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Parental Effort and Parasite Resistance in the Red-Bellied Woodpecker (*Melanerpes Carolinus*)

Matthew S. Schrader



THE FLORIDA STATE UNIVERSITY
COLLEGE OF ARTS AND SCIENCES

PARENTAL EFFORT AND PARASITE RESISTANCE IN THE RED-BELLIED
WOODPECKER (*MELANERPES CAROLINUS*)

By

MATTHEW S. SCHRADER

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The members of the Committee approve the thesis of Matthew S. Schrader defended on April 3, 2003.

Frances James
Professor Directing Thesis

Tom Houpt
Committee Member

Alice Winn
Committee Member

Approved:

Tom Roberts, Chairperson, Department of Biological Science

The office of Graduate Studies has verified and approved the above named committee members.

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ABSTRACT

I used a combination of observational and experimental approaches to investigate the potential for a trade-off between parental effort and parasite resistance to mediate the cost of reproduction in a population of Red-bellied Woodpeckers (*Melanerpes carolinus*) nesting in natural cavities in the Apalachicola National Forest in north Florida. In the observational part of this study, I examined how the prevalence of a haematozoan parasite (*Haemoproteus velans*) of the Red-bellied Woodpecker varies seasonally. I also investigated how infection with this parasite was associated with host mass, body condition, and overwinter survival. In the second part of this study, I used a brood manipulation experiment to test whether there is a trade-off between caring for an increased brood and resisting *H. velans*, and whether this trade-off is associated with a decrease in a component of residual reproductive value.

The observational study was conducted between May 2000 and July 2001. Analysis of blood smears taken from individual woodpeckers during this period indicated that the prevalence of *H. velans* peaked during the Red-bellied Woodpecker breeding season and was lowest during the winter months. Infection with *H. velans* was associated with low mass and poor body condition in males. Infection showed no association with female mass. There was no statistically significant association between infection with *H.*

velans and overwinter survival in males or females. However, males infected with *H. velans* tended to have lower overwinter survival than uninfected males.

The brood manipulation experiment was conducted during the spring and summer of 2002. There was no effect of the brood manipulation on male feeding rates, however the prevalence of *H. velans* in males caring for enlarged broods tended to be higher than the prevalence in males caring for reduced or control broods. Females caring for enlarged broods made more feeding trips per hour than females caring for reduced or control broods, however there was no effect of brood manipulation on the prevalence of *Haemoproteus* in females. There was no effect of brood manipulation on the success of second or third broods.

The results of this study suggest that there may be a trade-off between reproductive effort and resistance to *Haemoproteus* in Red-bellied Woodpeckers. This type of trade-off is generally thought to arise when limited energy must be partitioned between provisioning nestlings and resisting disease; however the results of this study indicate that a trade-off between caring for an enlarged brood and resisting haematozoa can arise even if parents do not increase their feeding rates. In addition, although there appears to be a trade-off between caring for an enlarged brood and resisting *Haemoproteus* this trade-off was not associated with a decrease in residual reproductive value, at least within one season.

INTRODUCTION

The existence of a trade-off between current reproductive effort and residual reproductive value is an essential component of models of life history evolution (Williams 1966). The importance of this trade-off, usually referred to as the cost of reproduction, to life history theory has motivated ecologists and evolutionary biologists to attempt to demonstrate its existence. Researchers have used several approaches to demonstrate the presence of a cost of reproduction with varying success (Reznick 1985). Ultimately, the cost of reproduction is an evolutionary phenomenon that arises because of genetic trade-offs. As such, the most appropriate way to demonstrate the cost of reproduction is to demonstrate genetic correlations among fitness traits, either through breeding designs or selection experiments (Reznick 1985). Another approach that has been used to demonstrate the cost of reproduction entails experimentally manipulating reproductive effort (e. g. brood manipulation experiments) and measuring the effect of this manipulation on residual reproductive value. Although this approach is not appropriate for demonstrating an evolutionary cost of reproduction, it can help to establish the physiological and ecological mechanisms that generate it (Roff 1992).

Brood manipulation experiments in populations of birds nesting in artificial cavities have demonstrated a trade-off between caring for enlarged broods and survival

and future fecundity (Askenmo 1979, Gustafsson and Sutherland 1988, Nur 1988), however the physiological and ecological mechanisms that generate these trade-offs are poorly known. Some recent studies have suggested that a trade-off between caring for an enlarged brood and resisting parasitic infections is one mechanism that may mediate the cost of reproduction in birds (Sheldon and Verhulst 1996). Evidence for a trade-off between reproductive effort and parasite resistance comes from observational and experimental studies that have demonstrated a positive relationship between a measure of reproductive effort (usually brood size or clutch size) and the prevalence or intensity of infections with haematozoan parasites (Gustafsson et al. 1994, Richner et al. 1995, Allander 1997, Oppliger et al. 1997). However, whether this trade-off results in decreased residual reproductive value is unclear. In addition, the presence of a trade-off between reproductive effort and resistance to haematozoa in birds has only been demonstrated in populations of birds nesting in nest boxes. Nest-box studies have provided important insights into many aspects of avian ecology (Blondel et al. 1989), however results from these studies are potentially biased (Linden and Møller 1989, Møller 1989, 1992, but see Koenig et al. 1992), and must be interpreted with caution. For example, the introduction of concrete nest boxes to a population of Great Tits (*Parus major*) has virtually eliminated nest predation and resulted in increased fledging success, population density, and late life mortality (McCleery and Perrins 1991, McCleery et al. 1996). It has been suggested that the increase in late life mortality seen after the introduction of predator-proof nest boxes is the result of a greater cost of reproduction due to increased competition and increased investment in reproduction (McCleery et al. 1996). Although the presence of a trade-off between reproductive effort and parasite

resistance has been demonstrated in nest-box populations, whether this trade-off occurs in more natural populations is unknown.

In this thesis I examine whether a trade-off between parental effort and haematozoa resistance is one mechanism that may mediate the cost of reproduction in a population of Red-bellied Woodpeckers (*Melanerpes carolinus*) nesting in natural cavities in the Apalachicola National Forest, Florida. In Chapter 1, I describe how the prevalence of a haematozoan parasite (*Haemoproteus velans*) varies seasonally in this population. I also describe how infection with *Haemoproteus* is associated with host mass and host condition. In addition, I describe how infection with *H. velans* affects the overwinter survival of its hosts. In chapter 2, I describe a brood manipulation experiment designed to test whether there is a trade-off between raising an increased brood and resisting *H. velans* in the Red-bellied Woodpecker. I also investigate whether this trade-off is associated with a decrease in a component of residual reproductive value (the success of second and third broods).

CHAPTER 1

SEASONAL PREVALENCE OF A HAEMATOZOAN PARASITE OF THE RED-BELLIED WOODPECKER (*MELANERPES CAROLINUS*) AND ITS ASSOCIATION WITH HOST CONDITION AND OVERWINTER SURVIVAL

INTRODUCTION

Interest in the potential role of parasites in the evolution and ecology of their hosts has grown substantially since Hamilton and Zuk (1982) proposed that mate choice based on parasite resistance is an important mechanism in sexual selection. Hamilton and Zuk's hypothesis proposed that females choose mates on the basis of condition-dependent secondary sexual characters that advertise parasite-resistant genotypes. This hypothesis was based on data suggesting a positive correlation between plumage brightness and the prevalence of protozoan blood parasites (haematozoa) in passerine birds. Much debate has followed about the strength of the evidence for Hamilton and Zuk's hypothesis (Hamilton and Zuk 1989, Read and Harvey 1989, Zuk 1989) and the practical issues involved in testing it (Cox 1989, Weatherhead and Bennett 1991, 1992).

Part of this debate concerns the potential for haematozoan parasites to affect host fitness and the ability of researchers to detect chronic haematozoan infections (Cox 1989, Weatherhead and Bennett 1991). More recently, a trade-off between reproductive effort and resistance to haematozoan parasites has been proposed as a physiological mechanism potentially involved in mediating the cost of reproduction in birds (Norris et al. 1994, Richner et al. 1995, Oppliger et al. 1997, Nordling et al. 1998). This trade-off is thought to arise when limited resources must be partitioned between reproductive effort (i.e., number of offspring) and disease resistance. Growing evidence for a parasite-mediated cost of reproduction in birds has caused avian ecologists to reconsider the role of disease in population dynamics and life-history evolution (Price 1991).

Although the role of haematozoan parasites in avian evolutionary ecology has engendered much interest, the biology of haematozoa in the wild has not been well studied. Much of what is known about avian haematozoa has been learned from laboratory studies of domestic animals or from studies of the effects of haematozoa on novel hosts (van Riper et al. 1986, Atkinson and van Riper 1991). Poor understanding of haematozoan biology in wild populations of natural host species has raised doubts about the role of these parasites in the ecology and evolution of their hosts. Specifically, seasonal variation in parasite prevalence and the paucity of evidence for fitness effects have caused some authors to question the value using haematozoa to test for parasite-mediated sexual selection and life-history trade-offs (Cox 1989; Weatherhead and Bennett 1991, 1992; Sheldon and Verhulst 1996).

Several studies have demonstrated the tendency of haematozoan infections to increase in frequency during the breeding season (e. g., Weatherhead and Bennett 1991,

Hatchwell et al. 2000). This trend has been referred to as the “spring relapse” and is thought to occur when hormone activity or the physiological stress associated with breeding causes relapse of chronic infections (Atkinson and van Riper 1991). Weatherhead and Bennett (1992) have suggested that spring relapse hinders the ability of researchers to determine accurately, from a blood smear, whether an individual is infected. Blood smears can only be used to detect circulating haematozoa, but noncirculating chronic infections may persist in the livers of infected hosts (Jarvi et al. 2001). Noncirculating chronic infections may not be detected from blood smears if the individual is sampled before or after the peak of the relapse. Understanding how parasite prevalence varies seasonally is an essential prerequisite to any study of the role of haematozoa in avian ecology and evolution.

The existence of either parasite-mediated sexual selection or a parasite-mediated cost of reproduction requires that the parasites involved negatively affect host fitness (Hamilton and Zuk 1982, Sheldon and Verhulst 1996). Laboratory studies of domestic species have shown haematozoa to have significant pathological effects on their hosts (Atkinson and van Riper 1991). In addition, *Plasmodium*, the haematozoan parasite that causes avian malaria, has been shown to limit the geographic distribution and abundance of Hawaiian land birds (van Riper et al. 1986). Few studies have assessed the effect of haematozoa on host fitness in the wild however, and evidence for negative associations between haematozoan infection and measures of host condition, which are often thought to reflect fitness, is mixed. Some studies have found no effect of haematozoa on survival rates or condition (reviewed by Bennett et al. 1988, 1993, Davidar and Morton 1993), whereas other studies have shown haematozoan parasites to affect negatively the immune

and condition indices and the reproductive success of their hosts (Ots and Horak 1998, Merino et al. 2000).

As part of a larger study examining the importance of a parasite-mediated cost of reproduction in the Red-bellied Woodpecker (*Melanerpes carolinus*), I examined the ecology of a haematozoan parasite (*Haemoproteus velans*) in a population of Red-bellied Woodpeckers in the Apalachicola National Forest northern Florida. In particular, I investigated (1) how the prevalence of *H. velans* varies seasonally in this population, (2) how infection with this parasite is associated with host condition, and (3) whether infection with *H. velans* affects host survival. It is necessary to understand these aspects of the biology of *H. velans* to assess the importance of a parasite-mediated cost of reproduction in the Red-bellied Woodpecker.

The Red-bellied Woodpecker is one of the most abundant woodpeckers in eastern North America. It is distributed across the eastern U.S., occurring west to the Great Plains and north to southern Ontario (Shackelford et al. 2000). Red-bellied Woodpeckers generally nest in dead trees, but in the Apalachicola National Forest many use cavities excavated by Red-cockaded Woodpeckers (*Picoides borealis*) in living pines.

Haemoproteus velans has been described in a number of woodpecker species, and it may be distributed throughout the worldwide range of the Picidae (Greiner et al. 1977). The lifecycle of *Haemoproteus* is similar to those of other haematozoa (Atkinson and van Riper 1991). Asexual reproduction occurs in noncirculating cells of the host and vector. Gametocytes are found in circulating blood cells, which are infective to bloodsucking vectors. Gametogenesis and sexual reproduction usually take place in the midgut of the vector. Species of *Haemoproteus* are the most common and probably the least

pathogenic of the avian haematozoa, although little is known of the biology of *Haemoproteus* in the wild (Atkinson and Van Riper 1991).

METHODS

I collected blood samples and body measurements from 196 adult Red-bellied Woodpeckers in the Apalachicola National Forest between May 2000 and July 2001. Most of the 151 individuals sampled between May 2000 and April 2001 were removed from cavities excavated by Red-cockaded Woodpeckers by as part of another study (Walters, unpublished). In addition, 25 males and 20 females were caught at nests between May and July 2001. Each individual collected between May 2001 and July 2001 was banded with a unique combination of three color-bands and a USFWS aluminum band. For each individual, approximately 100 μ l of blood was drawn from a brachial vein into a heparinized microhematocrit tube. This sample was used to prepare blood smears on two microscope slides according to the technique described by Bennett (1970). Blood smears were air-dried and fixed in absolute methanol. Birds were weighed with a spring balance to the nearest 0.1 g, and their tarsi were measured to the nearest 0.1 mm. The tarsus length of some birds was not measured. These birds were excluded from analyses that involved tarsus length.

Blood smears were stained with Giemsa stain within approximately one week of being taken. Slides were examined for the presence of haematozoa with a conventional light microscope at x400 and x1000 under oil emersion. The entire blood smear was scanned for infections so that low-intensity infections would not be missed. Although

screening blood smears for haematozoa is a relatively easy way to detect patent infections, subpatent infections may be impossible to detect by microscopy (Jarvi 2001). For the remainder of this paper, I refer to individuals with infections detected from blood smears as infected and individuals without detectable infections as uninfected, although these individuals may have subpatent infections that I was not able to diagnose from blood smears. I estimated the condition (mass corrected for size) of each individual from residuals of an ordinary least-squares regression of \ln mass on \ln tarsus. This type of analysis can be used to estimate body condition while controlling the effect of body size (Jakob et al. 1996). A separate regression was performed for each sex. Mass and body condition of infected and uninfected individuals were compared with ANOVA.

I estimated overwinter survival by recapturing or resighting adults banded at 23 sites during 2001 in the spring and summer of 2002. This estimate of overwinter survival is a function of survival, dispersal, and recapture probability, but here I assume that individuals not captured or seen during the 2002 breeding season were dead. I examined the association between infection with *H. velans* and overwinter survival with G-tests with William's correction for small sample sizes (Sokal and Rohlf 1995).

RESULTS

Approximately 25% of all individual woodpeckers sampled were infected with *H. velans*. A slightly larger percentage of males (26%, $n = 126$) than females (22%, $n = 70$) was infected with *H. velans*, but this difference was not statistically significant (G-test

with William's correction, 1 df, $G_{\text{adj}} = 0.436$, $P > 0.05$). No other species of haematozoa were found in any of the blood smears. The proportion of individuals infected with *H. velans* varied seasonally, with peaks occurring in July 2000 and July 2001 (Fig. 1.1).

Parasite prevalence in males varied seasonally in much the same way as in the entire sample. A larger proportion of males was infected during the breeding season than during the nonbreeding season (G-test with William's correction, 1 df, $G_{\text{adj}} = 20.03$, $P < 0.001$). Males infected with *H. velans* weighed less than uninfected males ($\bar{X}_{\text{infected}} = 71$ g, $\bar{X}_{\text{uninfected}} = 73.5$ g; ANOVA, $F_{(1,122)} = 8.71$, $P = 0.004$, Figure 1.2). Male tarsus length and male mass were significantly positively related, although tarsus length explained little of the variation in mass ($r^2 = 0.116$, $P < 0.005$, Figure 1.3). Infected males were in poorer condition than uninfected males ($\bar{X}_{\text{infected}} = -0.023$, $\bar{X}_{\text{uninfected}} = 0.008$; ANOVA, $F_{(1,110)} = 6.72$, $P = 0.011$, Figure 1.4). Because male mass and condition vary seasonally in the Apalachicola National Forest population (Schrader, unpublished), and because very few males were infected outside of the breeding season, I examined the association between infection with *H. velans* and male mass and condition using only males sampled during the breeding season (May–September 2000 and April–July 2001). Males infected with *H. velans* weighed less than uninfected males in the data set limited to breeding-season males ($\bar{X}_{\text{infected}} = 70.9$ g, $\bar{X}_{\text{uninfected}} = 73.4$ g; ANOVA, $F_{(1,81)} = 6.92$, $P = 0.01$, Figure 1.5). New condition values were calculated from the breeding-season data. Male mass and tarsus length were positively related during the breeding season ($r^2 = 0.14$, $P = 0.001$, Figure 1.6). Infected males were in poorer condition than

uninfected males in this data set ($\bar{X}_{\text{infected}} = -0.018$, $\bar{X}_{\text{uninfected}} = 0.010$; ANOVA, $F_{(1,68)} = 4.25$, $P = 0.043$, Figure 1.7).

Although parasite prevalence did not follow an obvious seasonal trend in the females (Fig. 1.1), a higher proportion of females were infected during the breeding season than during the nonbreeding season (G-test with Williams correction, 1 df, $G_{\text{adj}} = 9.09$, $P = 0.01$). Females infected with *H. velans* did not differ significantly in mass from uninfected females ($\bar{X}_{\text{infected}} = 67.6$ g, $\bar{X}_{\text{uninfected}} = 66.7$ g; ANOVA, $F_{(1,68)} = 0.68$, $P = 0.413$, Figure 1.2). Because female mass and tarsus length were not significantly related ($r^2 = 0.023$, $P = 0.303$, Figure 1.3), I did not calculate condition for females. I also examined the association between infection with *H. velans* and female mass using only females sampled during the breeding season. In this limited data set, female mass and infection were not associated ($\bar{X}_{\text{infected}} = 67.04$ g, $\bar{X}_{\text{uninfected}} = 66.2$ g; ANOVA, $F_{(1,31)} = 0.33$, $P = 0.569$, Figure 1.5). Female mass and tarsus length were not significantly related in this limited data set ($r^2 = 0.003$, $P = 0.767$, Figure 1.6), so I did not calculate condition for females.

Infection with *H. velans* had no significant effect on the probability that males would survive from the 2001 breeding season to the 2002 breeding season, although uninfected males tended to have higher over winter survival than infected males (4/8 infected [50%], 9/11 uninfected [82%], G-test with William's correction, 1 df, $G_{\text{adj}} = 1.98$, $P > 0.05$, Figure 1.8). Similarly, infection had no effect on the probability that females would survive from the 2001 breeding season to the 2002 breeding season (3/6 infected [50%], 6/15 uninfected [40%], G-test with William's correction, 1 df, $G_{\text{adj}} = 0.16$, $P > 0.05$, Figure 1.8).

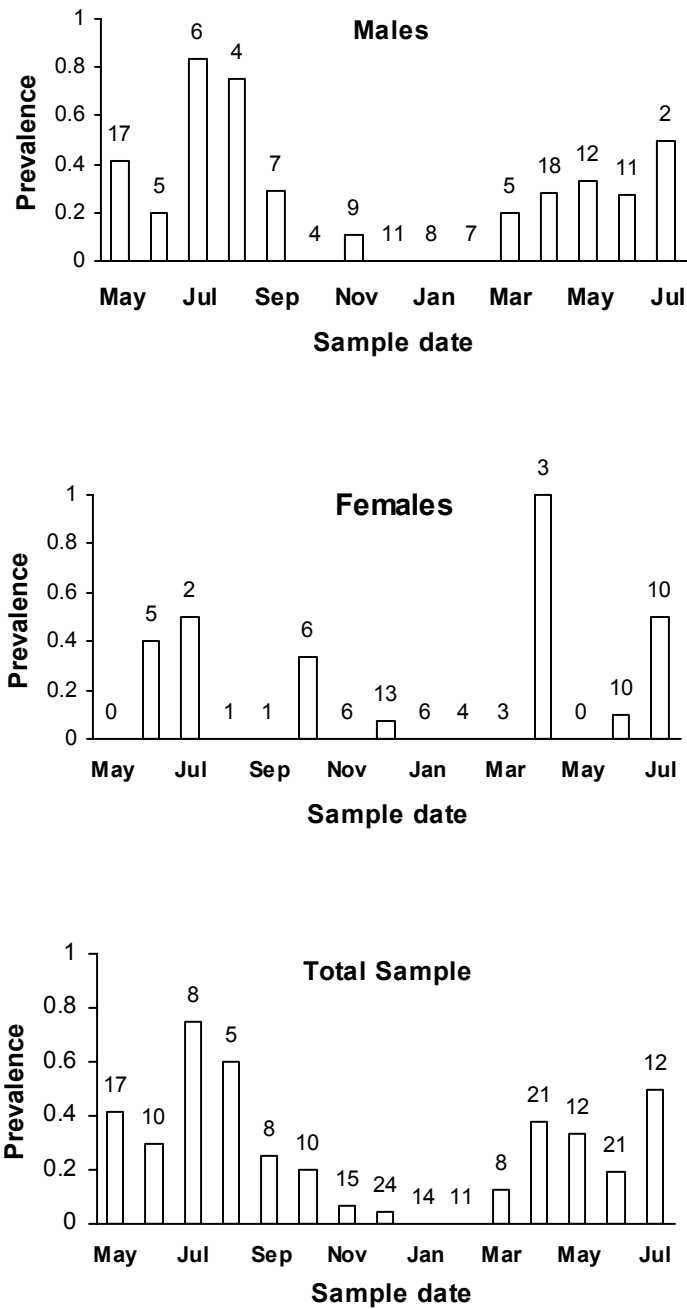


Fig. 1.1. Seasonal variation in the prevalence (proportion of individuals with detectable infections) of *Haemoproteus* infections in 126 males, 70 females, and the total sample (196 individuals). All individuals were collected between May 2000 and July 2001. Numbers above bars are sample sizes.

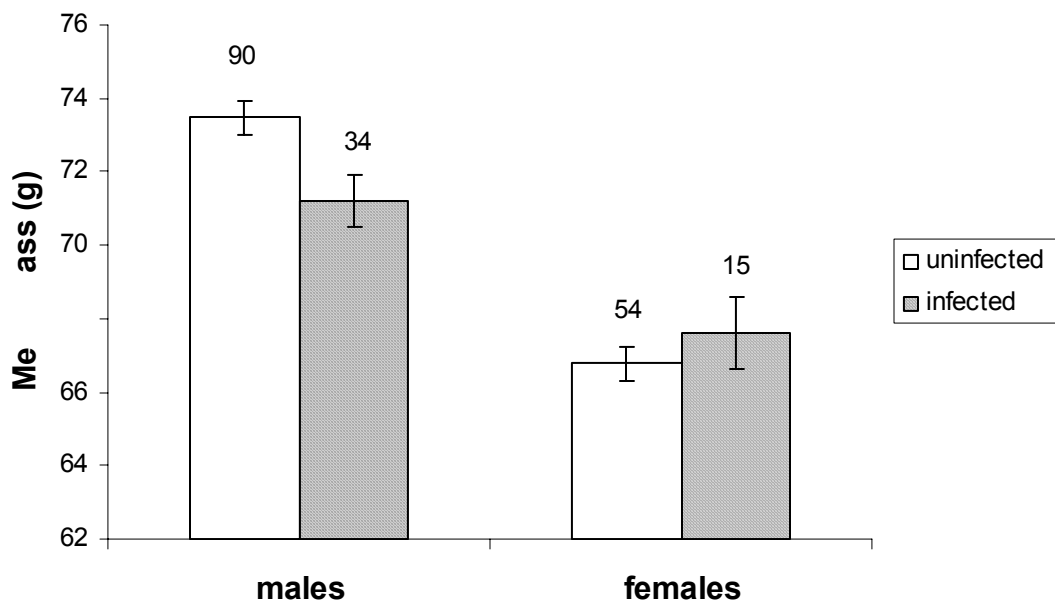


Figure 1.2. Mean mass (\pm SE) of uninfected (open bars) and infected (hatched bars) males and females. Numbers above bars are sample sizes.

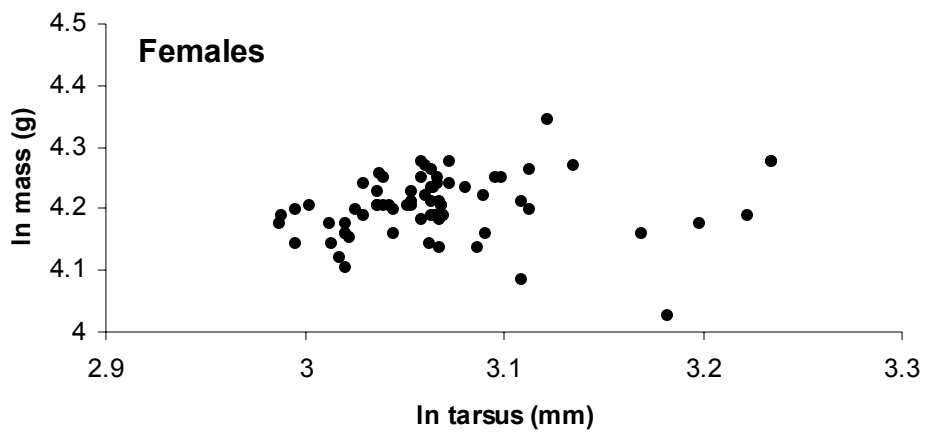
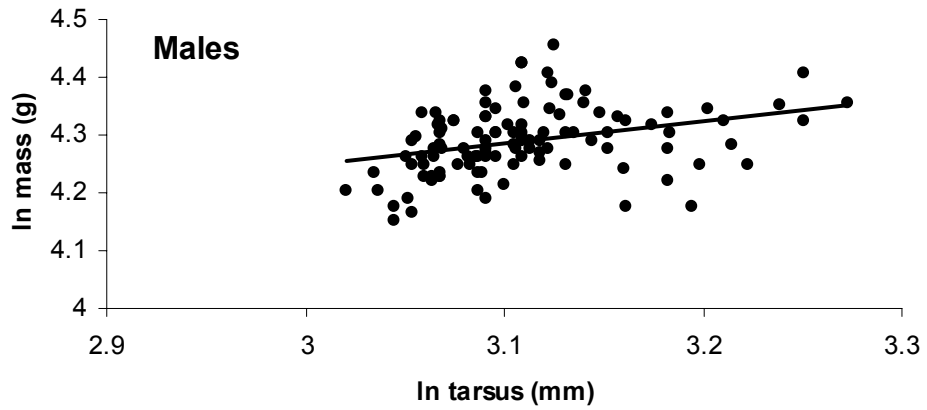


Fig. 1.3. The relationship between ln mass and ln tarsus length for males and females collected between May 2000 and July 2001.

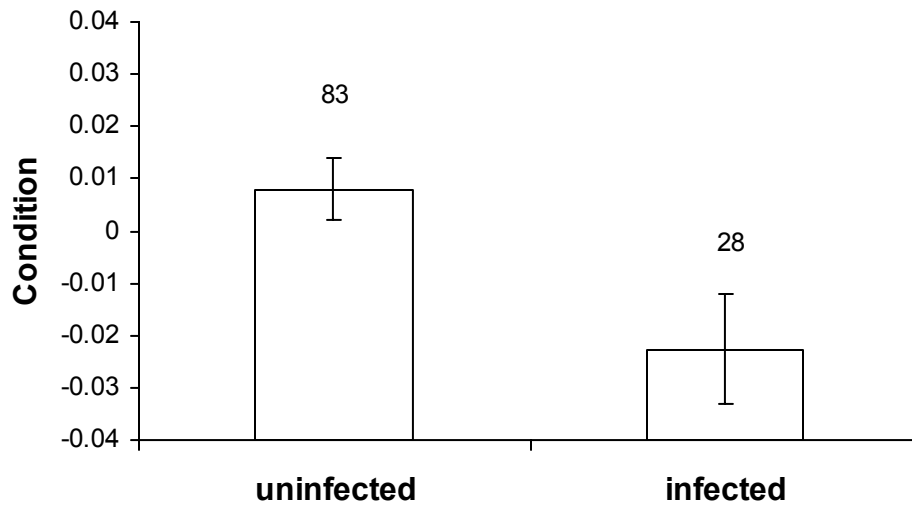


Fig 1.4. Mean condition (\pm SE) of uninfected and infected males. Condition was estimated using the residuals of the regression of \ln mass on \ln tarsus. Numbers above bars are sample sizes.

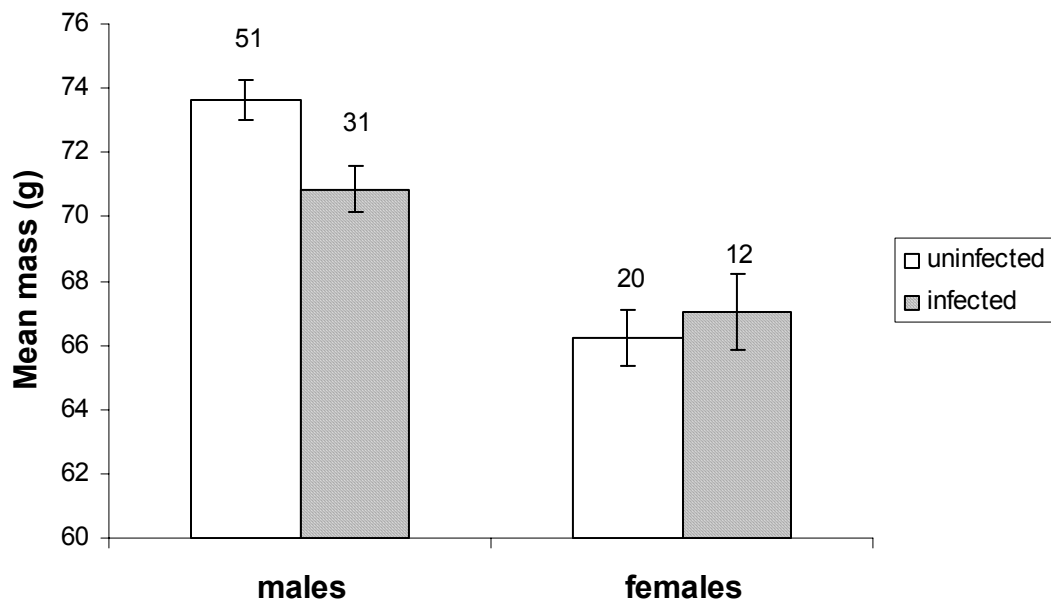


Fig 1.5. Mean mass (\pm SE) of uninfected (open bars) and infected (hatched bars) males and females collected during the breeding season (May- September 2000 and April- July 2001). Numbers above bars are sample sizes.

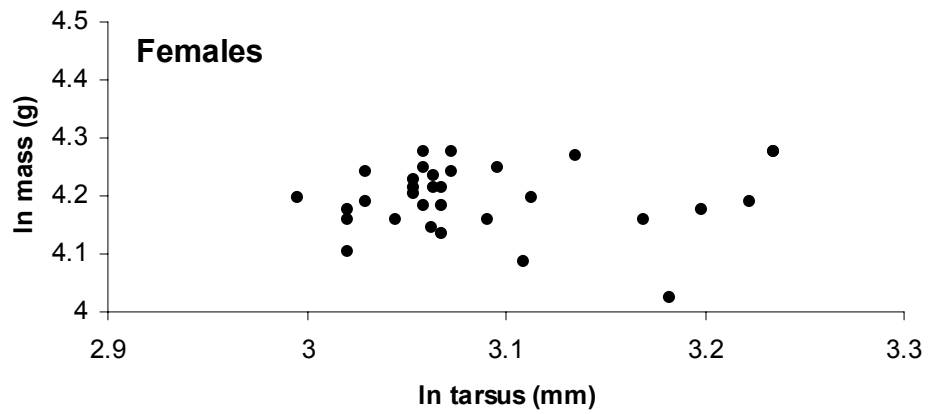
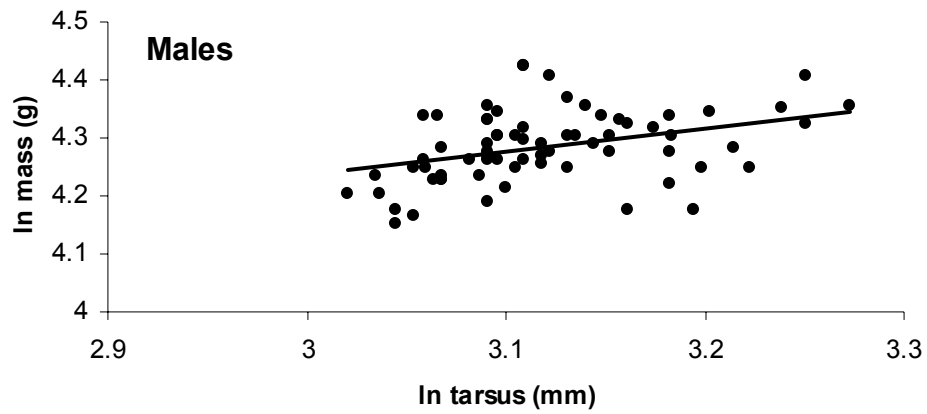


Fig. 1.6. The relationship between ln mass and ln tarsus length for males and females during the breeding season (May-September 2000 and April-July 2001).

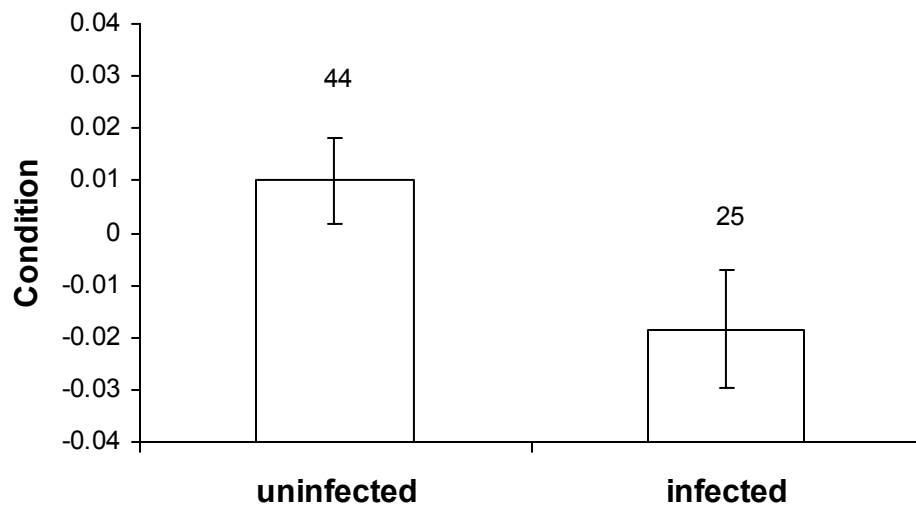


Fig. 1.7. Mean condition (\pm SE) of uninfected and infected males collected during the breeding season (May-September 2000 and April-July 2001). Condition was estimated using the residuals of the regression of \ln mass on \ln tarsus. Numbers above bars are sample sizes.

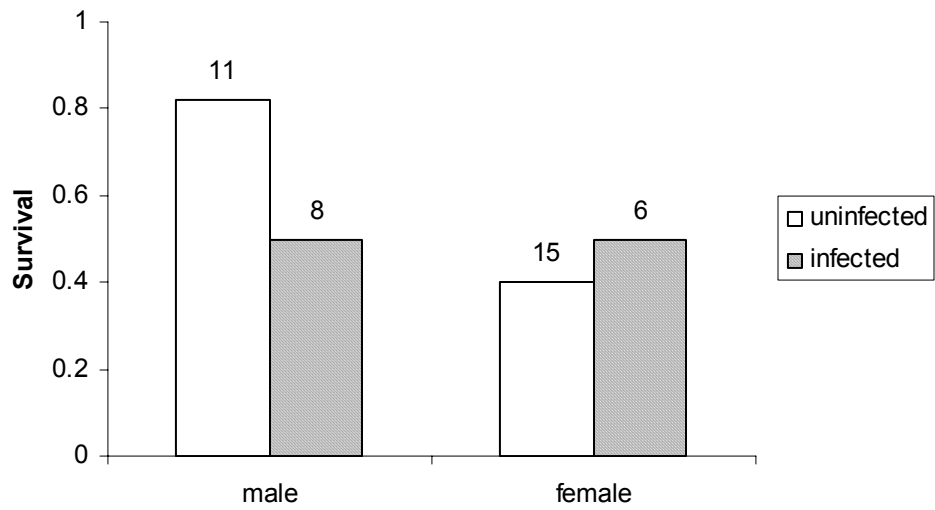


Fig. 1.8. Overwinter survival of uninfected (open bars) and infected (hatched bars) males and females. Numbers above bars are sample sizes.

DISCUSSION

The results of this study demonstrate that the prevalence of *Haemoproteus* varies seasonally in the Apalachicola National Forest Red-bellied Woodpecker population. Other studies in wild populations have demonstrated temporal differences in the prevalence of haematozoan infections (Janovy 1966, Weatherhead and Bennett 1991, 1992; Hatchwell et al. 2000; Deviche et al. 2001), but most have been conducted in migratory species on their breeding grounds, so their duration is usually limited to a few consecutive months. The study reported here revealed strong seasonal variation in parasite prevalence over a period of 15 consecutive months (Fig. 1.1). Parasite prevalence in this population ranged from a high of approximately 80% in July 2000 to a low of 0% in January and February 2001. During this study, parasite prevalence peaked during the middle of the Red-bellied Woodpecker breeding season and was consistent with the spring relapse phenomenon. The presence of a spring relapse has raised questions regarding some of the practical aspects of testing Hamilton and Zuk's hypothesis. For example, Weatherhead and Bennett (1991, 1992) have suggested that seasonal variation in parasite prevalence hinders the ability of researchers to detect infections from blood smears, because whether an individual tests positive may depend on when that individual was sampled. For example, individuals with chronic infections may not have circulating gametocytes, in which case, they would be considered uninfected on the basis of the analysis of a blood smear. This study further emphasizes the importance of considering seasonal variation in parasite prevalence in the attempt to

determine whether an individual is infected with haematozoa. The absence of any infected birds in our Jan and Feb 2001 samples suggests that individuals had fully recovered from prior infections, that chronic infections had become undetectable in peripheral blood by that time, or that infected individuals had died. Persistent stages of haematozoan parasites may reside in the liver of an infected host for the duration of the host's life and may serve as a source of parasites for relapsing chronic infections (Jarvi et al. 2001). It is therefore possible that the decrease in parasite prevalence observed in the winter is the result of chronic infections becoming latent, not complete recovery from summer infections. Recently developed PCR- based methods for diagnosing haematozoan infections (Jarvi et al. 2001) may increase the ability of researchers to detect haematozoa despite seasonal changes in prevalence.

An increase in the prevalence of haematozoa during the host's breeding season is often attributed to a relapse of chronic infections due to the physiological stress associated with breeding (Atkinson and van Riper 1991). This view is supported by experimental evidence that corticosterone triggers relapses of chronic *Plasmodium* infections (Applegate and Beaudoin 1970). In addition, many recent observational and experimental studies that have demonstrated a positive relationship between reproductive effort and the prevalence or intensity of haematozoa (Oppliger et al. 1997, Nordling et al. 1998). Red-bellied Woodpeckers in the Apalachicola National Forest usually attempt to raise 2–3 broods during each breeding season. First clutches are laid in mid to late April and second clutches in early July. The peak in *H. velans* prevalence I observed corresponds with the approximate fledge date of most second-brood chicks (late July and early August). A trade-off may therefore occur between raising a second brood and

resistance to *H. velans*. Future work examining how manipulating reproductive effort early in the breeding season (first clutches) affects parasite resistance and reproductive effort later in the breeding season (second and third clutches) may help increase our understanding of the relationship between reproductive effort and infection with *H. velans* in the Red-bellied Woodpecker.

Although good evidence suggests that infection with haematzoa is associated with physiological stress and reproductive effort, a number of additional factors may cause parasite prevalence to vary in the manner I observed. For example, infected birds may suffer higher overwinter mortality than uninfected birds. In this study, infection with *H. velans* did not affect overwinter survival of males or females, but uninfected males showed a nonsignificant tendency toward higher overwinter survival than infected males. These results are similar to those of Davidar and Morton (1993) and Dawson and Bortolotti (2000), who found no association between infection with *Haemoproteus* and return rates in Purple Martins (*Progne subis*) and American Kestrels (*Falco sparverius*) respectively. Although they found no association between infection and return rates, Dawson and Bortolotti found a significant negative relationship between the intensity of *Haemoproteus* infections and the probability that female American Kestrels would return to the study area. They found a similar relationship between return rates and infection intensity in males, but this relationship was not statistically significant. A similar relationship between infection intensity and overwinter survival may exist in the Apalachicola National Forest Red-bellied Woodpecker population, but I did not have intensity data on enough individuals to test this possibility.

In addition, the seasonal trend in parasite prevalence that I observed may be the result of new infections associated with the emergence of insect vectors. The vector for *H. velans* in the Apalachicola National Forest study is probably a biting midge (genus *Culicoides*). North Florida harbors a number of ornithophilic midges that may be potential vectors. The seasonal abundance of potential vectors in the study area varies by species, but a number of them are most abundant from April to October (Blanton and Wirth 1979). If the abundance of insect vectors increases over the same period as the increase in parasite prevalence, the increase is probably due in part to new infections. Relapses coincident with the emergence of insect vectors may also reflect a life-history strategy of the parasite (Kirkpatrick and Suthers 1988). For example, a correlation between vector abundance and some physiological change in the host could be exploited by the parasite to increase its chance of transmission to a new host. These possibilities are supported by Merila et al. (1995), who found that the prevalence of blood parasites in geographically separated Greenfinch (*Carduelis chloris*) populations was correlated with local vector abundance. A complete understanding of the association between vector abundance and prevalence of *H. velans* requires knowing the insect vector's identity, its seasonal abundance, and the prevalence of *H. velans* in the vector. I do not currently have these data.

A negative association between condition and infection with haematozoa is a necessary condition for validity of both Hamilton and Zuk's hypothesis and the suggestion of a trade-off between reproductive effort and resistance to haematozoa (Hamilton and Zuk 1982, Ots and Horak 1998), but many studies have failed to demonstrate such an association (Smith and Cox 1972, Bennett et al. 1988, Wiehn et al.

1997). In the absence of such an association, haematozoa might not be an important force in sexual selection and life-history evolution. However, this study revealed negative associations between infection with *H. velans* and male mass and condition. In addition, there was a tendency for infected males to have lower overwinter survival than uninfected males. These results suggest that infection with *H. velans* may be an important force in the evolutionary ecology of the Red-bellied Woodpecker. Current efforts to understand the relationships among reproductive effort, parasitism, and host condition may help to determine its importance.

Interestingly, mass of females was not associated with infection with *H. velans*. Dawson and Bortolotti (2000) found that the association between infection and condition in female American Kestrels was sensitive to the stage of the birds' nesting cycle. In their study, infection with *Haemoproteus* was not associated with condition in prelaying females but was negatively associated with condition in incubating females. A similar situation may exist in Red-bellied Woodpeckers, but because I did not know the nesting-cycle stage of most females I captured, I was unable to control for its potential effect. Another possibility is that the physiological demands of reproduction have a larger effect on female condition than does infection with *H. velans*. Female Red-bellied Woodpeckers in the Apalachicola National Forest often lay three clutches during a single breeding season, and they are responsible for most of the nestling provisioning (Schrader unpublished data). It may therefore be important to control for several measures of female reproductive effort (i.e., number of eggs laid, number of clutches laid, number of nestlings, and nestling age) during assessment of the effect of infection on female condition.

In conclusion, this study clearly demonstrated the presence of a spring relapse of *H. velans* infections in a population of Red-bellied Woodpeckers. In addition, the results of this study reemphasize the need to consider seasonal variation in parasite prevalence when screening individuals for haematozoa. Finally, the results of this study suggest that while infection with *H. velans* may not have a direct effect on host survival, it can have a negative effect on host condition.

CHAPTER 2

BROOD MANIPULATION AFFECTS PARASITE PREVALENCE BUT NOT FEEDING EFFORT IN MALE RED-BELLIED WOODPECKERS (*MELANERPES CAROLINUS*)

INTRODUCTION

The existence of a trade-off between current reproductive effort and residual reproductive value is an essential component of models of life history evolution (Williams 1966). The importance of this trade-off, usually referred to as the cost of reproduction, to life history theory has motivated ecologists and evolutionary biologists to attempt to demonstrate its existence. Researchers have used several approaches to demonstrate the presence of a cost of reproduction with varying success (Reznick 1985). Ultimately, the cost of reproduction is an evolutionary phenomenon that arises because of genetic trade-offs. As such, the most appropriate way to demonstrate the cost of reproduction is to demonstrate genetic correlations among fitness traits, either through breeding designs or selection experiments (Reznick 1985). Another approach that has

been used to demonstrate the cost of reproduction entails experimentally manipulating reproductive effort (e. g. brood manipulation experiments) and measuring the effect of this manipulation on residual reproductive value. Although this approach may not be appropriate for demonstrating an evolutionary cost of reproduction, it can help to establish the physiological and ecological mechanisms that generate it (Roff 1992).

Brood manipulation experiments in some species of birds have demonstrated a trade-off between current reproductive effort and survival or future fecundity (Askemno 1979, Gustaffson and Sutherland 1988, Nur 1988), however the mechanisms that give rise to this trade-off are largely unknown. Recent studies have suggested that a trade-off between reproductive effort and resistance to haematozoan parasites is one mechanism that can mediate the cost of reproduction in birds (Sheldon and Verhulst 1996).

Evidence for a trade-off between reproductive effort and parasite resistance comes from observational and experimental studies that have demonstrated a positive relationship between a measure of reproductive effort (usually brood size or clutch size) and the prevalence or intensity of infections with haematozoan parasites (Gustafsson et al. 1994, Richner et al. 1995, Allander 1997, Oppliger et al. 1997). In order for this trade-off to mediate the cost of reproduction, infection with haematozoa must result in decreased survival or future fecundity, however whether this requirement is met is unclear.

Although laboratory studies of domestic species have shown haematozoa to have significant pathological effects on their hosts (Atkinson and van Riper 1991), evidence that infection with haematozoa decreases host fitness in the wild is mixed. In some cases, infection is associated with decreased host survival, low host reproductive success, and poor host condition (van Riper et al. 1986, Ots and Horak 1998, Merino et al. 2000,

Schrader et al. 2003). Other studies however, have found no effect of haematozoa on host survival, condition, or reproductive success (reviewed by Bennett et al. 1988, 1993, Davidar and Morton 1993, Sanz et al. 2001). In addition, although there has been much recent interest in the importance of a trade-off between reproductive effort and haematozoa resistance in birds, this trade-off has only been demonstrated in populations in which pairs nest in nest boxes. Nest-box studies have provided important insights into many aspects of avian ecology (Blondel et al. 1989), however results from these studies are potentially biased (Møller 1989, 1992, but see Koenig et al. 1992). For example, the introduction of concrete nest boxes to a Great Tit (*Parus major*) population virtually eliminated nest predation and resulted in increased fledging success, population density, and late life mortality (McCleery and Perrins 1991, McCleery et al. 1996). It has been suggested that the increase in late life mortality seen after the introduction of predator-proof nest boxes is the result of a greater cost of reproduction due to increased competition and increased investment in reproduction (McCleery et al. 1996). While a trade-off between reproductive effort and resistance to haematozoa has been demonstrated in nest box populations of a few cavity-nesting species, it is unknown whether this trade-off is important in populations nesting under more natural conditions, or whether the trade-off only occurs in high density, low predation nest-box populations.

I investigated the importance of a trade-off between parental effort and resistance to a haematozoan parasite (*Haemoproteus velans*) in a population of Red-bellied Woodpeckers (*Melanerpes carolinus*) nesting in natural cavities in the Apalachicola National Forest (ANF) in north Florida, USA. Previous work in this population suggested the presence of a trade-off between reproductive effort and resistance to *H.*

velans. In particular, Schrader et al. (2003) found that the peak in *H. velans* prevalence in the ANF Red-bellied Woodpecker population coincides with the Red-bellied Woodpecker breeding season. In addition, Schrader et al. found that male Red-bellied Woodpeckers infected with *H. velans* were in poorer condition and tended to have lower overwinter survival than uninfected males, suggesting that if a trade-off between parental effort and resistance to *H. velans* exists, it has the potential to result in decreased residual reproductive value. Here I report the results of a brood manipulation experiment designed to determine whether there is a trade-off between caring for an enlarged brood and resisting *H. velans* in the Red-bellied Woodpecker, and if so, whether the trade-off is associated with a decrease in a component of residual reproductive value (the success of second and third broods).

METHODS

(a) *Study Species*

The Red-bellied Woodpecker is one of the most abundant woodpeckers in eastern North America. It is distributed across the eastern U.S., occurring west to the Great Plains and north to southern Ontario, and is found in a variety of habitats (Shackelford et al. 2000). Red-bellied Woodpeckers generally nest in dead trees or dead limbs in live trees, however in the ANF many pairs nest in cavities excavated in living pines by Red-cockaded Woodpeckers (*Picoides borealis*). Red-bellied woodpeckers in the ANF are host to *H. velans* (Schrader et al. 2003). The lifecycle of *H. velans* consists of asexual reproduction in the host and sexual and asexual reproduction in the vector which is

usually a biting midge or louse fly (Atkinson and van Riper 1991). Species of *Haemoproteus* are thought to be the most common and least pathogenic of the avian blood parasites (White et al. 1978, Atkinson and van Riper 1991).

(b) General Fieldwork

The study was conducted between April and September 2002 using pairs of banded Red-bellied Woodpeckers nesting in natural cavities in the ANF. I began locating nests in early April. Once nests were located, they were visited every 2-5 days to determine the dates of clutch initiation and completion, and clutch size. I matched each nest with two others based on the date of clutch initiation, clutch size, and proximity. Within each triplet of nests, I randomly assigned each nest to one of three treatments (reduced, control, or enlarged). When the oldest nestling in each nest was 5 days old, I removed 2 nestlings from nests in the reduced treatment group and added them to the nests in the enlarged treatment group. Brood size in the control group was unmanipulated, however when nestlings in these nests were 5 days old they were removed from the nest cavity, handled for approximately the same amount of time as nestlings in nests assigned to the other treatments, and replaced. Initially I assigned 15 nests to each of the treatment groups, however some nests failed before I was able to manipulate them, and others failed before the nestlings in them were 14 days old. After dropping these nests I ended up with 8 nests in the reduced treatment group, 10 nests in the control group, and 11 nests in the enlarged group.

When the nestlings in each nest were 14 days old, I measured the rate at which males and females fed nestlings. I recorded feeding rates at each nest by observing the

nest cavity from a distance with a spotting scope during a randomly assigned one-hour time period between 06:00 and 11:00. After recording the number of feeding trips parents made, I climbed each nest tree and counted the number of nestlings in the nest cavity. I counted the number of nestlings in each nest again when the nestlings were 22 days old. Red-bellied woodpeckers fledge 24-27 days after hatching, however I used the number of nestlings in the cavity 22 days after hatching as an estimate of fledging success because Red-bellied Woodpecker fledglings are difficult to locate.

I caught adults in the experiment to obtain blood samples, which I used to diagnose *H. velans* infections. Male Red-bellied woodpeckers roost in the nest cavity with the nestlings, so I was able to catch all males using a net on a telescoping pole as they left nest cavities in the morning. I caught adult males when first brood nestlings were 22-25 days old, however I wasn't able to catch females at the same time as the males because it was difficult to find where females roosted. Because I couldn't reliably catch females at the same time as males, I caught females while they were incubating completed second clutches. However, I was unable to catch most females who did not lay a second clutch and there were some females who laid second clutches that I was unable to catch. As a result, the sample sizes for the females are not the same as the sample sizes for the males. I collected two blood samples (approximately 50 μ l each) from the left brachial vein of each individual at the time of capture. This blood sample was used to make blood smears on two clean glass slides using the technique described by Bennett (1970). Blood smears were fixed in absolute methanol in the field and were stained with Geimsa stain approximately 1 week after being taken. Blood smears were scanned under oil emersion (1000X) to detect the presence of infected erythrocytes.

Hosts may harbor chronic haematozoan infections that are undetectable in smears of peripheral blood (Jarvi et al. 2001); however for the purposes of this study, I classified individuals with no infected erythrocytes in 200 fields of view as uninfected.

To examine the effect of manipulating first broods on future reproductive success, I monitored subsequent nesting attempts by each pair in the experiment. I began looking for the second clutches of each pair one week after the first brood nestlings fledged or the nest was discovered to have failed. For each second clutch I recorded the clutch size, brood size 7 days and 14 days after hatching, the number of fledglings, and whether or not pairs reused the first nest cavity or moved to a new nest tree. I began looking for third clutches one week after second broods fledged or the nest was discovered to have failed. For each third brood, I recorded the same data that were recorded for second broods.

(c) Statistical analysis

The effect of treatment on measures of breeding success (e.g. brood size, number of fledglings), were analyzed using either ANOVA, or in cases where the assumptions of ANOVA were violated, Kruskal-Wallis tests. Post-hoc comparisons among the treatment group means were made using Tukey's pair-wise comparisons, or distribution-free multiple comparisons based on Kruskal-Wallis rank sums with an experimentwise error rate = 0.05 (Hollander and Wolfe 1973). I examined the effect of treatment on parasite prevalence using the Cochran-Armitage trend test. This procedure tests for a linear trend between an ordinal independent variable (treatment) and a binary dependent variable (infected or uninfected) (Agresti 1996).

RESULTS

(a) Success of first broods

Since brood reduction is common in the Red-bellied Woodpecker (Shackelford et al. 2000), I compared the brood sizes in each treatment group immediately after manipulation to confirm that the parents in each treatment were caring for different sized broods. I also compared the brood sizes in each treatment when the nestlings were 14 days old (9 days after the manipulation) to confirm that brood reduction had not eliminated the effect of the brood manipulation. Brood size differed among the treatment groups immediately after the manipulation (Kruskal-Wallis test, $H_{adj} = 24.92$, $P < 0.0001$, Figure 2.1), and 14 days after hatching (Kruskal-Wallis test, $H_{adj} = 19.71$, $P < 0.0001$, Figure 2.1). There was also a significant effect of brood manipulation on the number of first brood fledglings (Kruskal-Wallis test, $H_{adj} = 11.83$, $P = 0.003$, Figure 2.1). This was mainly due to the fact that enlarged broods fledged more young than decreased broods ($P < 0.017$). Post-hoc comparisons among the treatment groups revealed that there were no statistically significant differences between the brood size of the reduced broods and control broods immediately after the manipulation ($P > 0.017$) or when the nestlings were 14 days old ($P > 0.017$). Although the post-hoc comparisons revealed no statistically

significant differences between the sizes of reduced and control broods, these tests are conservative (Hollander and Wolfe 1973) and there were clear differences between the mean brood sizes of each treatment group (Figure 2.1). Therefore, all subsequent analyses were performed both with the reduced and control groups pooled and with these groups considered separately. However, since pooling the reduced and control groups does not change the results of any further analyses, here I present only results of the analyses that consider each treatment separately.

(b) Feeding rates

Brood manipulation had different effects on male and female feeding rates. There was no effect of treatment on male feeding rate (ANOVA, $F_{(2, 24)} = 1.3$, $P = 0.29$, Figure 2.2), but there was a significant effect of brood manipulation on female feeding rate (ANOVA, $F_{(2, 24)} = 5.20$, $P = 0.013$, Figure 2.2). Females caring for enlarged broods made significantly more feeding trips per hour than females caring for reduced broods ($P = 0.018$). Females caring for enlarged broods also made more feeding trips per hour than females caring for control broods, however this comparison was marginally non-significant ($P = 0.09$).

(c) Parental infections

The prevalence of *H. velans* in males caring for enlarged broods was approximately double that of males caring for reduced and control broods (Figure 2.3), however effect of treatment on parasite prevalence in males was marginally non-significant ($M^2 = 2.53$, $P = 0.11$). In females, *H. velans* prevalence was highest in the

control group (Figure 2.3), and there was no significant linear relationship between treatment and parasite prevalence in females ($M^2=0.092$, $P= 0.76$).

(d) Success of second and third broods

Most females laid a second clutch (7/ 8 females caring for reduced first broods, 8/10 females caring for control first broods, and 9/ 11 females caring for enlarged first broods). Pairs caring for enlarged first broods tended to move to a new nest tree more often than pairs caring for reduced or control first broods (number using new tree/ total number renesting: 1/7 reduced, 1/ 8 control, and 4/9 enlarged, Figure 2.4), however this trend was not statistically significant (Cochran-Armitge test, $M^2= 2.43$, $P= 0.12$).

Females in the control group laid significantly smaller second clutches than females caring for enlarged or reduced first broods ($F_{(2, 21)}= 16.22$, $P< 0.001$, Figure 2.5).

However there was no effect of treatment on the size of the second brood when the nestlings were 7 days old ($F_{(2, 16)}= 1.47$, $P= 0.259$), 14 days old ($F_{(2, 16)}= 0.75$, $P= 0.49$), or 22 days old ($F_{(2, 16)}= 1.31$, $P= 0.297$, Figure 2.5). Few females laid a third clutch, however proportion of females laying a third clutch decreased with manipulated brood size (4/ 8, 2/ 10, and 0/11 females caring for reduced, control, and enlarged first broods respectively laid third clutches, Cochran-Armitage test $M^2= 6.2$, $P= 0.013$, Figure 2.6). No third clutches fledged any young.

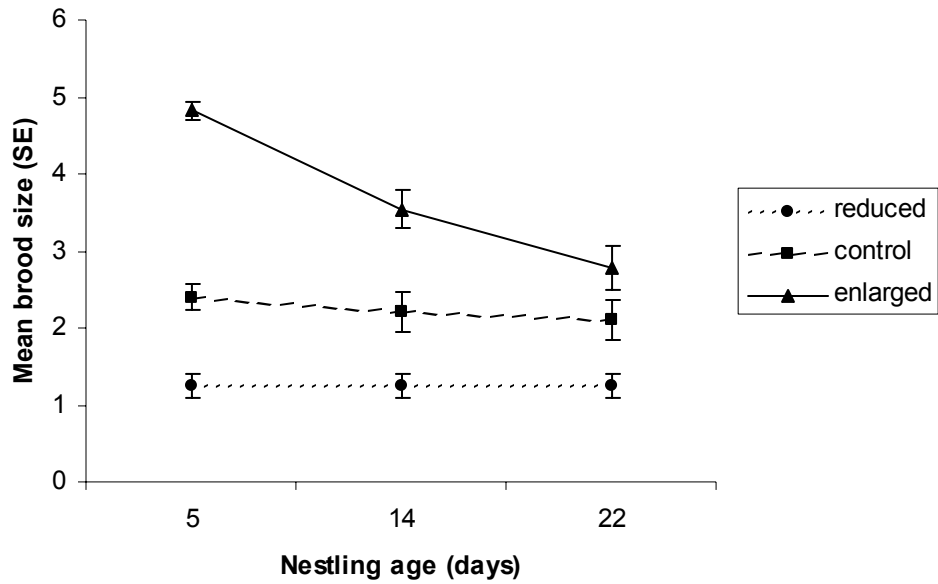


Figure 2.1. The mean (\pm SE) brood size of the reduced (●), control (■), and enlarged (▲) treatment groups 5 (●, $n=8$; ■, $n=10$, ▲, $n=11$), 14 (●, $n=8$; ■, $n=10$, ▲, $n=11$), and 22 (●, $n=8$; ■, $n=9$, ▲, $n=9$) days after the nestlings hatched. Brood size at 5 days was measured immediately after broods were manipulated.

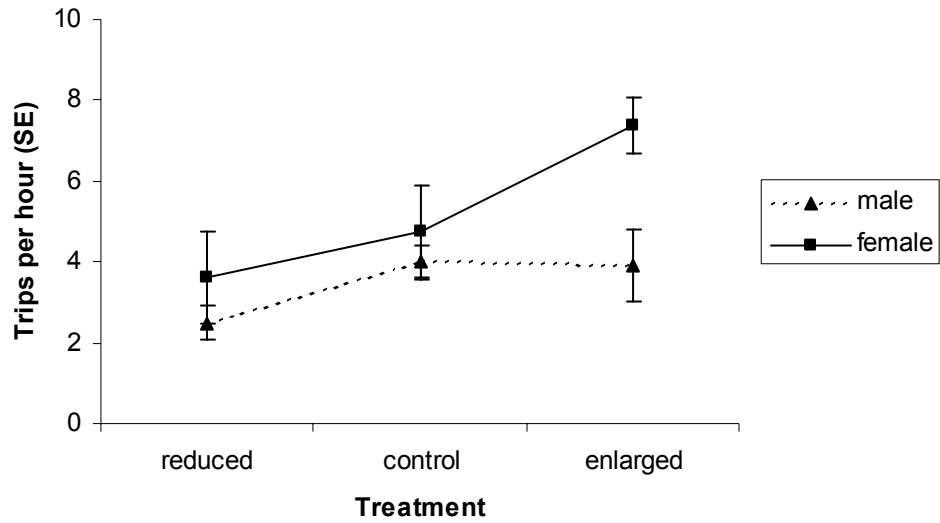


Figure 2.2. The mean number of feeding trips per hour (\pm SE) made males (\blacktriangle) and females (\blacksquare) caring for reduced ($n=8$), control ($n=8$), and enlarged broods ($n=11$). Feeding rate were recorded when nestlings were 14 days old.

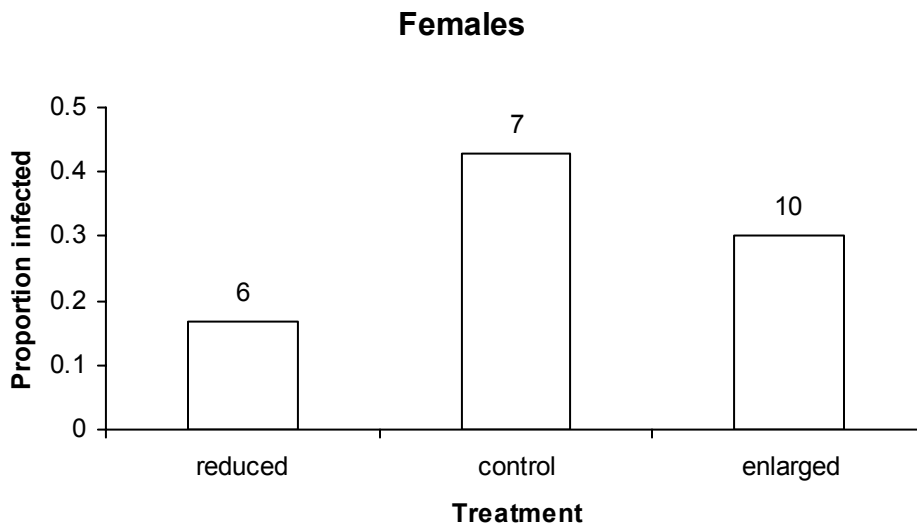
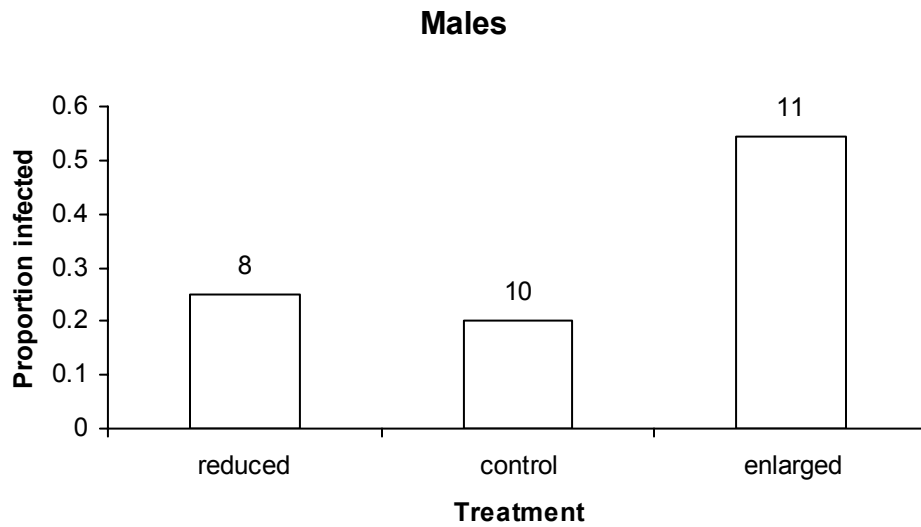


Figure 2.3. The prevalence (proportion infected) of *H. velans* in (a) male and (b) female Red-bellied Woodpeckers caring for reduced, control, and enlarged broods. Numbers above bars are sample sizes.

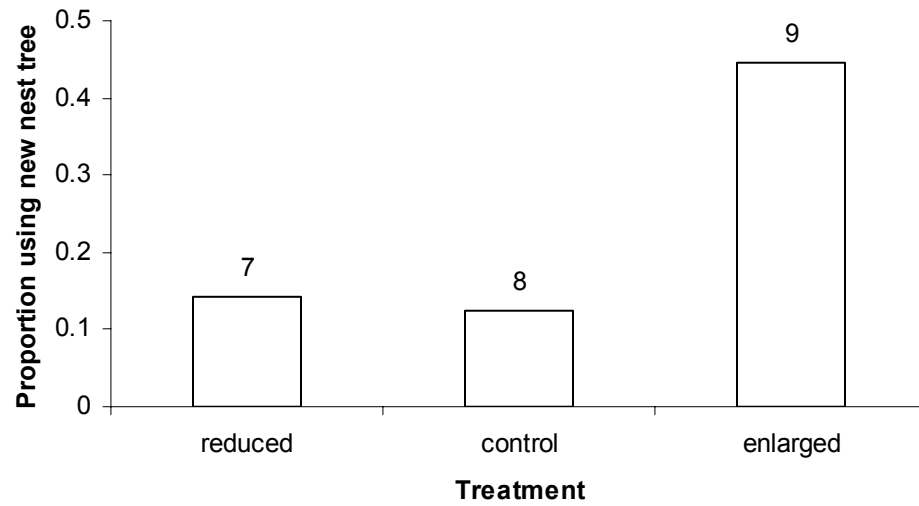


Figure 2.4. The proportion of pairs caring for reduced, control, and enlarged first broods that used a new nest tree for their second nesting attempt. Numbers above bars are sample sizes.

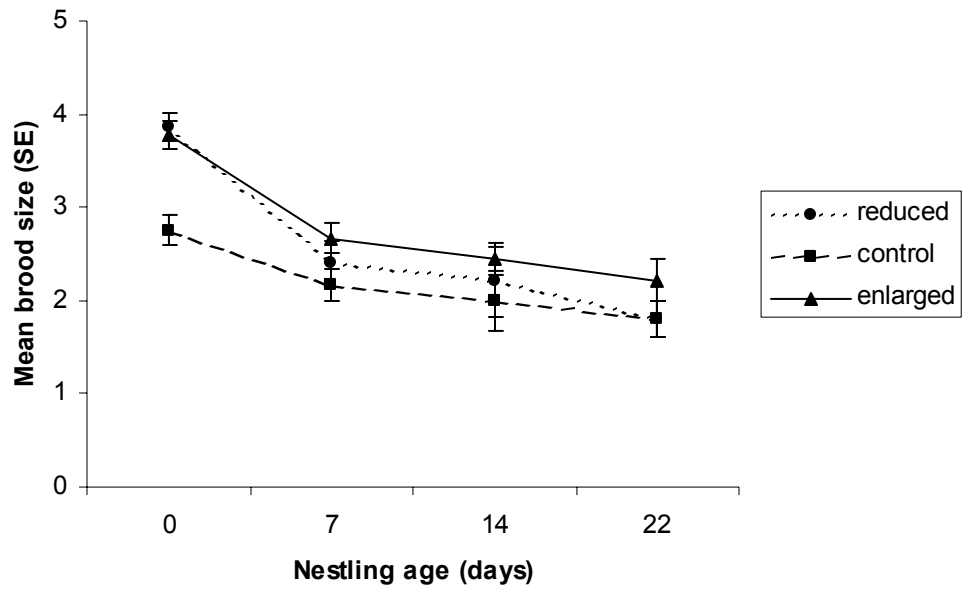


Figure 2.5. The mean second brood size (+/- SE) of pairs whose first brood was in the reduced (●), control (■), and enlarged (▲) treatment, 0 (●, n= 7; ■, n= 8; ▲, n=9), 7 (●, n= 5; ■, n= 5; ▲, n=9), 14 (●, n= 5; ■, n= 5; ▲, n=9), and 22 (●, n= 5; ■, n= 5; ▲, n=9) days after the nestlings hatched.

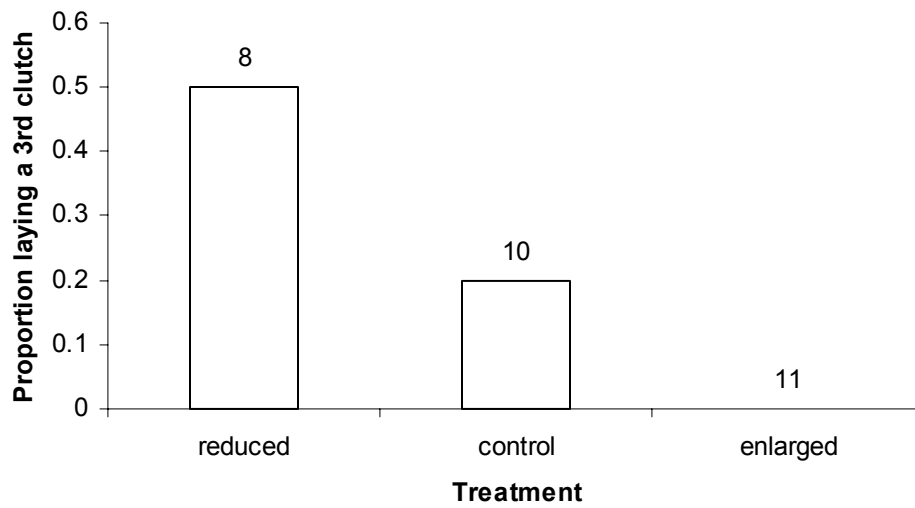


Figure 2.6. The proportion of females caring for reduced, control, and enlarged first broods that laid a third clutch. Numbers above bars are sample sizes.

DISCUSSION

The prevalence of *H. velans* in male Red-bellied Woodpeckers caring for enlarged broods was twice that of males caring for reduced or control broods, and almost twice that found for males sampled over approximately the same period in a previous observational study (Schrader et al. 2003). Although this result was not statistically significant, it suggests that there is a trade-off between caring for an enlarged brood and resisting *H. velans* infections in male Red-bellied Woodpeckers. To my knowledge this is the first study to attempt to demonstrate such a trade-off experimentally in a population of birds nesting in natural cavities. The results of this study are similar to those of studies conducted in nest-box populations, suggesting that the presence of a trade-off between reproductive effort and haematozoa resistance may be a general phenomenon in cavity nesting species. Although there appeared to be a trade-off between caring for an enlarged brood and haematozoa resistance in males, there was no such trade-off in females. This result is similar to those of Richner et al. (1995) who found a trade-off between caring for an enlarged brood and resisting *Plasmodium* in male Great Tits (*Parus major*). In their study, males caring for enlarged broods fed nestlings at higher rates and were more likely to be infected with *Plasmodium* than males caring for reduced or control broods, but there was no effect of brood manipulation on female feeding rates or *Plasmodium* prevalence. The results of Richner et al. support the assumption that a trade-off between reproductive effort and parasite resistance is the result of a conflict between the energetic demands of parental care and investment in the immune system (Sheldon and Verhulst

1996). In this study however, the increase in parasite prevalence in males caring for enlarged broods was not associated with an increase in male feeding rates, suggesting that there can be a trade-off between caring for an enlarged brood and resisting parasitic infections even if parents do not increase their feeding rates to match the manipulated brood size.

Parental feeding rates are often thought to reflect the amount of energy devoted to parental care, however the relationship between feeding rates and energy expenditure is not always positive (Moreno et al. 1995) and there are parental duties in addition to nestling provisioning (such as incubation, reviewed in Thomson et al. 1998), that may be costly. Under normal conditions, Red-bellied Woodpeckers parents appear to split most of the parental duties equally (Shackelford et al. 2000); however, male Red-bellied Woodpeckers spend the night in the nest cavity with their nestlings until just before the nestlings fledge, whereas females roost elsewhere. There are several potential costs of roosting in the nest cavity with the nestlings. One of these is increased exposure to ectoparasites. Most Red-bellied Woodpecker nests in my study site are infested with ectoparasitic louse flies (Schrader unpublished data). Studies of other species have found that the prevalence and intensity of nest ectoparasites increase with manipulated brood size (Saino 2002), and it is possible that a similar response to brood manipulation occurred in this experiment. If ectoparasites are transmitted bidirectionally between parents and offspring, it is possible that male Red-bellied Woodpeckers roosting in nest cavities containing enlarged broods were exposed to more ectoparasites than males caring for reduced or control broods. There are potential energetic costs associated with increased exposure to ectoparasites. For example, Christe et al. (1996) experimentally

manipulated the number of ectoparasites in nests of the Great Tit and found that females roosting in nest cavities infested with ectoparasites spent more time engaged in nest sanitation behaviors and less time sleeping than did females roosting in parasite-free nest cavities. If the ectoparasitic louse flies found in Red-bellied Woodpecker nests are capable of transmitting *H. velans*, then the increase in *H. velans* prevalence that I observed in males caring for enlarged broods may be the result of increased exposure to infective vectors. The relationship between brood size, louse fly abundance, and *H. velans* infections clearly needs further study.

To date, most studies that have demonstrated a trade-off between caring for an enlarged brood and resisting parasitic infections have interpreted the results in terms of a simple resource allocation model. However, Svensson et al. (1998) suggested that such a trade-off might be the result of stress-induced immunosuppression that arises independently of the amount of energy allocated to parental care. There is evidence that environmental stress can trigger relapses of haematozoan infections. For example, Oppliger et al. (1998) have shown experimentally that lizards living under crowded conditions have higher levels of corticosterone and a higher prevalence of haematozoan infections than lizards living in uncrowded conditions. It is possible that the trade-off between caring for an enlarged brood and resisting *H. velans* in male Red-bellied Woodpeckers is the result of stress-induced immunosuppression that is unrelated to parental effort.

There is some indirect evidence from this study that male Red-bellied Woodpeckers roosting with nestlings are subjected to environmental stress. As elsewhere (Shackelford et al 2000), Red-bellied Woodpecker parents in the ANF removed feces

from nest cavities only for the first few days after the nestlings hatched. After this, conditions within the nest cavity became increasingly unsanitary as feces, decaying eggshells, developing insect larvae, and occasionally even dead nestlings began to accumulate on the floor of the nest cavity. After the nestlings fledged, males usually stopped roosting in the nest cavity and began roosting in a nearby cavity. Most males returned to the original nest cavity for their second nesting attempt, however there was a tendency for males caring for enlarged first broods to choose a new tree for their second nest more often than males caring for reduced and control first broods. This result suggests that a nesting attempt decreases the quality of a cavity such that it is no longer suitable as a roost site or as a site for a second nesting attempt. However the relationship between conditions within the nest cavity and stress levels in males needs further study.

I found that female Red-bellied Woodpeckers caring for enlarged broods increased their feeding rates. Based on this result, I expected that if there were a trade-off between caring for an enlarged brood and resisting *H. velans* I would find it in females, not males. Contrary to this expectation, I found no evidence for a trade-off in females. Because the sample size for females was small I am reluctant to make any conclusions regarding the effect of brood manipulation on parasite prevalence in females. However, it is interesting that parasite prevalence in females was highest in the control group and that females in the control group laid significantly smaller second clutches than females caring for reduced or enlarged first broods. Red-bellied Woodpecker parents care for fledglings for 2- 6 weeks after they leave the nest. Since I was unable to catch females until after this period, it is possible that the treatment groups differed in the amount of post-fledgling parental care the fledglings required, and that these differences contribute

to the relationship between treatment, and parasite prevalence. For example, if fledglings from enlarged broods fledged in poorer condition than fledglings from reduced or control broods they may have suffered higher mortality between fledging and post-fledging independence. If this is the case, then females caring for control broods may have invested the most in parental care between the time of manipulation and the time of post-fledging independence. The relative importance of pre- and post-fledging parental care in generating trade-offs needs further study.

Although there was an effect of the brood manipulation on the size of second clutches, there was no effect of treatment on the number of fledglings produced by second broods. There was also no effect of treatment on the success of third clutches, although the proportion of females laying third clutches differed among the treatment groups (Figure 2.6). These results suggest that while there appears to be a trade-off between caring for an enlarged brood and resisting *H. velans* in male Red-bellied Woodpeckers, this trade-off is not associated with a decrease in residual reproductive value, at least within one season. Previous work in this system found that males infected with *H. velans* were in poorer condition and tended to have lower overwinter survival than uninfected males. Thus, it is possible that a trade-off between caring for an enlarged brood and resisting *H. velans* is one mechanism that mediates the cost of reproduction in males through decreased survival. More work is needed to determine whether a trade-off between reproductive effort and resistance to *H. velans* is one mechanism that mediates the cost of reproduction in the Red-bellied Woodpecker.

In conclusion, I found evidence for a trade-off between caring for an enlarged brood and resisting *H. velans* in male Red-bellied Woodpeckers that was not associated

with an increase in parental feeding effort. This suggests that a trade-off between caring for an enlarged brood and resisting parasites may not be the result of a simple energy allocation model. Instead, a combination of factors (increased exposure to ectoparasites and stress induced immunosuppression) may result in a trade-off between caring for an enlarged brood and resistance to *H. velans* in the Red-bellied Woodpecker. In addition, the results of this study suggest that several different mechanisms can mediate the cost of reproduction, and that the sexes may differ with respect to the importance of these mechanisms.

CONCLUSION

In conclusion, I found (1) that the prevalence of *H. velans* in the ANF Red-bellied Woodpecker population peaks during the Red-bellied Woodpecker's breeding season, (2) that infection with *H. velans* is associated with poor body condition and low overwinter survival in male Red-bellied Woodpeckers, and (3) there appears to be a trade-off between raising an enlarged brood and resisting *H. velans* in male Red-bellied Woodpeckers. Taken together, these results suggest that a trade-off between reproductive effort and resistance to *H. velans* may be one mechanism that mediates the cost of reproduction in the Red-bellied Woodpecker. However, this trade-off only appears to be important in males. It is possible that the cost of reproduction is mediated by several different mechanisms in the Red-bellied Woodpecker, and that sexes differ with respect to the importance of these mechanisms. In addition, although there appears to be a trade-off between caring for an enlarged brood and resisting *H. velans* in males, this trade-off is not associated with an increase in male feeding effort. It has been assumed that a trade-off between caring for an enlarged brood and resisting haematozoa can only be expected to arise if parents adjust their effort to match their manipulated brood size (Sheldon and Verhulst 1996). However, the results of this study suggest that such a trade-off can arise independently of parental effort, and that a simple energy

allocation model may not explain the presence of a trade-off between caring for an enlarged and resisting parasites in all cases.

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BIOGRAPHICAL SKETCH

Matthew S. Schrader
1504 Chuli Nene
Tallahassee, FL 32301
E-mail: Schrader@bio.fsu.edu

Department of Biological Sciences
Florida State University
Tallahassee, FL 32306-1100

Degrees:

B.S. Zoology, University of Florida, 1997
M.S. Biology, Florida State University, 2003

Area of Concentration:

Ecology and Evolution

Research Interests:

Evolutionary ecology, life history evolution, trade-offs, adaptation.

Teaching Experience:

Florida State University, Biology Department. Graduate Teaching Assistant, Introduction to Biology. Fall 1999, Spring 2000.

Florida State University, Biology Department. Graduate Teaching Assistant, Biological Science I Lab. Fall 2000.

Florida State University, Biology Department. Graduate Teaching Assistant, Biology of the Higher Vertebrates. Spring 2001, Spring 2003.

Florida State University, Biology Department. Graduate Teaching Assistant, Animal Diversity Lab. Fall 2001, Fall 2002.

Florida State University, Biology Department. Graduate Teaching Assistant, Pollination Biology. Spring 2002.

Professional / Research Experience:

University of Florida, Department of Zoology, Undergraduate Research Assistant. Fall 1997. Studied sexual allocation in a species of simultaneous hermaphroditic fish under Dr. Collette St. Mary.

Azruea Environmental Research and Consulting, Inc., Research Assistant, Aug 1998- July 1999. Conducted wildlife surveys on conservation lands, as well as laboratory work involving water quality assessment and waste-water chemistry.

Florida State University / U. S. Forest Service, Research Assistant, Summer 2000, Summer 2001, Summer 2002. Assisted in conducting the red-cockaded woodpecker breeding survey in the Apalachicola National Forest. Duties included locating and monitoring nests, banding chicks, and conducting fledge checks. This work was done as part of a large-scale experiment conducted by Dr. Frances C. James.

Awards / Honors:

American Ornithologists Union Student Research Grant, 2002

American Ornithologists Union Student Membership Grant, 2002

Florida Ornithological Society Cruickshank Memorial Award, 2001

Florida Academic Scholar, 1993- 1995

Publications

Schrader, M. S., E. L. Walters, and F. C. James, E. C. Greiner. 2003. Seasonal prevalence of a haematozoan parasite of the Red-bellied Woodpecker and its associations with host condition and overwinter survival. *The Auk*. In press.