patches, which are more frequently uninfected, and they may therefore start breeding earlier than later mated, *infected* females.

An alternative explanation for assortative mating is based on the finding that trypanosome infected Pied Flycatcher *Ficedula hypoleuca* males arrive at their breeding grounds later than uninfected ones (Rätti *et al.* 1993). Uninfected individuals of both sexes may arrive earlier as a consequence of their better body condition and subsequently preferentially mate with each other. In this case, presence of parasites does not influence mating directly, but uninfected pairs simply start to breed earlier. Furthermore, older birds may initiate their breeding earlier than younger birds, and since there may be some degree of correlation between age and parasitaemia (*see* above), the observed assortative mating could occur as a secondary consequence of assortative mating in respect to age.

In conclusion, our results suggest that the common blood parasite *Haemoproteus lanii* may impact the reproductive output of the red-backed shrike through its effects on timing of breeding. Moreover, male secondary sexual trait (black-and-white tail pattern) was negatively correlated with parasitism. Assortative pairing with respect to parasitism gives tentative support for the parasite-mediated sexual selection hypothesis, but further studies are required to separate causation from correlation.

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