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Blood parasites, clutch volume, and condition of Gadwalls and Mallards

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We analysed total clutch volumes and condition of female ducks relative to their haemosporidian blood parasite loads. Twenty-four percent of Gadwalls *Anas strepera* and 60% of Mallards *A. platyrhynchos* were infected with at least one type of blood parasite, although infection intensities were generally light. After controlling for potential covariates of clutch volume (clutch initiation date, female age, female mass, and female structural size), we found no significant relationships between clutch volume and parasitism. Mallards in poorer condition were more likely to be parasitised. However, because condition was not related to clutch volume, we conclude that the blood parasites we detected were relatively benign with respect to reproductive investment, at least at the intensities observed.

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Tradeoffs between parasite load and reproductive investment are of significant theoretical importance (Folstad and Karter 1992, Roff 1992, Stearns 1992, Forbes 1993). Although parasitism may reduce subsequent reproductive investment (Howard and Minchella 1990, Møller et al. 1990, Allander and Bennett 1995, Dufva 1996, Sorci et al. 1996, Van Vuren 1996), higher reproductive investment can also increase subsequent parasitism (Festa-Bianchet 1989, Norris et al. 1994, Richner et al. 1995). The latter positive correlation between investment and parasitism may arise because reproductively stressed hosts allocate less energy to immune function, and are thereafter more susceptible to parasites or are less able to clear them (Oppliger et al. 1996, Ots and Hõrak 1996). Similarly, a positive association could arise if individuals of high quality invest heavily in reproduction because they are able to sustain and combat heavy parasite loads without subsequent fitness costs (Oppliger et al. 1997, also see Reznick 1985). On the other hand, there may be no detectable relationship between parasitism and allocation to reproduction (e.g., Hausfater et al. 1990, Weatherhead et al. 1993, Wagner

et al. 1997), possibly because focal parasites are relatively benign and their effects are overwhelmed by other, more important factors (e.g., nutrition, age, other parasites, etc.).

We measured haemosporidian (phylum Apicomplexa, suborder Haemosporina) blood parasite loads after female duck hosts (Mallards *Anas platyrhynchos* and Gadwalls *A. strepera*) had made reproductive investments in clutch formation and incubation. Hence, these data were best suited to exploring whether investment was positively correlated with parasitism. The parasite genera we detected (*Haemoproteus*, *Leucocytozoon*, and *Plasmodium*) are all blood parasites vectored by flies (Diptera). When infected flies take blood meals, parasites enter host blood streams, proceed to various host organs, proliferate asexually for several days, and then invade blood cells as gametocytes, which is when prevalence is usually assessed (Atkinson and Van Riper 1991, Desser and Bennett 1993). In the Canadian prairies, prevalence ranges from 10 to 50% among adult Gadwalls and Mallards (Bennett et al. 1982, Robert Adlard pers. comm.). Many haemosporidian infections

are probably chronic, although they could also result from reinfection (Bennett and Bishop 1990, Weatherhead and Bennett 1991, 1992). Regardless, haemosporidians are probably acquired only on the breeding grounds (Bennett and Bishop 1990, Garvin and Remsen 1997). Because females make heavy reproductive investments on the breeding grounds, it is here that consequences of those investments, in terms of parasitism, may be most pronounced. The two duck species differ in several ways; Mallards are approximately 25% larger, have overlapping but slightly different nest habitat preferences, nest earlier in the year, reproduce earlier in life, and have smaller clutch sizes than do Gadwalls (Lokemoen et al. 1990, Greenwood et al. 1995, Clark and Shutler 1999, Shutler et al. 1998). Each of these factors may cause differences in parasitism between host species.

We used clutch volume as our index of female reproductive investment, because it is a more inclusive measure than is clutch size (Flint and Grand 1996). Not only do larger clutches require a larger initial metabolic investment (Carey 1996), they may also increase metabolic investment in incubation (Gloutney et al. 1996). Towards the end of incubation (i.e. after a large part of females' reproductive investment), we quantified blood parasite loads using blood smears (Bennett 1970). We note that our data are non-experimental and therefore do not necessarily indicate causation.

Methods

Field work was conducted in 1996 on the St. Denis National Wildlife Area, 40 km east of Saskatoon, Saskatchewan, Canada. Females were flushed from nests by dragging ropes or cables over herbaceous cover, and by walking and beating vegetation with bamboo canes in shrub-woodland cover. For each nest found, we recorded date, species, and clutch size, measured eggs with dial calipers (length and maximum

width to the nearest 0.1 mm), and candled eggs to determine stage of incubation (Weller 1956). Egg volume (cm^3) was computed following Hoyt (1979) as length $\times$ width^2 $\times$ 0.515. Clutch volume was the sum of individual egg volumes.

We used backdating to estimate date of clutch initiation, assuming that one egg was laid per day, and that no partial predation occurred before nests were found. To reduce nest abandonment, we waited until the last five days of incubation to capture females on their nests. Captured females were banded, measured for head size (linear distance from the back of the head to the tip of the bill; Dzubin and Cooch 1992), wing length, and mass, aged (using banding or web tagging information, or less often by plumage criteria similar to Krapu et al. 1979), pricked in the tarsal vein to provide blood for a smear, and then released.

One hundred fields of each blood smear were analysed at 400 × magnification for *Leucocytozoon*, and at 1000 × magnification for *Haemoproteus* and *Plasmodium* (Bennett 1970, pers. comm.). Twenty smears (10 for each species) were analysed by two different observers; high consistency was found between assessments (also see Shutler et al. 1996).

Statistical analyses were performed in SAS (1990). Because of their various differences (see Introduction), Gadwalls and Mallards were analysed separately. Aside from parasites, female clutch initiation date (Lack 1966, Welty 1982, Gill 1990, Rätti et al. 1993, Fowler 1995), age (Lack 1968, Welty 1982, Gill 1990, Sæther 1990, Beletsky and Orians 1996), condition (Ankney and MacInnes 1978, Galbraith 1988, Alisauskas and Ankney 1992), and body size (Welty 1982, Nol et al. 1997) can explain a significant amount of intraspecific variation in clutch size. These were covariates in analyses. Principal components analyses of wing length and head size failed to produce composite, structural size variables for either species that explained more variation than was expected by chance (Frontier 1976, Jackson 1993), so we used only original body measurement as covariates.

Table 1. Number of individuals of each duck species infected with haematozoa. One of each species had a single microfilaria.

Taxa detected	Gadwall (N = 29)			Mallard (N = 40)		
	Number infected	Modal intensity[1]	Maximum intensity[1]	Number infected	Modal intensity[1]	Maximum intensity[1]
Haemoproteus net-tionis	6	1	3	18	4	64
Leucocytozoon si-mondi	1	3	3	1	4	4
Plasmodium spp.	2	1	1	9	5	11
0 taxa	22		—	17		—
1 taxon	6		—	18		—
2 or more taxa	1		—	5		—

[1] For infected individuals only, the number of parasites per 100 fields. Not calculated for mixed infections because of variation in magnifications used.

Infections were often absent (and when present were generally light in our birds; Table 1), which meant that assumptions of normality were not met for parametric statistics. Hence, we used instead parasite status (infected or not infected) as a response variable in stepwise logistic regressions, with total clutch volume as the explanatory variable of interest, and clutch initiation date, female age, mass, head size, and wing length as covariates. We computed condition as mass divided by the cube of wing length (Searcy 1979), and repeated the above analyses substituting condition for mass and wing length. Significance was judged by Wald χ^2 test statistics and associated P values.

Results

We collected complete clutch and blood parasite data for 29 Gadwalls, and for 40 Mallards. Most (17) Gadwalls were of unknown age, and many (7) were 2 years old, so we did not use age as a covariate in Gadwall analyses. In contrast, 18 Mallards were 1-year old and 22 were 2 or more years old, so age was a covariate in Mallard analyses. Clutch sizes ranged from 6 to 12 (mean $\pm$ SD = 9.7 $\pm$ 1.7) for Gadwalls, and from 6 to 10 (8.2 $\pm$ 1.2) for Mallards. Clutch volumes ranged from 237 to 505 cm^3 (401 $\pm$ 84) for Gadwalls, and 254 to 479 cm^3 (374 $\pm$ 59) for Mallards. Clutch volume and clutch size were significantly correlated (r = 0.89 for Gadwalls, r = 0.90 for Mallards, Ps < 0.001) and results of analyses were similar if these variables were interchanged.

Of the Gadwalls and Mallards, 7 (24%) and 24 (60%), respectively, were infected with at least one blood parasite (Table 1). *Haemoproteus nettionis* was detected in 21% of Gadwalls, and 45% of Mallards, and *Plasmodium* spp. were detected in 23% of Mallards, so we repeated analyses comparing *Haemoproteus*-positive and *Haemoproteus*-negative individuals (hereafter *Haemoproteus* status), and comparing *Plasmodium*-positive and *Plasmodium*-negative Mallards only (hereafter *Plasmodium* status).

In tests of whether greater reproductive investment by Gadwalls was more likely to be associated with parasitism, no variables were left in models after stepwise logistic regression; this was unchanged when condition replaced mass and wing length. When forced into the logistic model, clutch volume was almost completely independent of parasite status (Wald $\chi^2 = 0.0$, P = 0.95). Similarly neither Gadwall clutch volume nor any covariates were associated with *Haemoproteus* status.

In the same tests on Mallards, no variables were left in the first stepwise logistic regression. When forced into the logistic model, clutch volume was almost completely independent of parasite status ($\chi^2 = 0.1$, P =

Table 2. Associations between Mallard parasitism by haemosporidians and covariates (non-significant covariates not shown). Each line in the table provides results of a separate stepwise logistic regression; values are Wald χ^2s.

Dependent variable	Covariate		
	Wing	Mass	Condition
Parasite status			3.7*
Haemoproteus status	6.6**	6.2**	
Haemoproteus status			7.1**

* P < 0.05, ** P < 0.01.

0.80). Substituting condition for wing length and mass, we found that ducks in better condition were less likely to have parasites (Table 2, Fig. 1); clutch volume was still unrelated to parasite status ($\chi^2 = 0.1$, P = 0.76). Female Mallards infected with *Haemoproteus* were lighter and had longer wings than did uninfected individuals (Table 2), but forcing clutch volume into this regression did not reveal a significant relationship with *Haemoproteus* status ($\chi^2 = 0.0$, P = 0.90). As was the case for parasite status, condition was significantly related to *Haemoproteus* status (Table 2), but forcing clutch volume into the model again revealed no significant association ($\chi^2 = 0.0$, P = 0.97). If *Plasmodium* status was the response variable, no significant associations were found.

Because of the significant association between parasitism and condition among Mallards, we tested whether condition was related to clutch volume, but we found no evidence of this (r = 0.11, P = 0.52). Similarly, condition and clutch volume among Gadwalls were also unrelated (r = 0.05, P = 0.78)

Discussion

We found no compelling evidence that parasitism by haemosporidians was related to female allocation to reproduction. To put our results in context, clutch
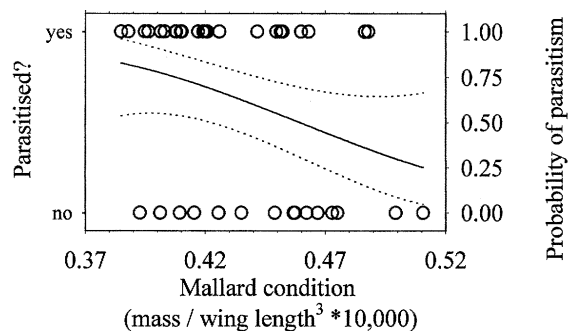

Fig. 1. Condition of parasitised and unparasitised female Mallards (open circles, left axis), and probability of parasitism from logistic regression (right axis, solid line). Dotted lines are 95% confidence limits.
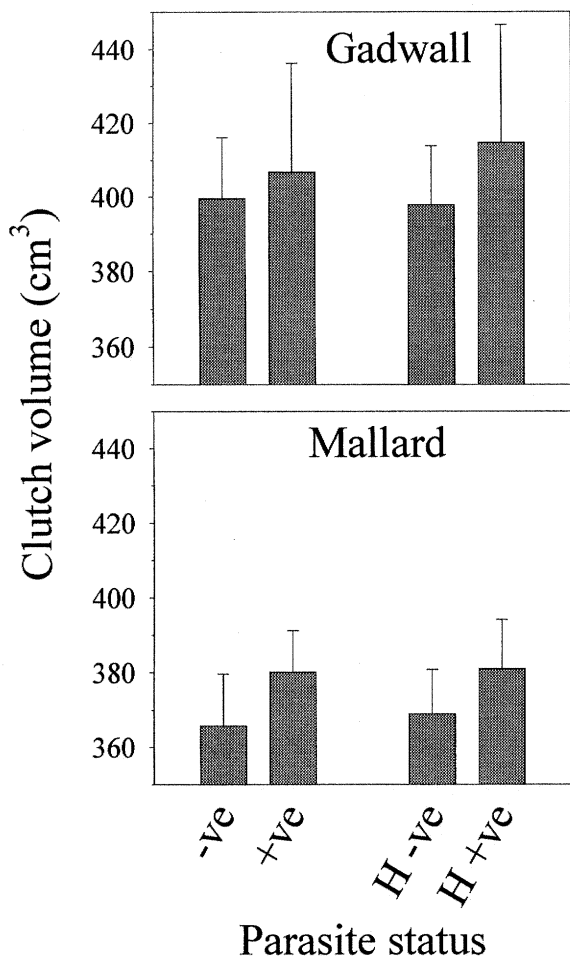
Fig. 2. Least squares means (standard errors are shown above bars) from general linear models (SAS 1990) with clutch volume as dependent variable, female mass as covariate, and either parasite status (uninfected denoted − ve, infected denoted + ve), or *Haemoproteus* status (uninfected denoted H − ve, infected denoted H + ve) as the variable of interest. Analyses done separately for Gadwalls and Mallards.

volumes of infected individuals were larger than those of uninfected individuals by about 30% of one egg (Fig. 2). However, these differences could be randomly related to variation in clutch size (and clutch volumes) among individuals, although the similar results for both species are suggestive. We did find evidence that Mallards in poorer condition were more likely to have parasites, suggesting either that these individuals had been forced to reduce energetic allocation to immunity, or that parasites had been an energetic drain on condition. However, condition and clutch volume were unrelated.

It is generally assumed that parasites cause hosts to reduce reproductive investment (Howard and Minchella 1990, Møller et al. 1990, Allander and Bennett 1995, Dufva 1996, Sorci et al. 1996, Van Vuren 1996) by competing with hosts for nutrients (Seebeck et al. 1971,

Eckert 1991, Crompton 1991), by forcing hosts to increase allocation to immune function (John 1994a, b), or by obliging hosts to allocate energy to repair damaged tissues (Holmes and Zohar 1990, Read and Skorping 1995). We can address this hypothesis indirectly; it predicts negative correlations between parasitism and investment. Although blood parasite status can change between years (Bennett and Bishop 1990, Weatherhead and Bennett 1991, 1992), it is highly consistent within years (Shutler et al. 1996). Assuming that parasitism at the time ducks were captured indicates whether they were parasitised before clutch initiation, the non-significant *positive* correlations between reproductive investment and parasitism are contrary to this hypothesis, and suggest that haemosporidians did not reduce reproductive investment. However, our results may indicate another tradeoff: that Mallards in poor condition reduced their allocation to immunity, possibly to maintain their reproductive allocation (cf. Oppliger et al. 1996, Ots and Hõrak 1996). Although this allocation decision may have had no effect on reproduction, it may have had other effects, such as on survival. This hypothesis requires further testing, but see Bennett et al. (1993).

The non-significant relationships between parasitism and reproductive investment could be because haemosporidians are benign. However, consider the case where hosts are already carrying a potentially harmful parasite (or are likely to encounter this parasite when reproduction has begun), but a sufficient immune defense keeps (or will keep) this parasite from proliferating. Because proliferation of this parasite is very costly to the host, each host may modulate its allocation to reproduction according to its current state of health, saving enough energetic reserves to keep the parasite at bay. Thus, all individuals would have no, or low intensity, infections, and reproductive investment would vary independent of subsequent parasitism (Sorci et al. 1996, Oppliger et al. 1997). This scenario parallels one wherein individuals optimise their reproductive investment according to their own capacity (Reznick 1985). We believe that this scenario is unlikely to apply to this system, because intense infections of haemosporidians are often observed in wild birds that otherwise appear healthy (Weatherhead et al. 1993, Shutler et al. 1996).

We interpret our results as suggesting that the parasites we observed are relatively benign. A variant of this hypothesis is that infection intensities we observed were too low to have any effect. Other studies have failed to detect significant effects of haemosporidians on unmanipulated, wild, avian hosts (Ashford 1971, Bennett et al. 1988, 1993, Weatherhead and Bennett 1991, 1992, Shutler et al. 1996), and our results are consistent with these. However, results from comparative (Hamilton and Zuk 1982, but see Read and Harvey 1989, Underhill and Kalejta-Summers 1995) and experimental stud-

ies (e.g., Norris et al. 1994, Richner et al. 1995, Ots and Hõrak 1996, but see Møller 1997) have revealed significant relationships between haemosporidians and allocation to other aspects of reproduction. Hence, although haemosporidians in our ducks are relatively benign in the short term, they are probably important influences on host evolution (Anderson and May 1979, Lee and Clayton 1995).

We used clutch volume as our measure of allocation to reproduction. There are other aspects of reproductive allocation that are independent of clutch volume that we could not measure. Because females are cryptic and are the sex that chooses mates, ornaments and displays are probably not important investments to them. However, female choice of nest site could influence both energy expended during incubation, and susceptibility to parasite vectors. With regard to the former, a female that chooses a nest site that experiences cooler temperatures (such as shady sites that afford greater cover from predators) may need to divert more energy to thermoregulation (Gloutney and Clark 1997), and perhaps less to immunity. There may also be similar tradeoffs among nest sites in terms of exposure to parasite vectors (Zuk and McKean 1996). Another investment we were not able to measure was energy used to form clutches that females lost, before we captured them, to predators. Each of these additional investments may not bias our results, but they may make it more difficult to detect an association between parasites and reproductive investment.

In comparison with our findings, negative (Korpimäki et al. 1993, 1995, Rätti et al. 1993), non-significant (Allander and Bennett 1995), and positive correlations (Norris et al. 1994) have been reported between clutch size and blood parasite infections. Of studies that have considered effects of parasites other than haemosporidians on clutch size, clutch size of Great Tits Parus major was not affected by fleas (Richner et al. 1993), clutch size of Lesser Snow Geese Chen caerulescens caerulescens was not affected by helminths (Clinchy and Barker 1994), but clutch size of Red Grouse Lagopus lagopus scoticus was lower for birds infected with nematodes (Delahay and Moss 1996 and references therein). Clearly, generalities cannot be made from these studies (additional studies summarised in Møller 1997). However, hosts can deal with costs of parasitism in different ways, and a crucial factor in allocation decisions is likely the magnitude of costs of focal parasites (Forbes 1993, 1996, Perrin et al. 1996, Sorci et al. 1996). Although there are some reports of haemosporidians causing mortality (Atkinson and Van Riper 1991, Desser and Bennett 1993), many of these reports are for domestic birds (Bennett et al. 1993), suggesting that costs of haemosporidian infection are generally low. Hence, in wild ducks, effects of haemosporidians on allocation decisions may be only minor.

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