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Mate Choice and Reproductive Success in the American Kestrel: a Role for Blood Parasites?

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Abstract

Blood parasites of breeding American kestrels, *Falco sparverius* (40 males and 27 females), were investigated to determine their connections to male showiness, mating success and host fitness. The only haematozoan found in the blood films was *Haemoproteus tinnunculi* (overall prevalence of 74% for females and 53% for males). In adult (+1-year-old) males, the subterminal tail band (character apparently used in female mate choice) was wider in infected males than in non-infected males. This was consistent with the Hamilton–Zuk hypothesis of parasite-mediated sexual selection. Our results also suggest that reproductive effort may increase susceptibility to parasitism. In yearling males, the proportion of individuals infected with *H. tinnunculi* was higher among those tending a large than a small brood at the time of fledging. Hunting effort (proportion of time spent in flight-hunting and wind-hovering) was also higher for males tending large broods than for those tending small broods, and it was higher for yearling than adult males on a given brood size. Reproductive effort may result in greater exposure and/or decreased ability to control chronic latent infections. Parasitic infections, in turn, may have detrimental effects on host fitness.

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Introduction

HAMILTON & ZUK (1982) proposed that some male ornaments, like plumage colouration and tail length, could signal the bearer's heritable resistance against parasites, and that therefore females should prefer extravagantly ornamented males as mates (READ 1988). Many studies have demonstrated that blood and other endoparasites may decrease the mating success of male vertebrates (KENNEDY et al. 1987; SCHALL & DEARING 1987; ZUK et al. 1990a,b; JOHNSON & BOYCE 1991; SPURRIER et al. 1991), but the connection between parasite load and male showiness remains unclear (SCHALL 1986; GIBSON 1990; HAUSFATER et al. 1990; PRUETT-JONES et al. 1990; TINSLEY 1990; BURLEY et al. 1991; WEATHERHEAD et al. 1991; HÖGLUND et al. 1992; KORPIMÄKI et al. 1995). Furthermore, there is no unambiguous evidence for the heritability of parasite resistance (CLAYTON 1991;

KIRKPATRICK & RYAN 1991). Alternative hypotheses to that suggested by HAMILTON & ZUK (1982) state that parasite-based female mate choice could lead to direct fitness benefits, without any heritable genetic gains (GRAFEN 1990a,b; KIRKPATRICK & RYAN 1991; PALOKANGAS et al. 1994). According to the resource provisioning model (CLAYTON 1991; KIRKPATRICK & RYAN 1991), females could choose unparasitized males if they are better providers of resources, such as parental care, than are parasitized males. This model does not require any inheritance for the resistance (CLAYTON 1991). Support for this model comes from the Eurasian kestrel, *Falco tinnunculus*, in which females appear to benefit from higher food provisioning rates of unparasitized males during the incubation and nestling periods (KORPIMÄKI et al. 1995).

Could reproductive effort, on the other hand, increase susceptibility to parasitism? The clearance of parasites, using techniques such as cell-mediated immunity and preening, may be costly to the host in terms of reproductive output (APANUS 1991; KEYMER & READ 1991; TOFT 1991). Consequently, a conflict would be expected between the investment in offspring and clearance of parasites: parental investment may limit the energy available for maintenance of the immune system, making hosts susceptible to parasitism. There are, however, only a few reports on the positive association between reproductive output and parasitism in the wild (FESTA-BIANCHET 1989), and to the best of our knowledge, only two recent studies with great tits, *Parus major*, have documented this in birds (NORRIS et al. 1994; RICHNER et al. 1995).

Parasitic infections, in turn, have been shown to have detrimental effects on the reproductive success of their hosts (SCHALL 1983; ALLANDER & BENNETT 1995; see MØLLER et al. 1990; LOYE & ZUK 1991; HOLT 1993 for reviews; but see also WEATHERHEAD 1990; WEATHERHEAD & BENNETT 1992; DAVIDAR & MORTON 1993). Such effects have also been found in some studies of birds of prey, including Tengmalm's owls, *Aegolius funereus* (KORPIMÄKI et al. 1993), Eurasian kestrels (KORPIMÄKI et al. 1995) and American kestrels, *Falco sparverius* (APANUS 1991).

The American kestrel is a monogamous, open-country raptor, with distinct intersexual division of duties during the breeding season. Males feed females after pair formation, whereas females hunt only occasionally before egg-laying. Thereafter, males provide for the whole family until the young are half grown (BALGOOYEN 1976). Males are smaller than females, a character typical of diurnal raptors (Falconiformes) and owls (Strigiformes) (ANDERSSON & NORBERG 1981; HAKKARAINEN & KORPIMÄKI 1991). Intersexual differences are also pronounced in the plumage colouration. The back of males is rufous with black spots. The tail of males is ventrally rufous, with a black subterminal band. Upper coverts and part of the wing secondary feathers of males are slate-blue, usually with black spots. Females are mostly brownish, with brown bars on the back and tail. The American kestrel is unique among the New World falcons in that the sexes differ in their plumage colouration already from the juvenile stage onwards (PALMER 1988).

In a recent study of parental abilities in American kestrels with respect to male plumage ornaments in eastern Pennsylvania, USA, WIEHN (1994, 1997) found that the male plumage colouration varied between and within age classes. Adult males (+1 year old) had brighter plumage than yearling (1-year-old) males. Furthermore, among age classes, differences in the plumage colouration of adult and yearling males are most distinct in the brightness of the tail, wing and dorsal feathers, and in the width of the subterminal band.

Migratory females usually arrived on breeding territories shortly after males, and pairs were usually formed within about 1 d of the males' arrival. Males with narrow subterminal bands seemed to acquire females fast. These males were the ones to provide the most food for their young and therefore during the nestling phase their partners had to do little hunting (WIEHN 1994, 1997). In the study population, pairs are formed annually (APANUS 1991; D. ARDIA & J. WIEHN, unpubl. data).

In this paper, our aim is to investigate in the American kestrel, whether levels of blood parasites are connected to male secondary sexual (morphological and plumage) characteristics, and therefore possibly to the mating success and the fitness of their hosts. In addition, we examine if breeding effort could increase the susceptibility of parent American kestrels to acquiring a parasitic infection or relapsing with a chronic latent infection.

Methods

Study Area

The study was conducted in east-central Pennsylvania, USA, in the vicinity of Hawk Mountain Sanctuary (40°N, 75°W), in 1993. The study area (about 800 km²) consists mainly of rolling farmland, with small woodlands breaking up the hayfields and pastures. Most kestrels in the study area breed in nest boxes (about 200) that are fastened to solitary trees. Before the breeding season, pellets and prey remains that had accumulated on the bottoms of the boxes were removed, and the boxes were provided with new wood shavings, which may have reduced the ectoparasite load (MØLLER 1989).

Breeding Performance and Parental Characteristics

The initiation of egg-laying was determined by regular visits to nest boxes. During incubation, nest boxes were checked to determine clutch size. Nestlings were marked with US Fish and Wildlife Service metal rings at the age of 2–3 wk and the surviving nestlings were counted when they were 3–4 wk old. After fledging, nest boxes were checked for the remains of dead nestlings.

Parent American kestrels (57 males and 58 females) were trapped with a swing-door trap attached to the nest box or with a bal-chatri, when the nestlings were around 1 wk old. Parents were aged as 1 (yearling) or +1-year-old (adult) using established plumage criteria (SMALLWOOD 1989). Birds were weighed to an accuracy of 1.0 g, and their wing and tail lengths were measured to the nearest 1.0 mm, and tarsus length to the nearest 0.1 mm. The width of the subterminal band was measured with sliding calipers to the nearest 0.1 mm from the 3rd rectrix, at the point of rachis. For scoring the plumage of males, J. W. ranked back, tail and wing colours into six categories, varying from 1 (dull) to 6 (bright). For ranking-criteria the Tikkurila Monicolour Nova paint colour cards and the colour cards of SMITHE (1975) were used. A male's tail and back are usually rufous, but vary from dull yellowish-brown to dark rufous. The colour of the back and tail was ranked as number 1 when yellowish-brown with the rank numbers (2–6) increasing as the intensity of reddish colour in the feathers increased. The ranking was based on following Tikkurila paint colour numbers [colour card number(s) of SMITHE (1975) in parentheses]: number 1 yellowish-brown – dull, Y 162 B (39); 2, Y 135 C (37, 139); 3, Y 095 C (340, 38, 240); 4, Y 129 C (40, 136); 5, Y 089 C (32); 6 (dark rufous – bright), Y 130 C. The colour of the wing (upper coverts and part of the secondary feathers) is usually slate-blue, and males were given a higher brightness rank with the increase in intensity of blue. The ranking of wing feathers was based on following colour card numbers [SMITHE (1975) in parentheses]: 1, J 168 A; 2, K 168 C (84, 87); 3, N 168 C (83); 4, N 162 C; 5, L 162 C; 6, M 168 C. The ranking was repeated by an independent observer (C. J. ROBERTSON), and ranking was found to be identical between the two observers. The brightness score was determined by taking the mean of back, tail and wing colours. Males were measured and ranked before their parasite load and breeding success were known.

Blood Sampling

Among the 115 parent kestrels trapped, blood was randomly sampled from 40 males and 27 females. To rule out possible seasonal changes in the parasite occurrence (APANUS 1991; WEATHERHEAD & BENNETT 1991, 1992), all parent birds were trapped when their nestlings were about 1 wk old.

A drop of blood from the brachial vein was collected in a microcapillary tube, transferred to a clean glass slide, smeared, air-dried, and fixed in absolute ethanol some hours later (BENNETT 1970). Slides labelled with the ring number, sex and age were sent to the International Reference Centre of Avian Haematozoa, where Gordon F. BENNETT determined the prevalence of parasitism (i.e. the proportion of infected birds in the sample population) and estimated parasite loads.

Haematozoa were quantified by counting the number of parasites on 100 fields under oil, using magnification of $\times 100$. The 100 fields were chosen on a line from one end of the slide to the other to compensate for differences in blood thickness which usually occur in smears. Although the method provides a standard approach for quantification of Haematozoa, the results represent estimates, rather than absolute values, of parasite load. For *Haemoproteus* spp., an infection of one parasite per field is roughly equivalent to an intensity of 1% and 1–5% is moderate intensity (G. F. BENNETT, pers. obs.).

Besides *Haemoproteus* spp., *Leucocytozoon toddi* and *Trypanosoma* infection can also be expected in the blood of American kestrels (APANUS & KIRKPATRICK 1988). Blood smears are, however, an inadequate method for detecting *Trypanosoma* infection (BENNETT 1962; APANUS 1991), and their infection rates, if any, remained unknown in this study.

Behaviour Recordings

During the time that young were 11–13 d old, behavioural observations were made on 20 pairs, 5 h per pair, divided into 2.5-h periods in the morning and afternoon of two days. Observations consisted of continuously recording (MARTIN & BATESON 1986) the occurrence of different behavioural acts. Recordings were made using 10 \times binoculars and a wide angle, 20 \times telescope. To avoid disturbing the birds, recordings were made at a distance of 150–300 m from the nest. Observations were made only on rainless days. The proportion of time spent actively hunting, i.e. directional flight between the nest and hunting area, flight bouts during hunting, and wind-hovering, was used as an indicator of an individual's hunting effort (MASMAN & KLAASSEN 1987, for energy requirements of different hunting methods.)

All statistical analyses were performed using SPSS for Windows software (NORUSIS 1993). To correct significance levels for correlations, we used the sequential Bonferroni procedure (RICE 1989) on a variable by table-wide level (in Table 2, yearling and adult males were handled as if they would have been in different tables). If a significance level is presented with Bonferroni correction, the term 'corrected p' will be used.

We used logistic regression [where infection was treated as a binary variable (non-infected/infected); HOSMER & LEMERSHOW 1989; TREXLER & TRAVIS 1993] to estimate infection probabilities of American kestrels. The brood size at fledging was used as an independent variable to estimate the infection probabilities. No logistic regression models with interaction terms (brood size \times parental age) were performed, as the power to produce significant interactions was low with given sample sizes. Instead, the probability of infection was analysed for each age class separately. When testing the probability of infection among yearling males and adult females, the brood size was treated as a continuous variable (as there were six different brood sizes for yearling males, 0, 1, 3, 4, 5 and 6, and seven for adult females, 0–6), whereas when testing the probability of infection among adult males and yearling females the brood size was treated as a categorical variable (as there were only two and four different brood sizes). The use of categorical independent variables is common in logistic regression and is thoroughly discussed with examples in HOSMER & LEMERSHOW (1989). Significance of the brood size was estimated using likelihood ratio statistics (HOSMER & LEMERSHOW 1989; NORUSIS 1993), and it is given by the change in deviance from null model (denoted as Δ Dev), which corresponds approximately to a χ^2 d distribution. All statistical tests are two-tailed.

Results

The only blood parasite detected in blood films of parent kestrels was *Haemoproteus tinnunculi* (overall prevalence 4% for females and 53% for males, Table 1). We found no sex- or age-class-related differences in the haemoproteid loads or prevalences (Table 1). The parasite loads of paired males and females were not correlated (Spearman rank correlation, $r_s = 0.05$, $n = 25$, $p = 0.82$). Sampling date did not have obvious relationships either to the haemoproteid load of males ($r_s = 0.07$, $n = 40$, $p = 0.68$) or females ($r_s = 0.05$, $n = 27$, $p = 0.80$). In addition, there was no difference in the sampling dates between

Table 1: *Haemoproteus tinnunculi*—load estimates (*Haemoproteus tinnunculi*—estimates were quantified by counting their numbers in 100 fields under oil ($\times 100$ magnification) for yearling (1-yr-old) and adult (+1-yr-old) male and female American kestrels

	Females		Males	
	Yearling	Adult	Yearling	Adult
No. of infected cells per 100 fields, mean	42.9	27.4	28.3	23.5
Median	21	18	0.5	0.5
SD	49.8	35.7	40.9	32.5
Range	0–160	0–115	0–115	0–108
Prevalence (%)	89	67	53	52
Age classes pooled (%)		74		53
Age classes and sexes pooled (%)			64	
n	9	18	19	21
Test ¹				
Load between:				
Age classes	U	194		64
	P	0.87		0.38
Sexes	U		446.5	
	P		0.22	
Prevalence between:				
Age classes	χ^2	—		0.00
	P	0.36		0.99
Sexes	χ^2		3.16	
	P		0.22	

¹The significance of the intersexual and age-class-related (1 and +1-yr-old) difference in the parasite load was tested by Mann–Whitney U-test and that of the prevalence by χ^2 test, except for that of the prevalence between age classes of females, which was tested by Fisher's exact test

infected and non-infected parent kestrels (mean \pm SD = 11 Jun. \pm 17 d vs. 12 Jun. \pm 16 d, Mann–Whitney U-test, U = 193.5, p = 0.87 for males; mean \pm SD = 17 Jun. \pm 25 d vs. 13 Jun. \pm 12 d, U = 69.5, p = 0.98 for females).

Among the plumage characteristics of adult males, the width of the subterminal tail band was related to their parasite status: it was significantly wider among the infected than non-infected individuals (mean \pm SE = 25.7 \pm 0.9 vs. 22.3 \pm 0.7 mm, t-test, t = 2.97, p = 0.008), whereas there was no obvious difference in yearling males (mean \pm SE = 24.8 \pm 0.8 vs. 26.4 \pm 2.1 mm, t = 0.77, p = 0.45). The intensity data gave similar results: the width of the subterminal band in adult males was positively correlated with the haemoproteid load estimate (Table 2; Fig. 1), but the same was not true for yearling males (Table 2). If only infected adult males were considered, the relationship between subterminal band and load estimate was still significant (r = 0.65, n = 11, p = 0.03; here parametric correlation coefficient is used as the parasite load data are normally

Table 2. Spearman rank correlations (r_s ; significance levels are corrected by the sequential Bonferroni procedure (RICE 1989); *corrected $p < 0.05$) between the plumage characteristics of yearling (1-yr old) and adult (+1-yr old) American kestrel males and the size of *Haemoproteus tinnunculi* load estimates (load estimate as in Table 1). Number of males is 19 yearlings and 21 adults

Male plumage characteristics	Yearling	Adult
Back colour	0.16	-0.12
Tail colour	0.03	0.12
Wing colour	-0.14	0.26
Brightness score ¹	-0.01	0.13
Subterminal band width	0.08	0.63*

¹Brightness score was calculated as the mean score of back, tail and wing colours

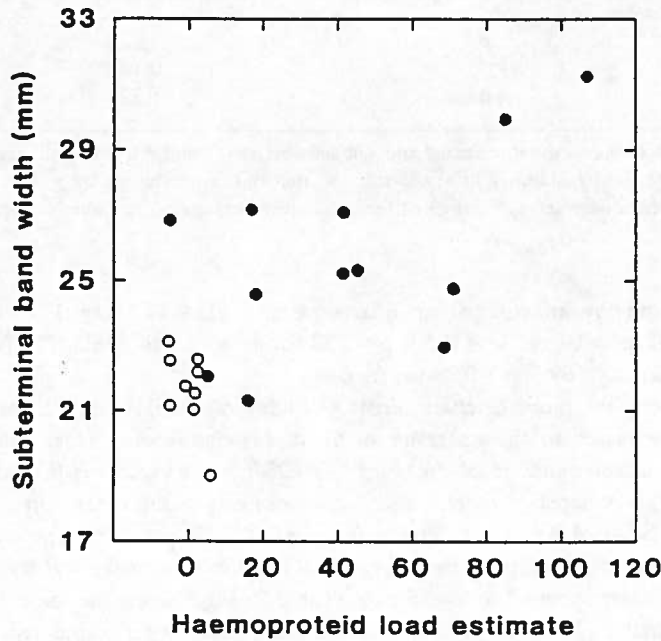


Fig. 1. Load estimate of *Haemoproteus tinnunculi* (number of infected cells per 100 fields) in relation to the subterminal band width of adult males. Circles represent parasite intensity estimates of zero; dots represent estimates over zero. Note: jitter option in SYGRAPH has been used to separate overlapping data points, and the option makes some parasite intensity estimates of zero fall below zero

distributed after excluding the zero values). The width of the subterminal band was not associated with the tail length ($r = -0.07$, $n = 56$, $p = 0.62$). Neither back, tail and wing colour, nor plumage brightness scores showed any obvious relationship to the parasite load estimates of yearling or adult males (Table 2).

We found no correlation between any other morphological trait we measured, and the haemoproteid load estimates of males and females (for all $p > 0.1$). Classifying males and females as infected and non-infected did not change the results. Neither we did find any correlation between laying date, clutch size, the number of fledglings produced and either male or female haemoproteid load estimates (for all $p > 0.1$).

Behavioural data showed that males tending large broods had higher hunting effort (proportion of time spent in flight-hunting and wind-hovering) than males tending small broods (Fig. 2). Among females there was no such clear tendency ($r_s = 0.33$, $n = 20$, $p = 0.16$). Comparisons between yearling and adult males showed that, when the brood size was controlled for, the hunting effort of yearling males was higher than that of the adult males (proportion of time used in flight-hunting and wind-hovering, mean \pm SD = 37.5 ± 30.6 (yearlings) vs. 20.0 ± 18.8 (adults), ANCOVA for arcsin-transformed hunting effort, $F_{1,19} = 5.20$, $p = 0.04$). In females, again, no such clear tendency was found (mean \pm SD = 3.6 ± 3.1 (yearlings) vs. 5.2 ± 2.9 (adults), ANCOVA for arcsin-transformed hunting effort, $F_{1,19} = 0.91$, $p = 0.35$).

We entered brood size at fledging into the logistic regression models to estimate the probability of parental infection. Only model (1), where the brood size estimates the

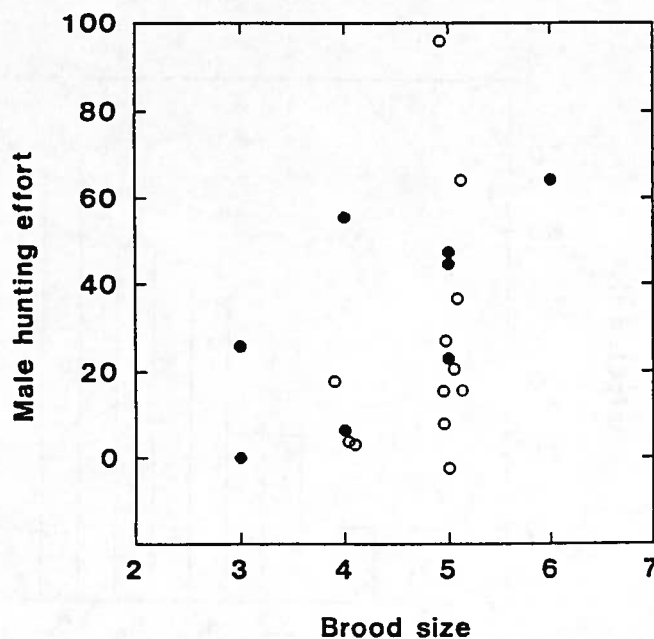


Fig. 2: Relationship between brood size and male hunting effort (proportion of time spent in flight-hunting and wind-hovering) ($r_s = 0.46$, $n = 20$, $p = 0.04$). Dots represent yearling males; circles represent adult males. Note as in Fig. 1

Table 3: Logistic regression models for the probability of infection (infected/non-infected) in relation to brood size at fledging. Deviance in null model for yearling males: 26.29; for adult males: 29.07; for yearling females: 6.28; and adult females: 20.60

Model	df	Δ Dev ¹	p
Infection of males			
(1) Yearlings	1	8.38	0.004
(2) Adults	3	6.04	0.11
Infection of females			
(3) Yearlings	2	1.78	0.41
(4) Adults	1	3.05	0.08

¹ See text for explanation.

probability of infection in yearling males, turned out to be significant (Table 3), whereas the models for adult males (2), or yearling (3) and adult (4) females were not significant (Table 3). Accordingly, in yearling males, the prevalence of infection increased with the number of fledglings (Fig. 3).

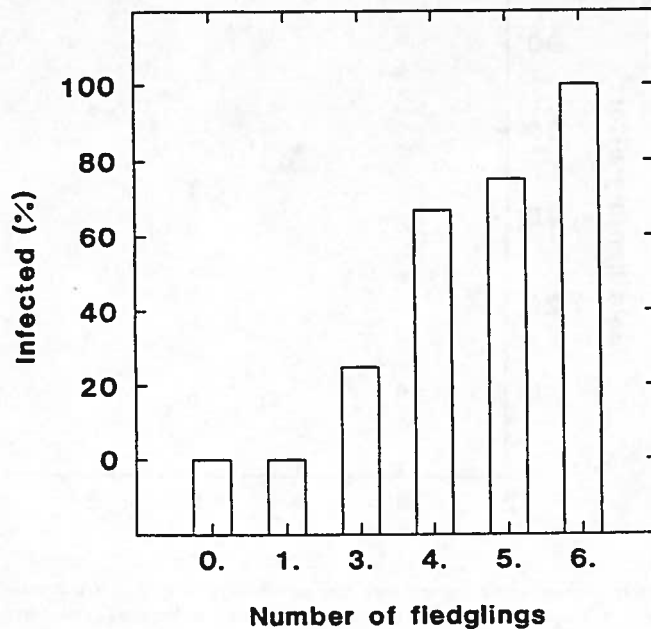


Fig. 3: The proportion of infected yearling males in relation to the brood size at the time of fledging. Number of cases (in increasing order of the number of fledglings produced): 1, 2, 4, 3, 8, 1

Discussion

Parasites and Sexual Selection

In general, our results support the prediction of the Hamilton–Zuk hypothesis, in that we found that among adult males, the width of the subterminal band was positively related to *Haemoproteus tinnunculi* load, and there is some evidence that males with narrow subterminal tail bands acquire partners sooner than males with wide subterminal bands (WIEHN 1994, 1997). However, it must be remembered that blood parasites could affect the plumage characteristics only at the time of moult. As American kestrels moult their flight and body feathers annually, starting concurrently with breeding and completing before autumn migration (PALMER 1988), inter-individual differences in plumage characteristics are potentially influenced by the parasite burden acquired during the previous summer transmission season. Parasite burdens of different intensities in the present breeding season may result from immunological variation between individuals as well as new infections acquired that year. Many blood parasite infections persist from one year to the next (BENNETT & BISHOP 1990).

The quality of tail feathers in adult kestrels is apparently affected (if not genetically determined) by the males' own ability to invest in moult during breeding. As the parasite intensities in individual American kestrel males are well repeatable between years (APANIUS 1991), we suggest that the tail ornamentation of adult males may be a condition-dependent 'handicap' revealing the vigour of males during the breeding season, at the onset of moult. The tail ornamentation may advertise that parasites have not stressed the male during moult, and therefore, the male has a great potential to be a good parent. However, susceptibility to vectors can confound these results. With a single exception, all known vectors of haematoproteids are ornithophilic species of the genus *Culicoides* of the dipteran family Ceratopogonidae (DESSER & BENNETT 1993). Even if there is no evidence that *Culicoides* are differentially attracted to different plumage colours (YEZERINAC & WEATHERHEAD 1995), males may have been differentially exposed to these vectors on their earlier breeding grounds, migration routes and overwintering sites, as vector densities may vary, for example, between localities and years (BENNETT & CAMERON 1974; DESSER et al. 1975; VAN RIPER et al. 1986; KIRKPATRICK & SUTHERS 1988; WEATHERHEAD & BENNETT 1991; BENNETT et al. 1995). In addition, most ornithophilic ceratopogonids have habitat preferences, especially with respect to height above the ground (BENNETT 1960).

In western fence lizards, *Sceloporus occidentalis*, the non-parasitized individuals are brighter in their colour than parasitized individuals (RESSEL & SCHALL 1989). In American kestrels, earlier work in the same study area indicates that in males there is an increase in plumage brightness with age (WIEHN 1994, 1997), stressing the importance of taking age into account when studying the parasite-trait relationships. Furthermore, parasites can be expected to affect, not only changes in colouration, but also size or the fine structure of sexual ornaments (MØLLER 1990). Moreover, plumage characters invisible to the human eye may confound the relationship between female preference and male plumage brightness (BENNETT et al. 1994). Recently, experiments have shown that Eurasian kestrels are able to see ultraviolet scent marks left by voles (VIITALA et al. 1995). American kestrels, too,

may be sensitive to ultraviolet light, and colours of feathers may look different in that spectrum (BURKHARDT 1989).

An earlier study indicates that haemoproteids are undetectable in all the nestlings in our study population (APANUS & KIRKPATRICK 1988), but during autumn migration, 69% of juvenile American kestrels are infected with *Haemoproteus tinnunculi* (KIRKPATRICK & LAUER 1985). This suggests that parasite transmission takes place after the nestling phase, but before the autumn migration. The prepatent period for *Haemoproteus* is 14–16 d (DESSER & BENNETT 1993). As the tail feathers of yearlings were grown the first time as juveniles in the nest (PALMER 1988), the plumage characteristics can actually be expected to reflect parasite status only in adult kestrels, not in yearling males. The feather characters of yearlings may be mostly determined by parental feeding and thus the tests of the hypothesis of parasite-mediated sexual selection are best restricted to adult individuals.

Parasites, Breeding Success and Investment in Reproduction

The Hamilton–Zuk hypothesis also connects parasites to the fitness of their host. Intraspecifically, there should be an inverse relationship between a host's fitness and its parasite load (READ 1988). An earlier study in the same population of American kestrels demonstrated that the higher a female's *Haemoproteus tinnunculi* load the fewer eggs she laid (APANUS 1991). However, APANUS (1991) also found that parasite load of females apparently increases over the course of the breeding season, and the increase is most marked among females with large broods. Accordingly, as in our study samples were taken in the early nestling phase, we are unable to judge whether female parasite load is related to clutch size. Furthermore, the power to detect any adverse effects of parasites may have been too low with given sample sizes. The fact that we did not find a negative correlation between male parasite load and breeding performance may simply be because the levels of haemoproteids circulating in male blood in our study may have been too low to have any adverse effects on host breeding success. Males with a narrow subterminal band, however, seem to provide the most food for their young and fledge relatively large numbers of young (WIEHN 1994, 1997). This is in accordance with the resource provisioning model (CLAYTON 1991; KIRKPATRICK & RYAN 1991), which states that female choice would lead to direct fitness benefits, without any heritable genetic gains (GRAFEN 1990a,b; KIRKPATRICK & RYAN 1991; PALOKANGAS et al. 1994). Whatever proximate mechanism (direct or indirect) is involved, it seems that subterminal tail bands appear to be reliable cues of male quality so that females mated with narrow-banded males gain reproductive success (WIEHN 1994, 1997).

Our results also suggest that a large brood size may increase the susceptibility to haematozoan infection. As an immunological response to parasites is usually costly for the host (KEYMER & READ 1991; TOFT 1991), and as parental investment is also costly (NUR 1988; DIJKSTRA et al. 1990; CLUTTON-BROCK 1991), hosts may need to trade-off investments in reproduction and clearance of parasites. In the chronic phase of *Haemoproteus* infection, the immune system of the host usually controls the parasite, but the infection may relapse due to both physiological and environmental stress (ATKINSON & VAN RIPER 1991).

During the nestling phase, the parental effort can be expected to be high, due to the

high food demands of young (MASMAN et al. 1989; TOLONEN & KORPIMAKI 1994). In Eurasian kestrels, the daily energy expenditure increases with increased brood size (MASMAN et al. 1989). Our observations showed that American kestrel males tending large broods spent more time in flight-hunting and wind-hovering (a good estimate of energy expenditure, MASMAN & KLAASSEN 1987) than males tending small broods. Moreover, yearlings spend more time in flight-hunting than adults on a given brood size level, suggesting the experience of adults in finding food (either due to better foraging skills or having a better-quality hunting territory) and thus being able to provide the family with less hunting effort than yearlings. Our finding that in the yearling males, the prevalence of parasitism was higher among those tending large than small broods, is in agreement with the hypothesis that parasitism is related to the increased reproductive effort.

An alternative, albeit not mutually exclusive, explanation for the association between the large brood size and infection might be the differential exposure of hosts to the parasite vectors (see Parasites and Sexual Selection). High reproductive effort may reduce time available for preening, and hence removal of potential haemoproteid vectors. Furthermore, the high reproductive effort may increase the time spent in sites with high vector densities.

The potential cost of parasitism requires evidence that infections reduce host fitness. Recently, such evidence has been accumulating, indicating that parasites can decrease both the breeding and mating success of wild animals (MÖLLER et al. 1990; LOYE & ZUK 1991; HOLT 1993; ANDERSSON 1994 for reviews). Therefore, parasite infections may have the potential to influence the evolution of life histories and female preference. Our study suggests both the causes and consequences of parasitism. However, we would like to underline that without manipulations of parasite burdens or reproductive effort, the interpretation of results may be ambiguous, and therefore such work is badly needed to further test these assumptions.

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