Parental Effort and Blood Parasitism in Tengmalm's Owl: Effects of Natural and Experimental Variation in Food Abundance

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Parental effort and blood parasitism in Tengmalm's owl: effects of natural and experimental variation in food abundance

Petteri Ilmonen, Harri Hakkarainen, Vesa Koivunen, Erkki Korpimäki, Adele Mullie and Dave Shutler

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We investigated the association between parental effort and susceptibility to haematozoan parasites in vole-eating Tengmalm's owls (*Aegolius funereus*) from 1993 to 1995. In a poor vole year (1993), almost all breeding Tengmalm's owls were infected with *Trypanosoma avium*, whereas in a good vole year (1994), only a few owls were infected. In a moderate vole year (1995), we found an intermediate prevalence of trypanosomes. In the moderate vole year, trypanosome-infected females were in poorer condition than were uninfected females. In the same moderate vole year, high parental effort was associated with increased susceptibility to haematozoan parasites for both genders, whereas in a good vole year no such association was found. In two breeding seasons (1996–1997) of relatively low vole abundance we tested whether supplementary food decreased parasite loads. In accordance with correlative data, trypanosome prevalence was lower among supplemented than control females. Our results support a hypothesis of a trade-off between parental effort and immunocompetence, and emphasize the importance of varying environmental conditions and physical condition of individuals on susceptibility to haematozoan infections.

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Costs of reproduction are defined as allocation tradeoffs between current reproductive effort and future reproductive potential, so that when organisms invest in current reproduction their future survival and/or breeding success will be reduced (Williams 1966, Charnov and Krebs 1974, Partridge and Harvey 1988). Costs of reproduction are thought to be incurred through somatic deterioration (Drent and Daan 1980, Partridge 1987) and by increased predation risk (Calow 1979, Magnhagen 1991). However, actual mechanisms underlying costs are still largely unknown (Lessells 1991). Recently, it has been suggested that parasites may mediate costs of reproduction (Møller 1993, Gustafsson et al. 1994, Norris et al. 1994). Several observational (Festa-Bianchet 1989, Ots and Hõrak 1996, Wiehn et al. 1997) and experimental studies (Norris et al. 1994, König and Schmid-Hempel 1995, Richner et al. 1995, Oppliger et al. 1996, Wiehn and Korpimäki 1998) have shown that high parental effort can increase host susceptibility to parasites. Because reproduction and immune defence are both thought to be energetically costly (Keymer and Read 1991, Toft 1991, Sheldon and Verhulst 1996), there may be a trade-off between allocation of resources to reproduction and immunity.

The magnitude of reproductive costs may be attributed to variation in environmental conditions among years (Schaffer 1974, Nur 1988). Tuomi et al. (1983) proposed that costs of reproduction may emerge only when resource levels are limited, but not if resource intake can be elevated. Interestingly, poor nutrition has often been found to be associated with

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impaired immunocompetence and susceptibility to disease (e.g. Chandra and Newberne 1977, Gershwin et al. 1985). Although annual variation in resource levels could potentially modify the cost of reproduction, environmental variation in food levels has mostly been ignored in previous studies on host-parasite interactions (see Møller 1993).

We investigated whether there is an association between parental effort and susceptibility to blood parasites in vole-eating Tengmalm's owl (*Aegolius funereus*) relative to prey availability. We expected that this association would be more pronounced under poor than good food conditions, when owls apparently have fewer resources for reproduction and immune defence. As indirect measures of parental effort we used clutch initiation date, clutch size and number and mass of fledglings. We also studied connections between parental body condition and parasite infections. To study experimentally the effects of resource levels on susceptibility of parent owls to parasitism, we food-supplemented female Tengmalm's owls during two years of relatively low natural food availability. We predicted that females provided with supplemented food would have more resources for both reproduction and immune defence, and would therefore have lower haematozoan prevalence than unfed control females.

Material and methods

Study organisms

Tengmalm's owl is a small, nocturnal predatory bird with a holarctic distribution that breeds in nest-boxes and natural cavities in coniferous forests. Voles of the genera *Clethrionomys* and *Microtus* are their preferred prey (e.g. Sulkava and Sulkava 1971, Korpimäki 1988). In our study area, like elsewhere in central and northern Fennoscandia, densities of these voles fluctuate cyclically with a period of 3–4 years (Hansson and Henttonen 1985, Korpimäki and Norrdahl 1989). In good vole years, voles represent 70–90% of the diet of breeding Tengmalm's owls, whereas in poor vole years this declines to 10–20% (Korpimäki 1988). At such times, alternative prey (shrews *Sorex* sp. and small passerine birds) are consumed (Korpimäki 1988). This considerably decreases reproductive success of Tengmalm's owls (Korpimäki and Hakkarainen 1991, Korpimäki 1992). In Tengmalm's owl, both genders have distinct roles in parental care; males do most of the hunting from courtship feeding until he end of the breeding season, whereas females incubate eggs and brood young until they are about three weeks old (Korpimäki 1981).

Tengmalm's owls harbour several blood parasites, such as intracellular haemosporidians *Haemoproteus noctuae*, *H. syrnii*, *Plasmodium circumflexum*, and *Leucocytozoon ziemanni*, and extracellular *Trypanosoma avium* haemoflagellates (Korpimäki et al. 1993). Haemosporidians and trypanosomes are transmitted by blood-sucking arthropods (Bennett 1961, Molyneux 1977, Atkinson and van Riper 1991). Although trypanosomes and haemosporidians are traditionally considered to be non-pathogenic in birds (Baker 1976, Fallis and Desser 1977), there is some evidence that both may cause histopathological changes (e.g. Becker et al. 1956, Molyneux et al. 1983, Atkinson et al. 1988), and dysfunction and stress in physiological systems of their hosts (Toft 1991 and references therein).

Observational data

Empirical data were collected in the Kauhava region, western Finland (ca 63°N, 23°E), during 1993–1995. Our study area covers 1300 km^2 and includes 500 nest-boxes and ca 30 natural cavities suitable for Tengmalm's owls.

In each study year nest-boxes were visited at least twice to determine all breeding attempts in our study area. Active nests were checked as many times as necessary to determine laying date, final clutch size, and number of fledglings (further details in Korpimäki and Hakkarainen 1991). Both female and male parents were trapped when their nestlings were 1–2 weeks old. Both fledglings and parents were weighed to the nearest 1 g with Pesola spring balances. As a measure of parental body condition, we used the residuals from a linear regression of body mass on wing length.

Vole abundance was monitored with snap-trap censuses from two separate areas (ca 14 km apart) within the main study area in early May. Trapping in both areas was done in four study plots representing the four main habitat types (spruce forest, pine forest, cultivated field, and abandoned field). In each study plot, 50 to 100 metal mouse snap-traps, baited with bread, were set 10 m apart in small mammal runs for four days (total 1680 trap nights/year) and were checked once a day (further details in Korpimäki and Norrdahl 1989). We standardized the total number of *Microtus* and *Clethrionomys* voles as the number of individuals caught per 100 trap nights.

Supplementary feeding experiment

To experimentally test the role of food abundance on susceptibility of parent owls to haematozoan infections, we provided supplementary food to females in two years (1996 and 1997) of relatively low natural food abundance. We provided females and their young with seven dead, newly hatched rooster chicks (average weight 40 g) per nest every third day from early incubation period until nestlings were two weeks old. This is a substantial improvement in food supply for females, because the mean daily food requirement for an adult Tengmalm's owl is 38 g, and for a nestling 30.5 g (Korpimäki 1981). Nests with matched laying dates served as unfed controls. We visited control nests as often as experimental nests to standardise disturbance to females.

Blood sampling

When nestlings were 1–2 weeks old, blood samples were taken from parent owls. A drop of blood from the brachial vein was collected in a microcapillary tube, transferred to a glass slide, smeared, air dried and fixed in absolute ethanol some hours later (Bennett 1970). Blood samples were Giemsa-stained and the prevalence of parasitism and the intensity of parasite burdens were determined by using a light microscope. Haemosporidian parasites were quantified by counting the number of parasites per 100 fields. Magnification used for leucocytozoids was 400 ×, and for *Haemoproteus* and *Plasmodium* 1000 × under oil. Trypanosomes were quantified using the hematocrit centrifuge method (Woo 1970). Blood was collected in 75 μl hematocrit tubes, which were subsequently stored at ambient temperature. Within 12 h of sampling, tubes were centrifuged for 5 min at 5000 RPM. Immediately thereafter, trypanosomes were counted by inspecting each tube for 5 min under a light microscope at 400 × magnification.

Statistical analyses

We used two different types of log-linear analyses: 1) hierarchical log-linear analyses, to study if parasite infections were dependent on each other, year or gender, and 2) logistic regression (Hosmer and Lemeshow 1989, Trexler and Travis 1993), to estimate infection probabilities of Tengmalm's owl parents relative to supplementation treatment. In logistic regression, year and treatment (supplementation or control) were treated as categorical variables, with indicator (dummy) coding. Both the main effects and their interactions were entered into analyses. In both hierarchical log-linear analyses and logistic regression, the model with best fit was chosen using backward (stepwise) model selection. In backward elimination the effect whose removal results in the least significant change in the likelihood-ratio χ^2 is eligible for elimination, provided that the observed significance level is larger than the criterion for remaining in the model (Norušis 1993). Both log-linear analyses were performed using SPSS for Windows software (Norušis 1993). We report only significant terms. For individuals sampled during two consecutive years, only one observation was chosen randomly for between-year analysis.

Results

Infections of *L. ziemanni*, *T. avium* and *Haemoproteus* (*H. syrnii* and *H. noctuae*) were detected from the blood samples of parent Tengmalm's owls (Table 1). Almost all individuals had *L. ziemanni* (Table 1), and thus we used only intensity of this species for statistical analyses. We treated each parasite species separately in analyses, because of their independence (Table 1).

Among-year differences in prevalence of *T. avium* were highly significant (Table 1) and varied inversely with changes in vole and owl densities (Fig. 1). In a poor vole year (1993), almost all breeding Tengmalm's owls had some trypanosomes, whereas in a good vole year (1994), only a few owls were infected (Fig. 1). During a moderate vole year (1995), we found an intermediate prevalence of trypanosomes (Fig. 1). Prevalence of *L. ziemanni* and *Haemoproteus* parasites did not vary among years (Table 1).

Haematozoan infections and body condition

In a moderate vole year (1995), *T. avium* infected females were in poorer body condition than uninfected ones (t-test: $t = 2.2$, df $= 21$, $P = 0.04$; Fig. 2), but this difference was not found in good vole year 1994 ($t = -0.7$, df $= 28$, $P = 0.51$). Body condition of males did not differ between *T. avium* infected and uninfected individuals in any year (1994, infected: $\bar{x} = 1.19$, S.D. $= 5.12$, $n = 11$; uninfected: $\bar{x} = 2.43$, S.D. $= 5.76$, $n = 17$; $t = 0.58$, df $= 26$, $P = 0.57$; 1995, infected: $\bar{x} = -1.09$, S.D. $= 6.28$, $n = 17$; uninfected: $\bar{x} = 3.15$, S.D. $= 7.68$, $n = 6$; $t = 1.3$, df $= 21$, $P = 0.19$). Sample sizes were too small to test for differences in body condition between

Table 1. Prevalences (% of individuals infected) for different haematozoan species present during the nestling period (both genders) in 1993–1995. Under number sampled, the first number refers to haemosporidian sample size and the last to trypanosome sample size. The dependence of parasites on each other, year and gender was tested with hierarchical log-linear analysis, using backward elimination of models (see Methods). First, significance for each term in the model is presented and, then, significance of the model involving all the terms ($P = 1$ in a model with perfect fit). LLR = log likelihood ratio χ^2. L, T and H refer to the parasite species, and Y to year.

Parasite		Females	Males
L. ziemanni	(L)	100.0	94.3
T. avium	(T)	46.6	64.0
Haemoproteus	(H)	12.3	7.5
Number sampled		65/58	52/50

Term	LLR	df	P
L	120.4	1	<0.0001
T × Y	21.7	2	<0.0001
H	70.5	1	<0.0001
Model	17.8	16	1.00

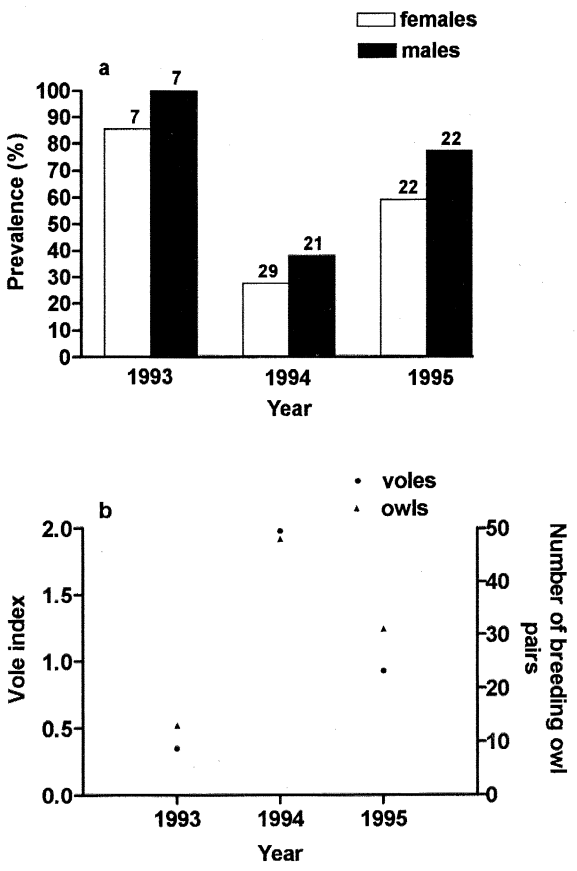

Fig. 1. a. Prevalence (% of infected individuals) of *Trypanosoma avium* in Tengmalm's owls during 1993–1995. Sample sizes are above bars. b. Vole indices (pooled number of *Microtus* and *Clethrionomys* voles snap-trapped per 100 trap-nights) and the number of breeding Tengmalm's owl pairs recorded in the whole study area in 1993, 1994 and 1995.

Haemoproteus infected and uninfected individuals, except for females in 1994, when no difference was detected (infected: $\bar{x} = 0.32$, S.D. $= 17.91$, $n = 5$; uninfected: $\bar{x} = 0.87$, S.D. $= 17.60$, $n = 26$; $t = 0.1$, df $= 29$, $P = 0.95$).

Parental effort and parasite infection

In the moderate vole year, males which raised heavy fledglings had high intensities of *L. ziemanni* (Table 2). In the same study year, *T. avium* infected males produced more fledglings than did uninfected individuals (Table 3). There was no difference in reproductive traits between *T. avium* infected and uninfected females (Table 3). However, in the moderate vole year females which produced large clutches had higher intensities of trypanosomes during the nestling period (Table 4). In females no connection between intensities of *L. ziemanni* and reproductive traits was found (Table 4).

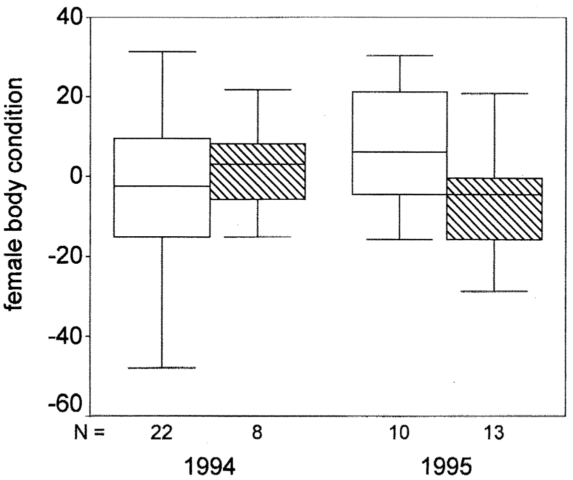

Fig. 2. Mean body condition (residuals from a linear regression of body mass on wing length) of *T. avium* infected (shaded box) and uninfected (open box) females in 1994 and 1995. Sample sizes are below bars. Boxes contain 50% of values falling between 25th and 75th percentiles and a line indicating median. Whiskers extend from the boxes to the highest and lowest values. Sample sizes are below boxes.

Supplementary feeding experiment

Prevalence of *T. avium* was significantly affected by supplementary feeding in females (Model with the best fit in logistic regression: LR $\chi^2 = 4.9$, df $= 1$, $P = 0.03$, Table 5). However, supplementation did not have any significant effect on *L. ziemanni* or *Haemoproteus* infection probabilities in females. In males, infection proba-

Table 2. Spearman rank correlation between *L. ziemanni* and *T. avium* intensities of male Tengmalm's owls and their breeding success in 1993, 1994 and 1995. Only infected individuals included. * = Bonferroni-corrected, $P < 0.05$.

1993	*L. ziemanni*		*T. avium*	
	r_s	n	r_s	n
Laying date	−0.45	11	0.06	8
Clutch size	−0.24	10	−0.63	7
No. of fledglings	−0.19	11	−0.47	8
Body mass of fledg.	−0.32	7	−0.10	5
1994	*L. ziemanni*		*T. avium*	
	r_s	n	r_s	n
Laying date	0.04	25	−0.36	11
Clutch size	−0.03	24	−0.01	11
No. of fledglings	−0.02	23	−0.03	11
Body mass of fledg.	0.30	20	0.36	8
1995	*L. ziemanni*		*T. avium*	
	r_s	n	r_s	n
Laying date	−0.01	23	−0.27	18
Clutch size	−0.08	20	0.30	17
No. of fledglings	0.29	16	−0.37	12
Body mass of fledg.	0.76	12 *	−0.20	10

Table 3. Differences in reproductive traits between *T. avium* infected and uninfected male and female Tengmalm's owls in 1994 and 1995. Means were compared with Mann-Whitney *U*-test. * = Bonferroni-corrected, $P<0.05$.

Males 1994	infected			uninfected			test	
	n	Mean	S.D.	*n*	Mean	S.D.	*U*	*P*
Laying date #	11	12.3	5.3	17	8.1	6.5	64.0	0.16
Clutch size	11	5.3	1.2	16	5.8	0.9	112.0	0.21
No. of fledglings	11	2.2	1.5	15	2.4	1.2	88.5	0.75
Body mass of fledg.	8	109.6	17.8	13	111.9	11.3	60.0	0.56
Males 1995	infected			uninfected			test	
	n	Mean	S.D.	*n*	Mean	S.D.	*U*	*P*
Laying date #	13	4.4	14.4	5	0.0	15.4	27.5	0.62
Clutch size	12	5.6	1.0	3	5.7	0.6	18.5	0.94
No. of fledglings	12	3.3	1.5	5	0.8	1.3	7.0	0.05 *
Body mass of fledg.	10	122.0	14.4	3	106.4	13.5	6.0	0.13
Females 1994	infected			uninfected			test	
	n	Mean	S.D.	*n*	Mean	S.D.	*U*	*P*
Laying date #	8	12.1	4.8	17	10.4	5.1	50.5	0.31
Clutch size	8	5.8	0.7	17	5.5	1.1	61.0	0.66
No. of fledglings	7	2.0	1.3	17	2.3	1.4	68.5	0.56
Body mass of fledg.	6	108.0	10.0	13	110.6	15.7	40.0	0.93
Females 1995	infected			uninfected			test	
	n	Mean	S.D.	*n*	Mean	S.D.	*U*	*P*
Laying date #	9	1.5	8.9	8	3.1	19.4	39.5	0.74
Clutch size	8	5.6	0.9	6	5.8	0.9	26.5	0.73
No. of fledglings	8	3.0	1.8	8	1.9	1.8	21.0	0.24
Body mass of fledg.	7	120.3	14.3	6	116.1	17.4	17.0	0.57

1 = 1 April.

bility for none of the haematozoan species was affected by food supplementation at the nests.

Discussion

Resource levels and susceptibility to haematozoan infections

We predicted that among-year variation in prevalence of haematozoan infections should be associated with variation in food conditions, if immunocompetence against parasites is related to resource levels. In accordance with our prediction, among-year *T. avium* prevalence for both female and male Tengmalm's owls was inversely related to vole abundance.

Body condition of female Tengmalm's owls varies both among years and within breeding seasons, and is dependent on abundance of voles in the field (Korpimäki 1990). It is possible that females in poor condition during the moderate vole year were not able to allocate enough resources to immune defence against blood parasites. We did not find, however, any connection between trypanosome infection and male body condition. Poor food conditions may not have drastic effects on male body condition because males apparently invest first in their own condition and only thereafter in the well-being of their female and young (Korpimäki 1990, Koivunen et al. unpubl. radio-telemetry study). Among-year variation in prevalence of trypanosomes in male owls is more likely dependent on energetic stress caused by increased hunting effort during poor vole years (see next section).

To our knowledge, an association between trypanosome infection and avian body condition has not been previously reported. The connection between haemosporidian infections and avian body condition (or body mass) has, however, been studied earlier, but no effects were found (Bennett et al. 1988, Weatherhead and Bennett 1992, Korpimäki et al. 1995; but see Shutler et al. 1999).

We tested experimentally effects of nutritional stress on susceptibility of owls to haematozoan infections by providing supplementary food to females during the incubation and early nestling phase in two years of relatively low vole abundance. Our results support, at least partly, our prediction; trypanosome prevalence among food-supplemented females was lower compared to unsupplemented control females, whereas no differ-

Table 4. Spearman rank correlation between breeding success and intensities of *L. ziemanni* and *T. avium* in female Tengmalm's owls during the nestling period in 1993, 1994 and 1995. Only infected individuals included. * = Bonferroni-corrected, $P < 0.05$.

1993	*L. ziemanni*		*T. avium*	
	r_s	*n*	r_s	*n*
Laying date	0.05	12	−0.49	7
Clutch size	−0.42	11	0.65	6
No. of fledglings	−0.10	12	0.36	7
Body mass of fledg.	−0.53	9	–	4

1994	*L. ziemanni*		*T. avium*	
	r_s	*n*	r_s	*n*
Laying date	0.30	26	−0.38	8
Clutch size	−0.20	26	−0.46	8
No. of fledglings	−0.36	25	0.00	7
Body mass of fledg.	0.20	18	−0.38	6

1995	*L. ziemanni*		*T. avium*	
	r_s	*n*	r_s	*n*
Laying date	0.28	22	−0.01	11
Clutch size	−0.02	19	0.77	10 *
No. of fledglings	−0.25	16	−0.36	8
Body mass of fledg.	0.15	13	−0.09	7

ence was found between the two groups in prevalence of *L. ziemanni* or *Haemoproteus*.

Factors other than food supply (e.g. annual variation in densities of vectors) may have affected the observed pattern in correlative data for among-year variation in prevalence of trypanosomes, but together with our experiment, our results are in agreement with other reports on associations between poor food conditions and susceptibility to disease (e.g. Chandra and Newberne 1977, Gershwin et al. 1985), and suggest that availability of resources has an important role in immunocompetence against parasites.

Parental effort and susceptibility to haematozoan parasites

The important finding in this study was that high parental effort can make Tengmalm's owls susceptible to haematozoan infections, especially in years of food scarcity. The observed positive association between parental effort and haematozoan infections in female and male parent owls is likely attributable to energetic trade-offs between allocation of resources to parental effort and immunocompetence (reviews in Toft 1991, Sheldon and Verhulst 1996, Møller 1997). This trade-off seems more likely to be manifested in increased parasitism during poor food conditions, whereas individuals breeding under good resource levels may be less likely to be parasitized.

In a moderate vole year, females with large clutches had high *T. avium* intensities during the nestling phase. Production and incubation of large clutches may have increased energetic and nutritional stress in female Tengmalm's owls, and thus decreased their ability to devote resources to immune defence against parasites. Avian egg production can be nutritionally and energetically costly (e.g. Ankney 1980, Alisauskas and Ankney 1985, Astheimer and Grau 1985). Chernin (1952) found that egg production may cause relapse of chronic latent *L. simondi* infections in domestic ducks. Female great tits (*Parus major*) manipulated to produce large clutches had higher prevalence of *Plasmodium* during the nestling phase than did control females (Oppliger et al. 1996). Daily energy expenditure of incubating females in hole-nesting passerine birds is ca three-fold compared to their basal metabolic rate (Westerterp and Bryant 1984, Moreno and Carlson 1989, Moreno et al. 1991), and energetic costs of incubation increase with clutch size (Biebach 1981, Haftorn and Reinertsen 1985, Moreno et al. 1991, Moreno and Sanz 1994, Gloutney et al. 1996).

Male Tengmalm's owls which were *T. avium* infected during the nestling period produced more fledglings than did uninfected ones in the moderate vole year. In the same year, males which produced heavy fledglings had high intensities of *L. ziemanni* during the nestling phase. Although we did not measure directly hunting effort or energy expenditure of male owls, an earlier study showed that males which produce large broods provide their young with a high number of prey items (Hakkarainen and Korpimäki 1995), and thus probably invest more in hunting than males which produce small broods. In general, raising a large number of nestlings can be energetically costly to raptors (e.g. Drent and Daan 1980, Masman et al. 1989, Deerenberg et al.

Table 5. Prevalence (% of individuals infected) of *T. avium*, *L. ziemanni* and *Haemoproteus* infection among female and male Tengmalm's owl parents of supplemented and control nests during the nestling period in 1996–1997. Number of individuals infected per total is given within parentheses.

	Females		Males	
Parasite	Supplemented	Control	Supplemented	Control
T. avium	36.4 (4/11)	81.8 (9/11)	72.7 (8/11)	80.0 (8/10)
L. ziemanni	100.0 (11/11)	100.0 (11/11)	90.9 (10/11)	90.0 (9/10)
Haemoproteus	9.1 (1/11)	0.0 (0/11)	9.1 (1/11)	20.0 (2/10)

1995). In addition, during poor vole years, male Tengmalm's owls have to work harder to satisfy food requirements of their mates and young than in good vole years, due to the low availability of voles and small size of alternative prey species (Hakkarainen and Korpimäki 1991). Male Tengmalm's owls with high parental effort in poor food conditions may have had less resources for immune defence against parasites. Similarly males with increased parental effort had decreased ability to raise immune response against experimental immunization with a novel antigen in captive zebra finches (*Taeniopygia guttata*) (Deerenberg et al. 1997) and wild barn swallows (*Hirundo rustica*) (Saino and Møller 1996).

Conclusions

We found that parasites may appear as potential cost of reproduction, especially if environmental resources are at a low level. Both observational and experimental data in this study suggest that nutritional status and availability of resources influence susceptibility to parasites. Our results are in accordance with a few other studies on avian parasitism in varying environmental conditions (de Lope et al. 1993, Møller 1993, Wiehn and Korpimäki 1998), and support the idea that the magnitude of reproductive costs may be dependent on the amount of resources available to an individual (Tuomi et al. 1983). Most previous studies on costs of reproduction and host-parasite interactions are based on data collected during only one breeding season, and thus have not considered possible effects of annual variation in resource levels. Our results are consistent with earlier findings of a trade-off between avian parental effort and immunocompetence, and underline the importance of studying the role of varying environmental resource levels on the magnitude of reproductive costs in terms of parasitism.

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