Changes in parental provisioning rates across the nestling period in response to ectoparasites in the North American barn swallow *Hirundo rustica erythrogaster*

By
Matt Aberle
Department of Ecology and Evolutionary Biology,
University of Colorado at Boulder

Defense Date: April 4, 2014

Thesis Advisor:
Professor Rebecca Safran, Department of Ecology and Evolutionary Biology

Defense Committee:
Professor Rebecca Safran, Department of Ecology and Evolutionary Biology
Professor Barbara Demmig-Adams, Department of Ecology and Evolutionary Biology
Professor Petger Schaberg, Department of Writing and Rhetoric
Professor Michael Breed, Department of Ecology and Evolutionary Biology

Glossary:

Altricial: Nestlings confined to the nest after hatching and completely dependent on parental care

Brood: Group of young produced by a parent at one point in time.

Clutch: Number of eggs laid by a female at one point in time.

Cross-Fostering: Experimental technique where half of the young from two broods are switched between paired nests, in order to parse out the genetic and environmental influences on different traits.

Ectoparasite: A parasite that lives on the exterior of its host; they are often haematophagous.

Grooming: Common behavior by birds to remove ectoparasites from their feathers with their beak.

Haematophagy: Act of feeding on the blood of another organism, common in parasites.

Immunoglobulin: Another term for antibodies, which attach to foreign bodies in the bloodstream to signal the immune system to destroy it.

Intensity: Number of parasites in or on an infected host.

Nestling Period: Span of time in which nestlings occupy the nest before fledging.

Nest Sanitation: Suite of behaviors done by parent birds to clean the nest, often involves removing nestling droppings and sometimes parasites. May help to decrease parasite infestation.

Provisioning: Act of a parent providing food to its offspring.

Sexual Signal Traits: Exaggerated physical male traits used by females in mate choice decisions. This process is known as sexual selection.

Abstract:

While parasites have long been documented, the large fitness cost to their hosts has only recently been addressed via studies of ecology and evolution. Large fitness costs apply to altricial nestlings confined to the nest and completely dependent on parental care. These costs are often passed on to their parents and can either be allayed or magnified through adjustments in parental behavior. My study employs manipulation of nest parasite loads and direct visual observation to assess how ectoparasitism (external parasites) by mites in nests of the North American barn swallow (*Hirundo rustica erythrogaster*) affects provisioning (feeding) behavior of parents. This study addresses the question of how provisioning rates are changing not only in response to ectoparasite intensity (number of parasites present), but also how parental responses differ across the nestling period (time nestlings occupy the nest) and between sexes. Early in the nestling period (Day 7), female provisioning rates decreased as parasite load increased, with no response by males. However, later in the nestling period (Day 13), males increased provisioning rates for parasitized nests, while females did not. These findings suggest that not only do parasites affect provisioning, but that responses are dynamic and change over the nestling period.

Introduction:

Parasites exploit host resources and can elicit significant immune and behavioral responses (Lehmann 1993, Zhong et al. 2005, Roberts et al. 2012). It is predicted that individuals suffering from parasitic infection face trade-offs when finite resources are lost to parasites or used for parasite defense; this trade-off can influence the degree of resources allocated to other processes such as growth, maintenance, and reproduction (Owen et al. 2010, Norris 2000). For example, ectoparasitism in cliff swallows (*Hirundo pyrrhonota*) can cause its hosts to lose the equivalent of one full year of reproductive success, which is quite dramatic for this short-lived bird (Brown et al. 1995). A similar trend was also observed in great tits (*Parus major*); when nests are infested by hen fleas (*Ceratophyllus gallinae*), both current and future reproduction is reduced for females (Fitze et al. 2004). When exposed to ectoparasites, purple martins (*Progne subis*) will also lay smaller clutches (number of eggs) (Moss and Camin 1970). The idea that sexual signal traits (sexually selected traits) may serve as parasite indicators, as shown by Hamilton and Zuk (1982), also demonstrates the potentially detrimental effects of ectoparasites on their host's ability to attract and acquire a mate.

The altricial nestlings of songbirds are particularly vulnerable to the effects of ectoparasites as they are confined to a nest and are completely dependent on their parents throughout early development (Tripet and Richner 1997). During this time nestlings cannot physically or physiologically escape parasite infestations, and have relatively immature and weak immune systems (Killpack et al. 2013). Indeed, many studies have revealed various negative impacts in altricial nestlings across many different avian species (Hamilton and Zuk 1982, Moss and Camin 1970). Barn swallow (*Hirundo rustica*) nestlings exposed to ectoparasites had lower mass and body condition at the time of fledging compared to nestlings not exposed to parasites

(Saino et al. 1998). Similarly, sand martin (*Riparia riparia*) nestlings, in response to ectoparasites, had higher amounts of circulating immunoglobulin (antibodies), lowered mass, and shorter tarsus lengths (Szep and Møller 1999). Hence, parasites impose important physiological costs in terms of nestling development, but another mediator of these costs may be determined by how parents respond to the presence of ectoparasites on their nestlings.

Parents have several options in responding to the presence of ectoparasites; for example, they can increase provisioning rates. Yet, this compensatory feeding behavior has an added cost on the parents; accordingly, a reduction in parental care in the face of nest parasites might also be an adaptive strategy. The parent-offspring conflict arises due to differences in the importance of survival and reproduction of parents and offspring. As individuals are always more related to themselves compared to their offspring, conflicts may arise when self-preservation is favored over costly parental care (Trivers 1974). Parasites often play an important role in mediating this conflict and can make the tradeoffs between parents and offspring fitness even more important (Johnson and Albrecht 1993, Szep and Møller 1999). These responses can also vary between sexes as a result of reproductive trade-offs between males and females (Trivers 1972).

While there is no clear pattern for how parents adjust their behavior in response to parasites, there are several questions remaining to be answered to understand the observed species-specific patterns. One of the primary unanswered questions is how parental responses and the impacts of ectoparasites change across the nestling developmental period. The effects of parasites on a newly hatched chick, with little to no immune response, might be quite different compared to a fully developed chick near fledging. Therefore, I hypothesize that parental behavioral responses to ectoparasites might also change across the developmental period. Further, how are males and females responding behaviorally to the ectoparasites; are they responding in a similar manner or do they exhibit different responses? I hypothesize, that due to trade-offs in current vs. future reproduction, males and females will have different responses to ectoparasites. Finally, while previous research has established that ectoparasites often have negative impacts on nestlings, it is unknown how that impact may change as parasite intensity increases. I hypothesize that the behavioral responses by parents for a nest with 20 mites will differ versus a nest infested by 100 mites or more.

In this study, I examine the link between the ectoparasitic northern fowl mite (*Ornithonyssus sylviarum*) and parental provisioning behavior in the North American barn swallow (*Hirundo rustica erythrogaster*) using an experimental manipulation of parasites. By concomitantly analyzing the degree to which parents react to differences in levels of parasite infestation across the early and late nestling period, I addressed the above questions directly in addition to whether or not the time spent at parasitized nests by parents changes.

Background:

Parents may respond to parasitized nestlings in a variety of ways that either impose additional costs or offset the physiological costs of ectoparasites. One possible change in parental care in response to the presence of ectoparasites is adjustment in feeding behavior (Johnson and Albrecht 1993, Tripet and Richner 1997). In order to offset the cost of parasites, parents may increase their feeding rate to enable offspring to compensate for lost resources (Bouslama et al. 2002, Hutrez-Bousses et al. 1998, Tripet and Richner 1997). For example, parasitized nests of blue tits (*Cyanistes caeruleus*) had higher overall provisioning rates by parents compared to non-parasitized nests and nestling growth rate and body condition were similar or equal across treatment groups (Bouslama et al. 2002, Tripet and Richner 1997). In another study of parasitized blue tits, nestling growth and body condition were lower than in unparasitized nestlings despite higher levels of provisioning (Hutrez-Bousses et al, 1998). This result suggests that parasitized nestlings would have been in even worse condition without increases in provisioning rates.

In an attempt to conserve their own resources for future broods (group of young) and increase their chances of survival, parents may also decrease their feeding rate if nestlings are parasitized. For example, in a study of European barn swallows, parents that have only one brood in a breeding season will invest significantly less time in caring for and feeding heavily parasitized nestlings compared to parents at nests with little to no infestation (Møller 1994). Male spotless starlings (*Sturnus unicolor*) will also decrease feeding rates if there are visual cues on the eggs indicating a parasitic infestation, leading to reduced body mass of parasitized nestlings (Aviles et al. 2009). Further, decreased provisioning has also been observed in the penduline tit (*Remiz pendulinus*), where patterns of reduced parental care were hypothesized to be related to either low parental quality or increased self-maintenance behavior of parents despite the fact that mites did not have an apparent effect on chick mortality or development (Darolova et al. 1997).

While there is clear evidence in certain species that provisioning behavior in response to ectoparasites is mutable, in other species parents exhibit no change in their provisioning rate. Such a lack of response in provisioning from parents has been observed in the common swift (*Apus apus*), although parents did spend more time at the parasitized nests (Walker and Rotherham 2011). Parent house wrens (*Troglodytes aedon*) also demonstrated no change in provisioning at the cost of the nestlings having reduced mass (Morrison and Johnson 2002). Similarly, marsh tits (*Parus palustris*) show no change in parental provisioning as a function of ectoparasite infection resulting in smaller nestlings (Nilsson 2003). In tree swallows

(*Tachycineta bicolor*), parents again presented no change in provisioning; but, in this system there were no negative effects on nestling growth and development (Thomas and Shutler 2001). Finally, in the pied flycatcher (*Ficedula hypoleuca*) parents showed no change in provisioning but females did increase grooming (parasite removal) and nest sanitation (cleaning behavior) (Cantarero et al. 2013). This could indicate that ectoparasites do not have a noticeable impact on nestling growth and development (Thomas and Shutler 2001), or that feeding rates are inflexible and thus unresponsive to parasite infestation (Walker and Rotherham 2011, Morrison and Johnson 2002). Provisioning rates can also be affected by other factors such as competing species (Ligon et al 2012), food availability, breeding experience, and the structure of the nest itself (Fargallo et al 2001).

Males and females may also differ in their behavioral responses to parasites. Many studies have observed differences in levels of parental care between males and females in the presence of parasites in the nest. These results could indicate a possible difference in the trade-off of costs between current and future brood possibilities and success for each parent (Trivers 1972). In a study that examined adjustments in time budgets for blue tits, researchers found that the density of fleas in the nest significantly increased the frequency of sanitary behaviors by females but not males (Tripet et al 2002). A different study observing great tits saw that males increased provisioning rates to parasitized nestlings with no change in female provisioning (Christie et al 1996a). In one case of nests infected with *Plasmodium spp.* males were observed increasing their provisioning rates at the cost of higher rates of malarial infection (Richner et al 1995). Differences in behavioral responses between parents however are not limited to provisioning; females will often increase nest sanitary behaviors in response to parasites

(Hurtrez-Bousses et al. 2000, Christie et al 1996b). Thus, underlying sex differences in provisioning behavior may be accentuated by the presence of parasites.

Methods:

I studied a population of barn swallows between early July and early August of 2013 as part of a reciprocal cross-fostering (swapping of young) experiment focused on the heritability and effects of parasites on feather color development in the North American barn swallow (*Hirundo rustica erythrogaster*). Provisioning observations were done on 42 nests at 11 different sites in Boulder County, Colorado.

I and other members of the field crew captured adult barn swallows at each field site with mist nets; each individual was marked with both a USGS metal band and a unique combination of color bands. We then conducted visual observations to match individual males and females, and thus breeding pairs, to their respective nests using their unique color combinations.

We monitored nests every three to four days to determine when eggs were laid and hatched. As part of the larger reciprocal cross-fostering experiment, parasite loads of different nests were experimentally manipulated. Nests were sterilized by heating the nest to 125^{o} C using a heat gun (Hund and Hund, *unpublished*) on day 2 of the nestling period (day 0 = hatch date). Nests were then either left sterile, or had 100 field-collected northern fowl mites (*Ornithonyssus sylviarum*) added to the nest. This parasite addition technique is similar to other studies done in the past (Møller 1994, Christie et al. 1996a, Christie et al. 1996b). Parasite levels were then monitored for both sterilized and parasitized nests as part of the cross-fostering experiment on days 2, 4, 6, and 12 of the nestling period (Parasite nests n = 23, Sterile nests n = 22). Mites were also counted on these days by placing a hand into the nest for 30 seconds and then counting the number of mites on the hand (Møller 1994), in addition to counting the number of mites on each nestling. All nests used in this study had the same brood size, four chicks, on day 2 of the experiment when cross fostering occurred.

Behavioral Observation Methods:

I, along with the help of two other crew members, conducted observations of parental feeding behavior on days 7 and 13 of the nestling period in order to see how provisioning behavior changes over time within a pair. The average nestling period lasts about 17 days, thus observations on days 7 and 13 captures both the early and late stages of nestling development. These observations took place in the mornings between 06:00 and 10:00 because this is the most active feeding time for Barn Swallows (Maguire and Safran 2010). After a 15-30 minute habituation period, allowing the birds to return to normal behavior, provisioning behavior was observed for one hour.

During this time period, the number of visits by both parents was counted. Male and female visits were tallied separately along with the specific behavior during each visit (feeding, visit without feeding, incubating). In analyzing the data though I used a total tally of visits, including all behaviors observed, as an indication of provisioning rates. Due to the distance and height of the nests from points of observation it was often too difficult to say which exact behaviors took place during each visit, total visits proved a more reliable indication of provisioning rates for this study.

We also recorded the times at which each visit occurred and how long each visit lasted in order to quantify the average length of visits by each parent as well as the average time in between visits. Parents were observed from as far away as possible while still being able to identify individual color combinations using binoculars in order to reduce disturbance as much as possible. Due to the layout of some field sites, we collected observations from behind a blind or longer habituation periods were provided before the commencement of data collection (Maguire and Safran 2010). Some nests (n = 36) were only observed on day 7 due to parents not showing up during the day 13 observation time period; thus the sample size for these two observation periods varies slightly.

Statistical Analysis:

I used the statistical package R version 3.0.3 to analyze data collected on day 7 (n=45 nests) and day 13 (n=36 nests, a subset of the 45 analyzed on day 7). I applied general mixed linear models using the "nlme" package (version 3.1-115). When warranted, I applied natural log transformations to normalize data distributions.

In addition to analyzing variables related directly to my initial research questions, I assessed whether other effects, including temperature, time of observation, and date, may contribute to understanding variation in parental care as a function of parasite infection. However, none of these additional parameters had a significant impact and were thus not included in my final models. The only parameter that had a significant impact and was thus included in the final models, was the site where observations took place.

Results:

Question 1: Are ectoparasites causing changes in parental provisioning behaviors early in the nestling period?

Effect of experimental treatment:

I found no significant difference in the number of overall parental visits (male and female combined) between the sterile and parasite treatment groups on day 7 of the nestling period ($F_{1, 31} = 1.96$, $P < 0.17$; Figure 1a). However, on day 7 females visited parasitized nests less often than sterilized nests ($F_{1, 31} = 7.01$, $P < 0.013$; Figure 2a) whereas male visits did not vary as a function of experimental treatment (Figure 2b). Conversely, the length of time spent at heavily parasitized nests during the early nestling period was greater compared to the length of time spent at nests with fewer ectoparasites ($F_{1, 25} = 6.81$, $P < 0.0151$; Figure 4a); this effect was due to increased length of visits by females at parasitized nests ($F_{1, 26} = 9.18$, $P < 0.006$; Figure 5a). There was no difference in length of visits by males between treatments (Figure 5b).

Effect of parasite intensity:

After nests are sterilized, ectoparasites have the opportunity to recolonize. I therefore quantified re-colonization and, in addition to examining experimental treatment outcomes, measured whether infection intensity influenced parental care. Similar to the effect of experimental treatment, I found that females visited nests with a high mite intensity less often than nests with lower mite intensities during the early nestling period ($F_{1, 31} = 5.79$, $P < 0.02$; Figure 3a). Yet the longer amount of time spent at parasitized nests by females was not driven by mite intensity ($F_{1, 26} = 0.2840$, $P < 0.60$; Figure 6a).

Question 2: Are ectoparasites causing changes in parental provisioning behaviors late in the nestling period?

Effect of experimental treatment:

While there was a trend for parents to visit nestlings in the parasitized treatment group more often on day 13 compared to nestlings in the sterilized treatment group, this trend was not significant ($F_{1, 33} = 2.43$, $P < 0.13$; Figure 1b). I also found no significant trend for female visits between parasite and sterile treatment groups in the late nestling period (Figure 2c). On the other hand, males visited parasitized nests more often than sterilized nests ($F_{1, 26} = 5.60$, $P < 0.026$; Figure 2d). Interestingly, parents overall spent more time at parasitized nests than at sterilized nests on day 13 ($F_{1, 25} = 4.42$, $P < 0.05$, Figure 4b). Although males on day 7 did not spend more time at parasitized nests, they did so on day 13 ($F_{1, 33} = 12.24$, $P < 0.0014$, Figure 5d). Similar to day 7, females also were also observed to spend more time at parasitized nests on day 13 ($F_{1, 33} = 8.44$, $P < 0.007$, Figure 5c).

Effect of parasite intensity:

Despite the significant effect of treatment on male visit rate, male visit rate did not vary as a function of mite intensity ($F_{1, 26} = 0.081$, $P < 0.78$; Figure 3b). The extra time spent at parasitized nests by females was not significantly driven by mite intensity, ($F_{1, 33} = 3.04$, $P < 0.09$, Figure 6b); nevertheless, mite intensity had a highly significant effect on males ($F_{1, 33} = 14.61$, $P < 6e-04$, Figure 6c), with males spending more time at nests as mite intensity increased.

Discussion:

Parental responses during the early nestling period.

Early in the nesting period (day 7) females with parasites in their nests visited less than females in sterile nests. This response appeared to be driven by parasite intensity, where the more mites that were in the nest, the less the female visited (Figure 2a). While there was a significant response by females as a function of both experimental treatment and parasite intensity, I found no influence of either of these factors on male visit rates. I *a priori* predicted that parental behavior might be influenced by parasite avoidance, as blood mites have negative consequences for both adults and nestlings (Møller 1990, Gallizzi et al. 2008, Morrison and Johnson 2002). Instead, I found that female visits were significantly longer for parasitized nests than sterilized nests (Figure 5a). Thus, while females visited parasitized nests at a lower rate, they actually spent more time in the nest, clearly not avoiding parasite exposure and perhaps even increasing their own vulnerability to these haematophagous (blood-feeding) mites (Hutrez-Bousses et al. 2000).

Prolonged visitation by females may also indicate that females are prioritizing behaviors besides provisioning to care for parasitized nestlings that may be less costly. This result aligns with findings of other studies that show females may allocate more time to nest sanitation when under varying physiological conditions including negative states like parasitism (Cantarero et al. 2013) or more positive states like increased body temperature (Spencer 2005). Occasionally, females will even decrease sleep to engage in sanitary behaviors in response to ectoparasites (Christie et al. 1996b). Alternatively, females could be providing higher quality food which leads to fewer visits due to increased search effort as hypothesized by Nilson (2003). This may not have been the case Nilson's study though due to parasitized nestlings having a reduced growth rate. Another potential explanation for lengthy visits by females could be longer feeding bouts as proposed by Walker and Rotherham (2011). However, I do not know for certain the specific behaviors done during each visit, so this may or may not have been the case in the present study.

Parental responses during the late nestling period

Interestingly, the patterns I found during the early nestling period were quite different from those of the late nestling period. Males, not females, altered their behavior between days 7 and 13 by visiting parasitized nests more often than sterilized nests, with no significant difference in female visits as a function of parasite presence or intensity (Figures 2c and 2d).

Males responded to the presence or absence of mites (the treatment effect) rather than mite intensity (Figure 3b). A possible explanation for an increase in male parental care of parasitized nestlings late in the nestling period is that males may be holding off on increased nestling investment to see if nestlings are likely to survive. If nestlings survive until day 13 while exposed to parasites, regardless of intensity, this may indicate to the male parent that they are more fit than nestlings that do not survive, and the male will thus gain a greater reproductive benefit by investing more heavily in them at this stage of development.

Does this mean that males are taking on more of the responsibilities of nestling care later on in the nestling period? This seems unlikely for two reasons (i) females did not decrease provisioning rates between the early and late nestling periods for parasitized nests (Figures 2a and 2c) and (ii), males visited sterilized nests less than females did on day 13 (Figures 2c and 2d). A more likely explanation is that there is a sex-related difference in the trade-offs between current vs. future reproduction being accentuated by mites. For females, there is greater advantage in investing in future broods while the opposite is true for males; males may increase feeding rate to avoid divorce if breeding success is low (Christie et al. 1996a). Richner et al.'s (1995) study of great tits further supports this hypothesis, observing that males will also increase feeding effort to combat *Plasmodium spp.* while females do not. The results of my study also agree with these findings, especially with Christie et al. (1996a) showing that males increased feeding visits close to 50% to parasitized nests (Figure 2d). Since their data was also collected from observations on day 13, combined with the findings of my study, it appears that this trade-off does not impact male feeding until later on.

My findings of an increase in male care to parasitized nestlings only during the late nestling period opens up several possibilities. One explanation for why males are only responding later in the nestling period is that males and females pick up on passive cues of parasitic infestations at different points in time (Aviles et al 2009). Alternatively, perhaps nestlings are behaving differently as a function of parasite infection during the early and late nestling period. Prior research has shown that nestlings will significantly increase their rates of begging when exposed to parasites (Christie et al. 1996a, Cantarero et al. 2013). Conversely, nestlings also may be too weak to sufficiently beg and alert their parents to an increased need for food as demonstrated in Darwin's small ground finch (*Geospiza fuliginosa*) (O'Connor et al. 2013). The idea of nestling begging in response to ectoparasites however is controversial as other studies have shown no correlation between the begging of tree swallow (*Tachycineta bicolor*) nestlings and ectoparasites (Thomas and Shutler 2001). Because I did not collect data on begging behavior, I lack information about how variation in begging rate is influenced by parasites or whether this is in turn influencing parental behavior.

Interestingly I found evidence that males may be altering other behaviors besides provisioning. The fact that males spent significantly more time at parasitized nests during each visit on day 13 (Figure 5d) contradicts previous findings that males do not engage in nest sanitary behaviors exhibited by females (Christie et al. 1996b, Hutrez-Bousses et al. 2000). This is further supported by my observation that visitation length was significantly correlated with mite intensity as well. As mite intensity increases, there could be a higher need for nest sanitation behavior from males. Although I cannot say for certain the exact behaviors done during each visit due to the height of the nests, elongated male visits points to other behaviors besides provisioning taking place. The fact that males are increasing both visitation and the length of each visit suggests that males are taking on a greater cost of parental care during the latter part of the nestling period. If nestlings have lived this long with heavy parasite infestation it may demonstrate that they have a greater chance at survival and may be worth the extra investment. Since males typically have a lower chance of future reproduction than females, that could explain the increased investment by males and not females.

Conclusion

This study is unique in that it shows not only how parental provisioning rates for parasitized and sterilized nests change over time, but also how male and female rates change differently across the nestling period. Further, my results highlight the difference between parental behaviors as a function of the presence or absence of mites compared to the intensity of infestation. The differences in male and female behaviors not only inform differences across both the early and late nestling periods, they also inform sex-specific tradeoffs between current and future investment in reproduction. Previous research on this question has not focused on how parasite infections may mediate life history trade-offs between the sexes. Future research on the specific behaviors done by both males and females during these visits could not only help further specify these trade-offs and costs on parents and offspring, but also how they are changing over time.

As of yet there is no definitive pattern of how parasites affect parental provisioning across different species. A potential explanation for this could be varying life history traits across species such as food sources, habitat, and frequency of reproduction (Christie et al. 1996a). Another factor that may be contributing to inconsistent findings across studies is the type of parasite being observed (Cantarero et al. 2013). Not only is there significant differences in the species of parasite being observed, the level of parasite intensity across studies varies as well. The effects of 20 fleas vs. 150 mites may not be able to be compared directly. Observed differences in behavior between sexes has also been inconsistent in past research. Here, the decreased frequency of visits by female barn swallows on day 7 supports the idea of future reproduction being prioritized amongst females, whereas male barn swallows increasing visitation on day 13 supports the idea of current reproduction being prioritized amongst males (Trivers 1972). Still, these trade-offs, and how they change across the nestling period, needs to be more closely analyzed in future research.

Acknowledgements:

I would personally like to thank Professor Rebecca Safran and Amanda Hund for all of their help and mentorship. Without their generous assistance I would not have been able to complete this study. Special thanks also to Joey Hubbard for her additional assistance and mentorship. I also give my thanks to Caroline Glidden and Hannah Burke for assisting me in conducting behavioral observations, and the 2013 Safran Lab field crew for help identifying banded adults and collecting data necessary for my study. I would also like to thank Professor Barbara Demmig-Adams for her help and advice on writing my thesis and for being a part of my defense committee. I also thank Professor Michael Breed for being on my committee and discussing my study with me and giving advice. I would also like to thank Professor Petger Schaberg for taking time to be a part of my defense committee. Finally, I thank the University of Colorado at Boulder for providing me funding through the Undergraduate Research Opportunity Program grant, as well as the NSF for providing me with additional funding through their research experience for undergraduates grant.

Table 1: *Past studies on provisioning and ectoparasites*

Species	**Effect of ectoparasites on Provisioning**	**Type of Parasite**	**Studies**
Blue Tit (*Cyanistes caeruleus*)	Increase or just an increase in females only (Tripet et al 2002)	Ticks, Hen fleas, Blowflies, Bird fleas	Bouslama et al. 2002, Hutrez-Bousses et al. 1998, Tripet and Richner 1997, Tripet et al. 2002
Barn Swallow (*Hirundo rustica*)	Decrease (in single broods) No effect (double broods)	Tropical Fowl Mites	Møller 1994
Common Swift (*Apus apus*)	No effect	Louse Flies	Walker and Rotherham 2011
House Wren (*Troglodytes aedon*)	No effect	Blowfly larvae	Morrison and Johnson 2002
Great Tit (*Parus major*)	No effect (Gallizzi K 2008, and Fitze 2004), Males increased rate (Christie P. 1996), No effect on female rates (Christie P. 1996b)	Hen Fleas, Ticks	Gallizzi et al. 2008, Christie et al 1996, 1996b, Fitze et al. 2004
Tree Swallow (*Tachycineta bicolor*)	No effect	Avian Fleas, blowflies	Thomas and Shutler 2001, O'Brien and Dawson 2005
Pied Flycatchers (*Ficedula hypoleuca*)	No effect	Mites, blowfly larvae, hen fleas	Cantarero et al. 2013
Penduline Tit (*Remiz pendulinus*)	Decrease	Northern fowl mite and Northern feather mite	Darolova et al. 1997
Marsh Tit (*Parus palustris*)	No Effect	Fleas	Nilsson 2003
Spotless Starling (*Sturnus unicolor*)	Males decrease	Carnid flies	Aviles et al. 2009

<u>Figures:</u>

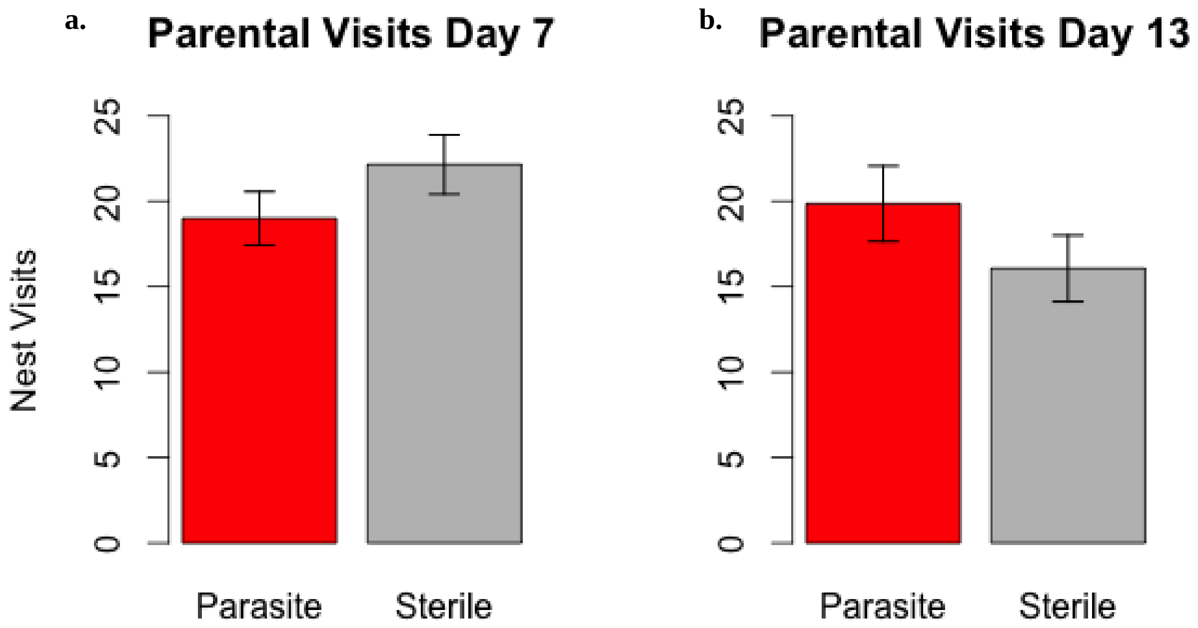

Figure 1: *Mean total parental visits per treatment.* Mean number of the total visits, by both males and females combined, to parasite treatment nests (red bars, n = 23) and sterile treatment nests (grey bars, n = 24). **1a** shows the difference between treatment groups on day 7. **1b** shows the difference between treatment groups on day 13.

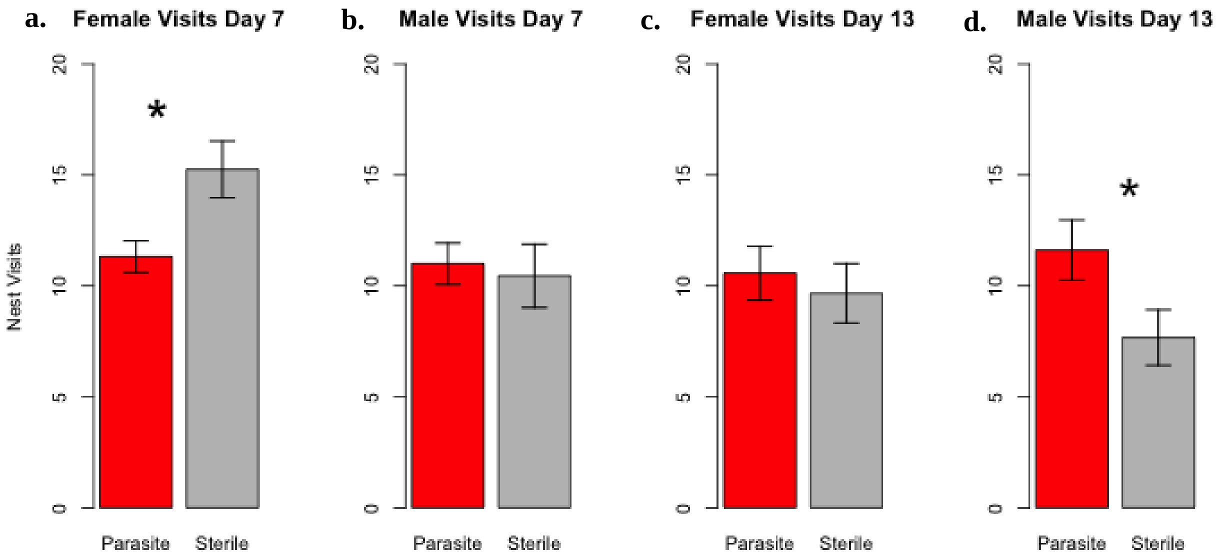

Figure 2: *Mean total female and mean total male visits per treatment.* Mean number of the total visits by males and females, separated out by sex, to parasite treatment nests (red bars, n = 23) and sterile treatment nests (grey bars, n = 24). **2a** shows female visits between treatment groups on day 7. Significance is denoted by the asterisk. **2b** shows male visits between treatment groups on day 7. **2c** shows female visits between treatment groups on day 13. **2d** shows male visits between treatment groups on day 13. Significance is denoted by the asterisk.

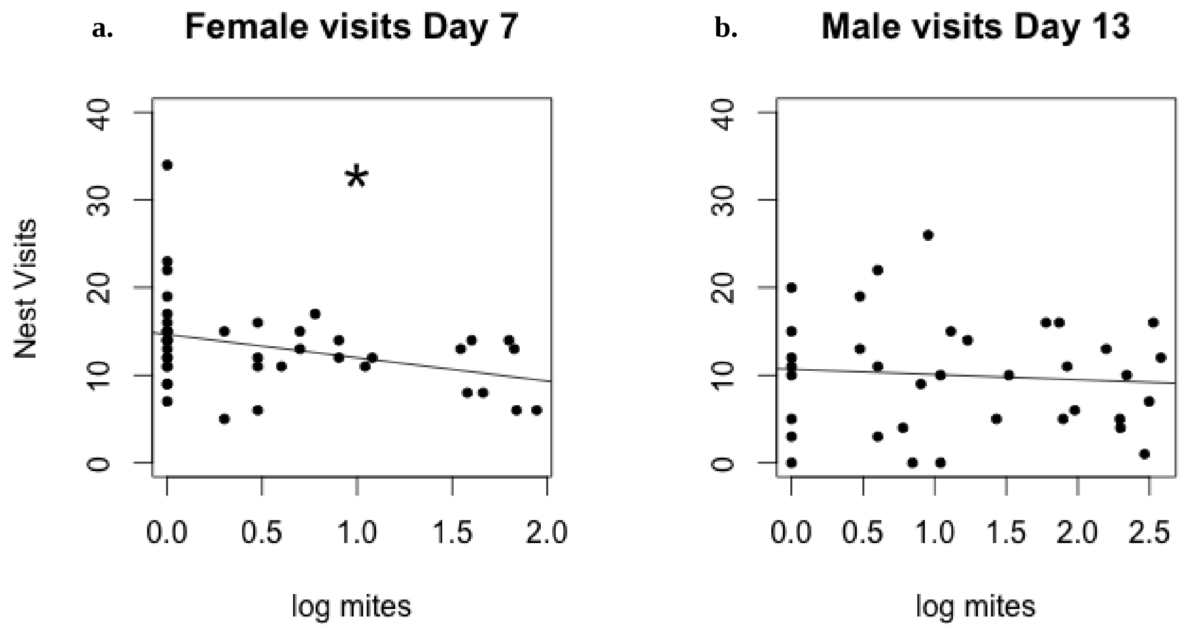

Figure 3: *Mean total female visits and mean total male visits as a function of mite intensity*. Mean total number of visits by females to parasite treatment nests (n = 23) on day 7 and mean total number of male visits to parasite treatment nests on day 13. The number of mites on each day was log transformed to normalize the distribution as shown on the x-axis. This test was only done for these two groups since there was no significant response by males on day 7 and females on day 13 just looking at treatment. **3a** shows the correlation between number of mites and total nest visits for females on day 7 with an asterisk to denote significance. **3b** shows the correlation between number of mites and total nest visits for males on day 13.

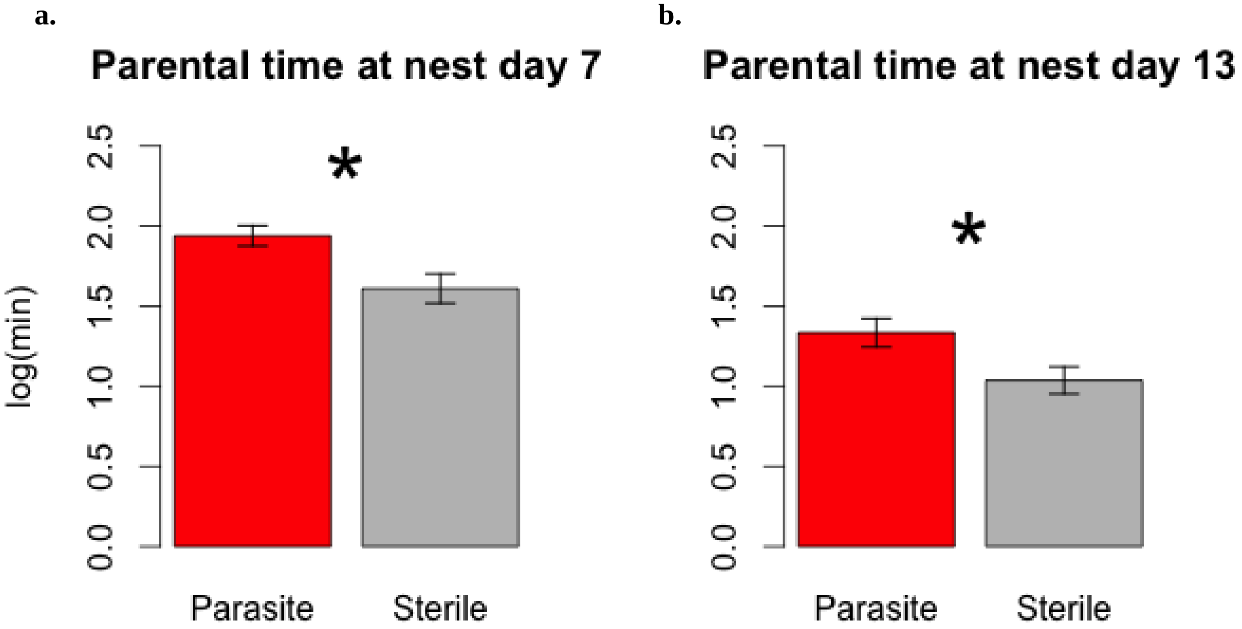

Figure 4: *Mean length of parental visits per treatment.* Mean visit length of both males and females combined to parasite treatment nests (red bars, n = 23) and sterile treatment nests (grey bars, n = 24) in minutes. Average length of visit was log transformed to normalize the distribution as shown on the y-axis. **4a** shows the difference between treatment groups on day 7 with significance denoted by the asterisk. **4b** shows the difference between treatment groups on day 13 with significance denoted by the asterisk.

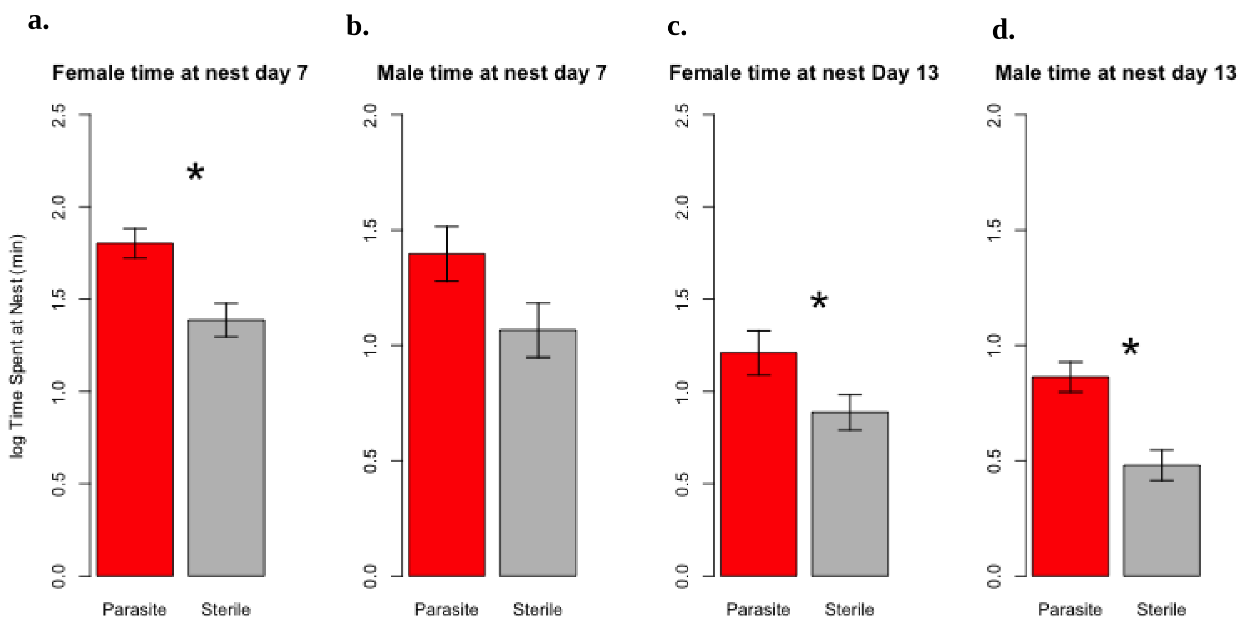

Figure 5: *Mean length of female visits and mean length of male visits per treatment.* Mean length of female visits and male visits, separated out by sex, to both parasite treatment nests (n = 23) and sterile treatment nests (n = 24) in minutes. Average length of visit was log transformed to normalize the distribution as shown on the y-axis. **5a** shows female visit length between treatment groups on day 7. Significance is denoted by the asterisk. **5b** shows male visit length between treatment groups on day 7. **5c** shows female visit length between treatment groups on day 13. Significance is denoted by the asterisk. **5d** shows male visit length between treatment groups on day 13. Significance is denoted by the asterisk.

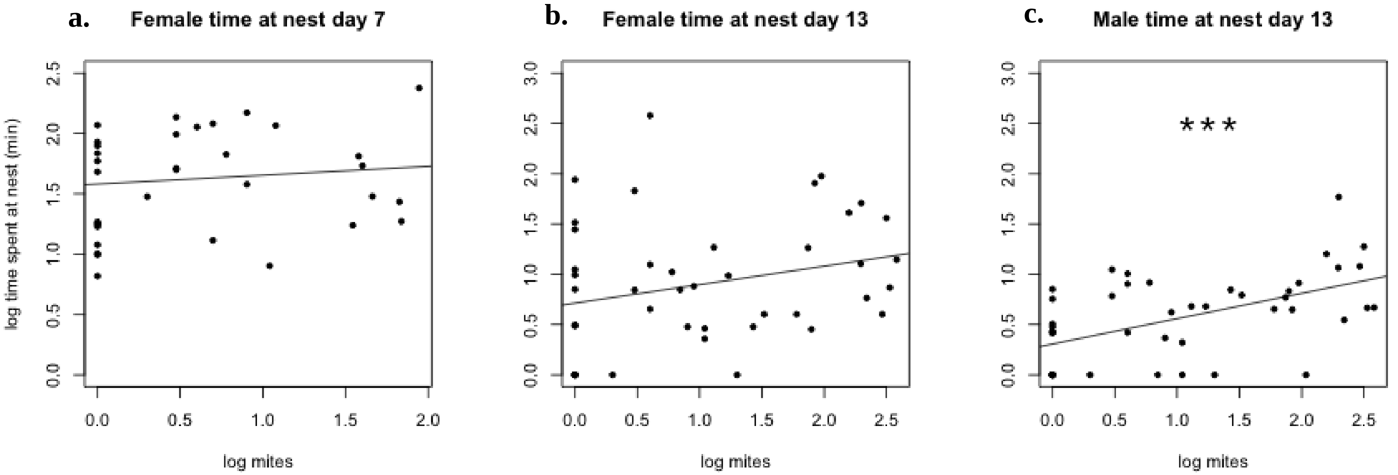

Figure 6: *Mean length of female visits and mean length of male visits as a function of mite intensity.* Mean length of visits by females to parasite treatment nests (n = 23) on day 7 and 13 and mean length of male visits to parasite treatment nests on day 13 in minutes. The number of mites on each day was log transformed to normalize the distribution (x-axis) as well as the average time spent at the nest (y-axis). This test was only done for these three groups since average length of male visits on day 7 showed no significant response just looking at treatment. **6a** shows the correlation between number of mites and average visit length for females on day 7. **6b** shows the correlation between number of mites and average visit length for females on day 13. **6c** shows the correlation between number of mites and average visit length for males on day 13 with three asterisks denoting high significance.

References:

Avilés, J. M., Pérez-Contreras, T., Navarro, C. and Soler, J. J. 2009. Male spotless starlings adjust feeding effort based on egg spots revealing ectoparasite load. - Anim. Behav. 78: 993–999.

Bouslama, Z., Lambrechts, M. M., Ziane, N., Djenidi, R. and Chabi, Y. 2002. The effect of nest ectoparasites on parental provisioning in a north-African population of the Blue Tit *Parus caeruleus*. - Ibis (Lond. 1859). 144: E73–E78.

Brown, C. R., Brown, M. B. and Rannala, B. 1995. Ectoparasites Reduce Long-Term Survival of their Avian Host. - Proc. R. Soc. B Biol. Sci. 262: 313–319.

Cantarero, A., López-Arrabé, J., Redondo, A. J. and Moreno, J. 2013. Behavioural responses to ectoparasites in pied flycatchers *Ficedula hypoleuca*: an experimental study. - J. Avian Biol. 44: 1–9.

Christe, P., Richner, H. and Oppliger, A. 1996a. Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. - Behav. Ecol. 7: 127–131.

Christe, P., Richner, H. and Oppliger, A. 1996b. Of great tits and fleas: sleep baby sleep . . . - Anim. Behav. 52: 1087–1092.

Darolova, A., Hoi, H. and Schleicher, B. 1997. The effect of ectoparasite nest load on the breeding biology of the Penduline Tit *Remiz pendulinus*. - Ibis (Lond. 1859). 139: 115–120.

Fargallo, J. a., Blanco, G., Potti, J. and Viñuela, J. 2001. Nestbox provisioning in a rural population of Eurasian Kestrels: breeding performance, nest predation and parasitism. - Bird Study 48: 236–244.

Fitze, P., Tschirren, B. and Richner, H. 2004. Life history and fitness consequences of ectoparasites. - J. Anim. Ecol. 73: 216–226.

Gallizzi, K., Alloitteau, O., Harrang, E. and Richner, H. 2008. Fleas, parental care, and transgenerational effects on tick load in the great tit. - Behav. Ecol. 19: 1225–1234.

Hamilton, W. D. and Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? - Science 218: 384–7.

Hurtrez-Bousses, S., Blondel, J., Perret, P., Fabreguettes, J. and Renaud, F. R. 1998. Chick parasitism by blowflies affects feeding rates in a Mediterranean population of blue tits. - Ecol. Lett. 1: 17–20.

Hurtrez-Boussès, S. and Renaud, F. 2000. Effects of ectoparasites of young on parents' behaviour in a Mediterranean population of blue tits. - J. Avian Biol. 31: 266–269.

Johnson, L. S. and Albrecht, D. J. 1993. Effects of Haematophagous Ectoparasites on Nestling House Wrens, *Troglodytes aedon*: Who Pays the Cost of Parasitism? - Oikos 66: 255–262.

Killpack, T.L., Oguchi, Y. & Karasov, W.H., 2013. Ontogenetic patterns of constitutive immune parameters in altricial house sparrows. - J. Avian Biol. 44: 513–520.

Lehmann, T., 1993. Ectoparasites: direct impact on host fitness. - Parasitol. Today. 9: 8–13.

Ligon, R. a, Siefferman, L. and Hill, G. E. 2012. Invasive ants alter foraging and parental behaviors of a native bird. - Ethology 118: 858–866.

Maguire, S. E. and Safran, R. J. 2010. Morphological and genetic predictors of parental care in the North American barn swallow *Hirundo rustica erythrogaster*. - J. Avian Biol. 41: 74–82.

Møller, A. P. 1990. Effects of Parasitism by a Haematophagous Mite on Reproduction in the Barn Swallow. - Ecology 71: 2345–2357.

Møller, A. P. 1994. Parasite Infestation and Parental Care in the Barn Swallow *Hirundo rustica* - A test of the Resource-provisioning model of Parasite-mediated Sexual Selection. – Ethology 97: 215–225.

Morrison, Brian and Johnson, L. S. 2002. Feeding of House Wren Nestlings Afflicted by Hematophagous Ectoparasites: A Test of the Parental Compensation Hypothesis. - Condor 104: 183–187.

Moss, W. and Camin, J. 1970. Nest parasitism, productivity, and clutch size in purple martins. - Science 168: 1000–1003.

Nilsson, J. 2003. Ectoparasitism in marsh tits: costs and functional explanations. - Behav. Ecol. 14: 175–181.

Norris, K., 2000. Ecological immunology: life history trade-offs and immune defense in birds. Behav. Ecol. 11: 19–26.

O’Brien, E. L. and Dawson, R. D. 2005. Risk of ectoparasitism perceived reduces primary reproductive investment in tree swallows *Tachycineta bicolor*. - J. Avian Biol. 36: 269–275.

O’Connor, J. A., Robertson, J. and Kleindorfer, S. 2013. Darwin’s finch begging intensity does not honestly signal need in parasitised nests. - Ethology 119: 1–10.

Owen, J. P., Nelson, A. C. and Clayton, D. H. 2010. Ecological immunology of bird-ectoparasite systems. - Trends Parasitol. 26: 530–539.

Richner, H. 1995. Are clutch in birds and brood size patterns shaped by ectoparasites? - Oikos 73: 435–441.

Richner, H. 1997. Host responses to ectoparasites : food compensation by parent blue tits. - Oikos 78: 557–561.

Richner, H. and Tripet, F. 1999. Ectoparasitism and the trade-off between current and future reproduction. - Oikos 86: 535–538.

Richner, H., Christe, P. and Oppliger, a 1995. Paternal investment affects prevalence of malaria. - Proc. Natl. Acad. Sci. U. S. A. 92: 1192–4.

Roberts, L., Janovy, J. & Schmidt, G. 2012. Foundations of parasitology. – McGraw-Hill.

Saino, N., Calza, S., Møller, A. P. and Moller, A. P. 1998. Effects of a Dipteran Ectoparasite on Immune Response and Growth Trade-Offs in Barn Effects of a dipteran on immune and growth ectoparasite response in barn swallow, *Hirundo rustica*, nestlings. - Oikos 81: 217–228.

Spencer, K. A. 2005. The effects of body state on nest sanitation and provisioning effort in breeding barn swallows (*Hirundo rustica*). - Can. J. Zool. 83: 1360–1364.

Szép, T. and Møller, A. 1999. Cost of parasitism and host immune defence in the sand martin *Riparia riparia*: a role for parent-offspring conflict? - Oecologia 119: 9–15.

Thomas, K. and Shutler, D. 2001. Ectoparasites, nestling growth, parental feeding rates, and begging intensity of tree swallows. - Can. J. Zool. 79: 346–353.

Tripet, F., Glaser, M. and Richner, H. 2002. Behavioural responses to ectoparasites: time-budget adjustments and what matters to Blue Tits *Parus caeruleus* infested by fleas. - Ibis (Lond. 1859). 144: 461–469.

Trivers, R. L. 1972. Parental and investment and sexual selection. -In: Campbell B. (ed.), Sexual Selection and the Descent of Man. Aldine, 137—179.

Trivers, R. L. 1974. Parent–offspring conflict. Amer. Zool. 14: 249–264.

Walker, M. and Rotherham, I. 2011. No evidence of increased parental investment by Common Swifts *Apus apus* in response to parasite load in nests. - Bird Study 58: 37–41.

Zhong, D., Pai, A. & Yan, G., 2005. Costly resistance to parasitism: evidence from simultaneous quantitative trait loci mapping for resistance and fitness in *Tribolium castaneum*. Genetics. 169: 2127–35.