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Absence of Blood-parasitization Effects on Lesser Kestrel Fitness

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Blood parasites were thought to be benign to their avian hosts, but recent reviews uncovered important alterations in birds infected with blood parasites (Atkinson and van Riper 1991, Bennett et al. 1993). Hamilton and Zuk (1982) proposed that secondary sexual traits evolved as signals of parasite resistance that are used in mate choice. This hypothesis has been the focus of recent research and reviews (Gibson 1990, Pruett-Jones et al. 1990, Weatherhead 1990, Clayton 1991, Weatherhead et al. 1991, Weatherhead and Bennett 1991, 1992, Lozano 1994, Seutin 1994). Recent studies also have focused on possible detrimental effects of haematozoan infection on reproductive effort (Apanius 1993, Norris et al. 1994), breeding success (Davidar and Morton 1993, Korpimäki et al. 1993, Allander and Bennett 1995), male spring arrival (Rätti et al. 1993), dominance (Weatherhead et al. 1995), and bird survival (Davidar and Morton 1993). Weatherhead (1990) failed to find any fitness cost caused by blood parasites.

The Lesser Kestrel (*Falco naumanni*) is a migratory colonial falcon with strong sexual dimorphism in plumage. Adult males are brightly colored, whereas females and juveniles of both sexes are dull (Cramp and Simmons 1980). We report on levels of parasitization by haematozoa in a Lesser Kestrel population and relate these to hosts' reproductive effort, clutch size, and survival.

Methods.—Our study was conducted in Los Monegros (northeastern Spain; 41°25'N, 0°11'E), where a large population of Lesser Kestrel breeds in abandoned farm houses (Tella et al. in press). Adult birds were caught while roosting or attending nests; captures occurred from spring arrival (March) to the end of the breeding season (July) in 1993 and 1994. Nestlings were sampled in 1993. We took 498 blood samples from the brachial vein of as many hosts. Thin blood smears were individually labelled, air dried, fixed with 100% methanol, and stained with Giemsa (Bennett 1970). A 100× oil-inmersion lens was used to count blood parasites in 100 microscope fields on each smear. Fields were chosen in a line from one end of the slide to the other to compensate for differences in the thickness of the smear (Weatherhead and Bennett 1991). Haemoparasite prevalence was defined as the percentage of infected individuals in a sample, and intensity as the number of parasites per infected bird per 100 microscope fields. The identity of parasite species was determined at the International Reference Centre for Avian Haematozoa (Memorial University of Newfoundland, Canada).

We were able to age most of the birds as they were banded when young. Clutch size was determined in focal pairs, after successive visits to estimate egg losses due to predation (Tella et al. in press). A two-factor ANOVA showed no differences in clutch size between years ($F_{1,107} = 1.774$, $P = 0.18$), but significant differences between first-year and older females ($F_{2,107} = 4.257$, $P = 0.016$). Thus, we only analyzed clutches from after-first-year (AFY) females and pooled years. Laying and hatchling dates were estimated according to the length of the eighth primary feather of the largest chick in each brood (Negro et al. 1992). Based on these data, we grouped the known parents into the prelaying (March to beginning of May), incubation (most birds until beginning of June), and nest-

TABLE 1. Number and percentage (in parentheses) of infected and uninfected Lesser Kestrels depending on sex and year.

Year	Infected	Uninfected
	Males	
1993	1 (1.28)	77 (98.72)
1994	1 (1.11)	89 (98.89)
Total	2 (1.19)	166 (98.81)
	Females	
1993	5 (4.59)	104 (95.41)
1994	5 (4.95)	96 (95.05)
Total	10 (4.76)	200 (95.24)
	Total	
	12 (3.17)	366 (96.83)

ling (until middle July) periods. We resampled several birds in differents periods of the 1994 breeding season to measure their reproductive effort.

To avoid pseudoreplication, we randomly selected one blood sample from birds that were caught more than once in the same year. However, we considered smears taken from the same bird in different years as independent samples, as blood parasitization can change depending on year and bird's age (Gibson 1990, Weatherhead and Bennett 1991, Davidar and Morton 1993, Allander and Bennett 1994, Norris et al. 1994, Seutin 1994). We compared prevalences between years using chi-square tests, with Yates' correction when the expected values were lower than five (Zar 1984).

Results.—The only blood parasite found in our Lesser Kestrel population was *Haemoproteus tinnunculi*. It was detected in 3.17% of adult birds (n = 378; Table 1), and there were no differences in prevalence between the two years of study (1993, 3.20%; 1994, 3.14%; X^2 = 0.0, P = 0.97). Intensity ranged from 1 to 95 infected erythrocytes per 100 inspected microscope fields (median = 21.5, lower quartile = 9, upper quartile = 53.5, n = 12). None of the sampled nestlings (n = 85) were infected.

Prevalence was higher in females than males (Table 1; X^2 = 3.87, $P < 0.05$ for pooled data). All infected birds were more than two years old, this age-related trend being only significant in the case of females (X^2 = 4.47, $P < 0.05$). However, of 64 adults and 4 nestlings taken in 1993 and resampled in 1994 (3 of them parasitized in 1993), only 1 adult shifted status from infected to uninfected.

Regarding the reproductive effort and seasonal variations, no trends in either sex were found in the percentage of parasitized birds throughout the sampling period (males, X^2 = 1.81, P = 0.40; females, X^2 = 0.16, P = 0.92; Table 2). Furthermore, only 1 of the 28 birds resampled in successive periods in 1994 changed from unparasitized to parasitized status.

Clutch size of AFY parasitized females ($\bar{x}$ = 4.66 ± 0.70, n = 9) did not differ from that of unparasitized ones of the same age group ($\bar{x}$ = 4.61 ± 0.70, n = 65; Mann-Whitney U-test, z = −0.046, P = 0.96). Blood parasitization apparently did not affect Lesser Kestrel survival, although the sample size of infected birds was very small for a meaningful comparison; 2 of 6 infected birds, and 90 of 179 uninfected birds returned from 1993 to 1994 (X^2 = 0.16, P = 0.68).

Discussion.—Our study is the first to report *Haemoproteus tinnunculi* parasitizing the Lesser Kestrel. This parasite is broadly distributed in falconid species from the Old and the New World (Peirce et al. 1990, Bennett et al. 1992a). However, its prevalence in the studied Lesser Kestrel population (3.17%) is much lower than that shown by this or other blood parasites in most of well studied avian hosts (28–100%; see Gibson 1990, Pruett-Jones et al. 1990, Weatherhead and Bennett 1991, 1992, Apanius 1993, Davidar and Morton 1993, Korpimäki et al. 1993, Rätti et al. 1993, Allander and Bennett 1994). The causes of the scarcity of haematozoa in our Lesser Kestrel population are not clear, but might be due to the local absence of suitable vectors (ornitophilic ceratopogonids). Lesser Kestrels breed in open, arid regions (typically steppes). In the tundra, another treeless habitat, both sedentary and migratory birds are almost free from blood parasites, while they are heavily parasitized in forested boreal environments (Bennett et al. 1992b, Earlé and Underhill 1993). In forested areas of North America, 85% of American Kestrels (*Falco sparverius*) are parasitized by *H. tinnunculi* (Apanius 1993). Further studies are needed to evaluate these differences (Bennett et al. 1992b). A low density of vectors might also explain that the risk of infection increases with the age of the bird, due to the longer time of exposure, at a lower rate than in highly parasitized species (Weatherhead

TABLE 2. Prevalence (number with percent in parentheses) of *Haemoproteus tinnunculi* in adult male and female Lesser Kestrels in relation to reproductive status.

Breeding period	Male		Female	
	Infected	Uninfected	Infected	Uninfected
Prelaying	2 (2.33)	84 (97.67)	5 (4.72)	101 (95.28)
Incubation	0 (0.00)	49 (100.00)	4 (5.33)	71 (94.67)
Chick rearing	0 (0.00)	28 (100.00)	1 (3.45)	28 (96.55)

and Bennett 1991, Davidar and Morton 1993, Allander and Bennett 1994, Seutin 1994).

As in other species (e.g. Korpimäki et al. 1993, Norris et al. 1993), more female than male Lesser Kestrels were parasitized. This fact may be related to reproductive effort decreasing the host's ability to control chronic infections and/or a greater exposure of females to vectors (Norris et al. 1994). Our results do not support the first hypothesis, since prevalence did not increase intrasexually during the breeding season. Furthermore, males feed the females during the prelaying period to improve the female's body condition (Donázar et al. 1992), and studies using doubly labelled water showed that males tend to spend more energy than females during the chick-rearing period (J. L. Tella, J. A. Donázar, and F. Hiraldo unpubl. data). Taking into account that Lesser Kestrel females invest more time in nesting activities than males (Negro 1991), sex differences in blood parasitization could be related to the spatiotemporal pattern of activity of vectors.

Blood parasitization does not appear to affect individual fitness of Lesser Kestrels given that there is no apparent reduction of clutch size or adult survival. Variation in male spring arrival (up to two months) also cannot be attributable in this population to blood-parasite loads (Rätti et al. 1993, but see Davidar and Morton 1993). Our results also have implications concerning the relation between blood parasites and plumage brightness in birds (Hamilton and Zuk 1982). Variability in the highly colored plumage of male Lesser Kestrels can hardly be explained by haematozoa infestations, unless the population that we studied is exceptional in terms of its low parasite prevalence. Thus, we provide additional evidence that, at least in large populations of some species, processes of mate choice and sexual selection are not mediated by blood-parasite infestation (Bennett et al. 1992b, Earlé and Underhill 1993, Seutin 1994).

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An Association of Habitat with Color Dimorphism in Finches

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Sexual dimorphism in the color of birds is often attributed to sexual selection (Møller and Birkhead 1994), although there are alternative explanations (e.g. Baker and Parker 1979). One of the more puzzling observations is that many closely related species differ in degree of dimorphism. For example, the House Sparrow (*Passer domesticus*) is dimorphic and the Tree Sparrow (*P. montanus*) monomorphic. Understanding differences such as these would be aided if environmental associations with dimorphism could be detected. In one of the few examples of such an association, Crook (1964a, b) showed that the forest-dwelling weaver finches have dispersed territories and are monogamous and monomorphic, whereas savannah species are colonial, polygynous, and dimorphic. In this note I demonstrate an association of habitat with dimorphism across finches on five different continents.

Schluter (1986) presented lists of finch species occurring in similar habitats in five different regions of the world (North America, South America, Europe, Africa, Australia). Finches come from four different families (the Emberizidae, Frigillidae, Estrildidae, and Ploceidae), and no species are held in common across all five regions investigated (for detailed discussion of dataset, see Schluter 1986). Distributions of monomorphic and dimorphic finches in different habitats are shown in Figure 1. Following Schluter (1986) and Schluter and Ricklefs (1993), I used a two-way ANOVA (region × habitat) to test for differences between habitats in the proportion of finch species that are monomorphic. Since there are no replicates per cell, the interaction term cannot be tested and is used as the error term in the ANOVA. There is a significant difference among habitats ($F_{8,10} = 4.8$, $P < 0.05$). There is no significant difference among region ($F_{4,10} = 1.1$, $P > 0.4$). Tests weighting by sample size in each habitat and after arcsin-transforming the data gave similar significance values.

Reasons for the association of sexual dimorphism with habitat are unclear. While an association between habitat and mating system does seem to be generally upheld across bird species (Vehrencamp and Bradbury 1984), the association between mating sys-