

Effects of Ectoparasites and Reproductive Class on Roost-Switching and Foraging Behavior of
Indiana Bats (*Myotis sodalis*)

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ABSTRACT

Ectoparasites of bats have been known to cause harm to their hosts and to affect roost-switching. Little research exists on effects ectoparasites may have on roosting and foraging behavior of the federally endangered Indiana bat (*Myotis sodalis*). From 2008 through 2010, I collected ectoparasite data and documented roost-switching and foraging behavior of Indiana bats on habitat restoration lands owned by the Indianapolis International Airport (IND) in central Indiana. I tested for differences in roosting and foraging behavior between bats with varying ectoparasite loads, and for differences in ectoparasite load, roost-switching frequency, and foraging behavior between different reproductive classes of Indiana bats. I used the volume of ectoparasites of each Indiana bat when analyzing data. I found a significant difference in roost-switching frequency and ectoparasite volume between reproductive classes. Neither reproductive class nor ectoparasite load significantly affected any aspect of foraging behavior. Indiana bats in this study apparently maintained moderate loads of ectoparasites which may not affect foraging and roosting, but the insignificant results found in this study may have been due to a small sample size. The significant difference in roost-switching between reproductive classes likely demonstrates variation in bat thermoregulation. Lactating females and pregnant females have a higher need for group thermoregulation and switch roosts less frequently than post-lactating females and volant juveniles. Because ectoparasites have been found to increase in maternity colonies, volant juveniles and post-lactating females may disperse from the main colony roost and switch roosts more often to avoid higher intensities of ectoparasites.

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Effects of Ectoparasites and Reproductive Class on Roost-Switching and Foraging Behavior of Indiana Bats

Introduction

The primary objective of this study was to document the effects ectoparasites of *Myotis sodalis* have on roost-switching and foraging behavior of their hosts and also to examine seasonal variation in ectoparasite loads, roost-switching, and foraging behavior of *M. sodalis*. Ectoparasites are organisms that parasitize the exterior of a host and can be found on the skin, on hair, or in various body orifices. Many ectoparasites include arthropods such as insects and numerous mite species that consume a variety of resources directly from their host. Some ectoparasites, such as fleas and mites of the family Spinturnicidae, feed on blood, whereas others like mites of the family Demodecidae feed on epithelial cell contents (Desch et al. 1972, Mullen & Durden 2002). These mites can be found in hair follicles and are also in the oral cavities of bats (Desch et al. 1972, Mullen & Durden 2002). Ectoparasitism can affect both fitness and survival of hosts (Hart 1992). The host is habitat for any parasite, and over-consumption of resources would be detrimental to both host and parasite. Decreased fitness or mortality of the host may occur, and parasites could perish with no host to serve as the environment. Although ectoparasites rely on the health of their hosts, ectoparasites still may cause harm to hosts; for example, demodecid mites cause mange in domestic and wild mammals (Mullen & Durden 2002). In avian ecology, Brown and Brown (1986) found that the swallow bug *Oeciocercus*

vicarius reduced survivorship of Cliff Swallow nestlings (*Hirundo pyrrhonota*). Higher intensities of *Spinturnix myoti* increased grooming for *Myotis myotis*, which led to the negative effect of weight loss associated with higher metabolism (Giorgi et al. 2001). Animals may not directly succumb to effects of parasitism, but the cost of ectoparasite loads may reduce fitness when there are intense periods of energetic stress (Hart 1992). Given these negative effects, animals with lighter parasite loads and those that employ behaviors that reduce parasitism should have a higher fitness or greater probability of survival.

Natural selection has produced behavioral adaptations in both parasite and host that allow animals to survive and reproduce despite heavy ectoparasitism and tends towards maintenance of moderate levels of ectoparasites (Price 1980; Hart 1992). As a response to higher loads of ectoparasites, bats have been known to increase the frequency of roost-switching (Lewis 1996; Reckardt and Kerth 2006, 2007; Bartonicka and Gaisler 2007) and grooming (ter Hofstede and Fenton 2005). These examples demonstrate some effects ectoparasites can have on various bat species.

Abundances of ectoparasites may vary between the reproductive periods of the host (Christe et al. 2000; Ritzi 2004; Kanuch et al. 2005). *Spinturnix myotis* times its reproductive cycle with that of its bat host *M. myotis* by massively infesting newborns with gravid females (Christe et al. 2000). Similarly, mites increase in abundance during the pregnancy and lactation periods of *Nycticeius humeralis* and *Eptesicus fuscus* (Ritzi 2004), which form large maternity colonies in the summer. It is not unreasonable to expect that *M. sodalis*, which exhibits similar reproductive behavior, would also display the same variation in ectoparasite loads.

Roost-switching behavior in bats has been associated with a variety of factors including ambient temperature and humidity, type of roost, microclimate of roosts, disturbance, parasite or

predator avoidance, bats' awareness of available roosts, proximity to foraging sites, and maintaining social contacts and information exchange (Lewis 1995; Lewis 1996; Rabe et al. 1998; Weller and Zabel 2001; Willis and Brigham 2004; Russo et al. 2005; Reckardt and Kerth 2006, 2007; Barclay and Kurta 2007; Bartonicka 2007; Ellison et al. 2007). Aside from these influences, roost-switching frequency may vary between reproductive periods (Kurta et al. 2002). Pregnant female *M. sodalis* in Michigan have been shown to switch more often than lactating females (Kurta et al. 2002). It is reasonable to expect *M. sodalis* in other areas to behave similarly. Lactating bats should switch less frequently than other reproductive classes because they must return to roosts to feed non-volant offspring and it is energetically costly to transport offspring to new roosts.

The reproductive period of bats may also influence roost selection (Kerth and König 1999; Garroway and Broders 2007). Along with *M. sodalis*, *M. septentrionalis* is typically sexually segregated during the summer with females forming maternity colonies and males roosting solitarily (Garroway and Broders 2007). Garroway and Broders (2008) suggested that lactating *M. septentrionalis* choose roosting sites with a higher exposure to sunlight, which raises the temperature of the roost. This would appear to be a strategy that provides heat to develop young and to reduce costs of internal thermoregulation during a reproductive period in which offspring survival would be negatively affected by torpor (Racey and Swift 1981; Wilde et al. 1995; Wilde et al. 1999). Bats in maternity roosts may switch roosts less frequently because of the thermoregulatory benefits of roosting in large groups. Given that *M. sodalis* also forms sexually segregated maternity colonies, the roost selection of this species may also be influenced by reproductive period, but see Lacki et al (2009) for differences in roost selection between these

M. sodalis and *M. septentrionalis*. Areas with high solar exposure are characterized by lower clutter that could be beneficial for newly volant juveniles (Garroway and Broders 2008).

Roost-switching is especially effective against parasites that spend a portion of their life-cycle off the host. Lausen and Barclay (2002) reasoned that switching roosts and avoiding their reuse could reduce loads of ticks that remain in the roost when they are not feeding. Roost-switching is a successful strategy for *M. bechsteinii* against the parasitic fly *Basilina nana* (Bartonicka and Gaisler 2007; Reckardt and Kerth 2006, 2007). Switching roosts may allow bats to interrupt the life cycles of parasitic mites such as those in the family Macronyssidae, which leave the host to deposit eggs in the roost (Radovsky 1967; Ritzi 2004). Although roost-switching has been demonstrated to be a successful strategy against some bat flies, it may have little impact on parasites that never leave the host such as mites of the family Myobiidae (Pearce and O'Shea 2007). Roost-switching could be a beneficial strategy only for bats afflicted with parasites whose life history requires them to leave the host but not for parasites that spend their whole life on a host.

The amount of time an ectoparasite spends in a roost and off the host varies among species. *Basilina nana* pupates off the host in the roost and emerges at least 29 days after being deposited by an adult female (Reckardt and Kerth 2007), and the eggs of different species of parasitic mites can take 15 to 60 hours to hatch depending on the temperature, humidity, and species of mite (Radovsky 1967; Dood 1987). The egg, larva, and deutonymph stages of macronyssid mites occupy host roosts (Radovsky 1967), and these stages provide the opportunity for bat hosts to use roost-switching as an effective anti-parasite behavior.

Temperature and relative humidity also affect survival and egg production of at least some parasitic mites, for example *S. occidentalis*, *S. antrozoi*, and *Chiroptonyssus robustipes*

(Radovsky 1967; Dood 1987). Measuring the temperature and humidity of roosts may demonstrate the appropriate conditions for ectoparasites to grow and reproduce at faster rates, thus potentially increasing the frequency of roost-switching by bats.

Determining the role of ectoparasites in roost-switching by bats can provide more insight into their roosting strategies. Although variation in roost-switching has been found between species (Lewis 1995), differences between individuals within a species that have varying ectoparasite loads may result in more heavily parasitized individuals switching roosts more often.

Because it has been found that increased metabolism of bats is associated with higher loads of ectoparasites (Giorgi et al. 2001), a bat would also require more resources. Foraging for longer periods of time may be a strategy bats use to meet this need. It might be possible to show this relationship by comparing foraging behavior of bats with varying ectoparasite loads.

Increasing a bat's allocation of resources to anti-parasite behavior such as more grooming bouts or time spent searching for other suitable roosts (Lewis 1996) may also result in a greater need for resources. If the bat's energy budget is affected by the ectoparasites or anti-ectoparasite behavior, it would likely be reflected in greater nightly foraging durations. It is hypothesized here that obtaining more resources should be a priority for bats that are more heavily parasitized and are thus losing a larger amount of resources than bats with lighter loads.

In this study, I collected ectoparasite data from *M. sodalis* in an area where chiropteran ectoparasite communities have been well documented (Whitaker 1982; Ritzi 2004; Whitaker et al. 2007). I tested the prediction that ectoparasite load varies seasonally on *M. sodalis* as seen with *E. fuscus* and *N. humeralis* where loads increase during the pregnancy and lactation periods (Ritzi 2004). I predicted that bats will switch roosts more frequently, forage for longer periods,

and have a greater foraging range when afflicted by higher loads ectoparasites than bats with lighter loads. In addition to comparing roost-switching and foraging behavior to ectoparasite data, I also tested predictions that lactating bats will switch roosts less often, forage in smaller areas, and forage for longer durations than pregnant, post lactating, and volant juvenile bats.

Methods

The study area for this project was near the Indianapolis International Airport (IND) on lands located southwest of IND at the intersection of Hendricks, Marion, and Monroe Counties, Indiana. The IND has committed to a mitigation project on these lands for *Myotis sodalis* since 1992 (Ritzi et al. 2005; Whitaker et al. 2006). Part of this effort was the installation of 3204 artificial roost structures on mitigation lands (Ritzi et al. 2005; Whitaker et al. 2006). These structures included 259 triple and 715 single birdhouse style boxes (Ritzi et al. 2005; Whitaker et al. 2006). Although *M. sodalis* were not detected using the boxes as roosts until approximately 10 years after they were installed (Ritzi et al. 2005; Whitaker et al. 2006), the population has made regular use of a small sample of these boxes in recent years and, since 1997, there has been an ongoing project that monitors this population (Whitaker et al. 2007; Whitaker et al. 2008; Whitaker et al. 2009).

I had a unique opportunity to explore the impacts of ectoparasites on bats by linking surveys of ectoparasites with information on foraging and roosting of bats that was already being collected as part of a long-term study of bat communities near IND. Bats were captured between 15 May and 15 August 2008-2009 and 10 April and 15 August 2010 using standard mist-netting techniques and placed temporarily in small Ziploc bags. Each bat was placed in a new bag to prevent cross contamination of parasites or pathogens between individual bats. Data taken for

each bat included mass, right forearm length, age, sex, reproductive condition, and species. I identified reproductive classes as pregnant females by gently palpating the abdomen, lactating females by bare patches around nipples or presence of milk, post-lactating females by desiccated nipples and new hair growth around the nipples, and volant juveniles by the presence of epiphyseal-diaphyseal gaps (Brunet-Rossinni & Wilkinson 2009). The body of each individual was then examined alive for parasites with head-mounted magnifying lenses (Ritzi 2004). For each bat, I began by examining the dorsal side, starting with the right wing then moving to the uropatagium, the left wing, the furred body, and the head. The bat was carefully flipped over, and I examined the ventral side starting with the left wing followed by the uropatagium, the right wing, the furred body and the head. Examining each region of a bat's body separately standardized the samples taken from each individual. The membranous surfaces of each bat such as the wings and uropatagium were examined for approximately 30 seconds while the furred areas of a bat were examined for approximately 1 minute because of the increased difficulty of finding parasites hidden by fur. The number of parasites on each body region was recorded and vouchers taken when ectoparasites could not be identified in the field. Vouchers were identified using available keys and literature (Rudnick 1960; Radovsky 1967; Radovsky and Beck 1971; Whitaker 1982; Ritzi 2004) and confirmed by J.O. Whitaker, Jr.

Common measures of ectoparasite loads include prevalence (total hosts infected with a parasite divided by total hosts examined), abundance (total parasites found divided by total hosts examined), and mean intensity (total parasites found divided by total hosts infected with parasites). For this study, I also characterized the ectoparasite load of each individual bat by the volume of ectoparasites. When comparing ectoparasite volume and roost-switching data, I only used the volume of ectoparasites that will potentially spend time off the host. I used an Olympus

BX41 microscope and an Olympus DP21 camera and software (Olympus Corporation, Tokyo, Japan) to find the surface area of a vouchered parasite in μm^3 on a slide. Using calipers, I measured the thickness of 7 coverslips which was 0.65 mm. Therefore, the thickness of each coverslip was $0.65 \text{ mm}/7=0.093 \text{ mm}$. I found the thickness of slides using the same method, and, using 5 slides, the thickness was 0.99 mm per slide. The combination of slide and coverslip is 1.083mm, and this number was subtracted from the thickness of a particular vouchered ectoparasite. I multiplied the thickness of a parasite by the area to find its volume and repeated this for each species, sex, and life stage of ectoparasite found on each bat to be tracked. I multiplied the volumes by the number of ectoparasites found on each bat to estimate an individual bat's total volume of ectoparasites.

After examining a bat for ectoparasites, a model LB-2 radio transmitter (Holohil Systems Ltd, Carp, Ontario, Canada) was attached to the mid scapular region of the bat with Skin-Bond Cement (Smith & Nephew, Inc., Largo, Florida). Transmitters were no more than 5-10% of body mass. I used a TRX-2000S PLL Synthesized Tracking Receiver (Wildlife Materials Inc, Carbondale, IL) and a 3 or 5 element antenna (Wildlife Materials Inc, Carbondale, IL) to track bats to their roosts until the transmitter failed. Roost-switching frequency was defined as the total times a bat switched roosts divided by the total days the bat was tracked to a roost minus 1 because it cannot be ascertained whether or not a bat has switched roosts on the first day of tracking (Kurta et al. 2002). I only used the volume of ectoparasites that spend a portion of their lives off the host (*M. crosbyi* and *M. insignis*) when comparing these data to roost-switching.

The foraging ranges of the bats were determined using radio telemetry, as has previously been successful for several species (Fellers and Pierson 2002; Duchamp et al. 2004; Walters et al. 2007; Whitaker et al. 2007). Duchamp et al. (2004) compared both foraging time and

foraging ranges between *E. fuscus* and *N. humeralis* and different reproductive conditions.

These methods are commonly used to determine habitat preferences of bats with software such as Geographic Information System (ESRI ArcMap 9.2, 2006) (Fellers and Pierson 2002; Duchamp et al. 2004; Walters et al. 2007). However, these methods were also useful in examining relationships between ectoparasite loads and the host's foraging behavior.

I tracked the foraging of each Indiana bat for 3-6 nights by obtaining triangulated locations during nightly foraging. At least 3 azimuths were taken simultaneously from specific tracking locations at 2-5 minute intervals during a bat's nightly foraging. The telemetry data were converted into point data using the computer program Locate (V. Nams 2000), and these data were loaded into a Geographic Information System (ESRI ArcMap 9.2, 2006) and overlain on a Digital Ortho Quarter Quadrangle photographic map (US Geological Survey, 1998) and a photomap of the state produced by the Indiana State Geological Survey (2005). I was able to determine the total foraging area (km^2) of each bat from the GIS software that I used to compare the ranges of bats with varying ectoparasite loads. I also compared the average nightly foraging area (km^2) between reproductive classes which I found by creating a minimum convex polygon for each night a bat was tracked, finding the sum of the areas, and dividing by the total tracking nights.

Data were analyzed with analysis of variance (ANOVA) and linear regression in SPSS version 11. I reported means \pm standard error where appropriate. The independent variables in this study were reproductive class and ectoparasite load. These were tested for an effect on the dependent variables, which were roost-switching frequency, foraging range, average foraging duration, and average nightly foraging area. I also tested whether or not there is a difference in ectoparasite load between reproductive classes. When testing for interactions between

ectoparasites and roost-switching, I used only the volume of ectoparasites species that potentially spend a portion of their life cycle in the roost as an independent variable. The foraging areas and ectoparasite volumes were log-transformed for normality. Each year at least 6 individuals of *M. sodalis* were captured and tracked to roosting areas and foraging ranges. When possible, additional bats were tracked in order to gain a reasonable sample size.

Results

From 2008-2010, I captured a total of 55 individuals of *M. sodalis*, from which I collected enough data to compare ectoparasite volume with reproductive class for 34 individuals (10 pregnant females, 6 lactating females, 8 post-lactating females, and 10 volant juveniles; Table 1).

Of the 55 individuals of *M. sodalis* I captured, I attached transmitters to 35. Of these, I was able to track the roost-switching and compare it with reproductive class of 28 individuals. Unfortunately, I was only able to combine ectoparasite data and roost-switching frequency for 19 individuals. Some transmitters failed before I had enough time to successfully track roost-switching, and I was not able to collect ectoparasite data from every bat captured.

I was able to collect adequate foraging data for analysis of 27 individuals. Of the 27 individuals of *M. sodalis* from which I obtained foraging data, I was only able to collect enough data to find both average foraging duration and foraging area for 20 individuals. Some transmitters failed before I had enough time to successfully track nightly foraging or roost-switching. Other bats moved out of the range of our equipment, and, although we typically compensate by moving tracking positions, we could not follow some because we were tracking several bats simultaneously. Both male juveniles and female juveniles were grouped together,

and adult males were excluded from this study because no foraging data was collected from adult males.

I quantified the parasite loads of bats by the total volume of their ectoparasites. Ectoparasite species found on *M. sodalis* included *Myodopsylla insignis* (Siphonaptera; Ischopsyllidae), *Cimex adjunctus* (Hemiptera; Cimicidae), *M. crosbyi* (Acari; Macronyssidae) and *S. globosus* (Acari; Spinturnicidae; Table 2). Using an Olympus BX41 microscope and an Olympus DP21 camera and software (Olympus Corporation, Tokyo, Japan), I was able to find the area for each sex and reproductive class of each of these species. Using these measurements, I calculated the volumes for each ectoparasite which are as follows: *S. globosus* male= $23.44 \mu\text{m}^3 (\pm 23.440)$, female= $72.59 \mu\text{m}^3 (\pm 8.52)$, nymph= $23.44 \mu\text{m}^3 (\pm 2.41)$; *M. crosbyi* male= $0.44 \mu\text{m}^3 (\pm 0.24)$, female= $0.95 \mu\text{m}^3 (\pm 0.46)$, and protonymph= $0.19 \mu\text{m}^3 (\pm 0.10)$; *M. insignis* male= $553.10 \mu\text{m}^3 (\pm 118.70)$; Table 3).

Pregnant females had the highest abundance of ectoparasites (mean= 6.50 ± 1.71) followed by post-lactating females (mean= 3.88 ± 1.46), lactating females (mean= 3.67 ± 1.52), and volant juveniles (mean= 0.70 ± 0.37) (Table 1), but these differences were not significant (ANOVA $F=2.159$; d.f.=3,30; $P=0.114$). I did, however, find a significant difference between each reproductive class and the mean total volume of ectoparasites (ANOVA $F=9.614$; d.f.=3,30; $P=0.000$; Table 4). Post-lactating females had the highest volume of ectoparasites ($154.24 \mu\text{m}^3 \pm 4.22$) followed by lactating females ($121.45 \mu\text{m}^3 \pm 20.27$), pregnant females ($119.43 \mu\text{m}^3 \pm 24.33$), and juveniles ($24.18 \mu\text{m}^3 \pm 16.50$; Table 4).

Variation in roost-switching and ectoparasite load was compared between different reproductive classes of *M. sodalis*. I did not use *C. adjunctus* in my analyses because the two individuals I recorded were on bats that I was not able to fully examine for ectoparasites. Both

male juveniles and female juveniles were grouped together, and adult males were excluded from this study because none were tracked long enough to yield sufficient data.

A significant difference in roost-switching frequency was found between reproductive classes of *M. sodalis* (ANOVA $F=3.453$; d.f.=3, 25; $P=0.032$; Figure 1). Lactating females had the lowest roost-switching frequency with a mean of 0.345 ± 0.121 followed by pregnant females ($0.426, \pm 0.069$), post-lactating females ($0.601, \pm 0.094$), and volant juveniles ($0.727, \pm 0.086$).

The volume of ectoparasites that spend a portion of their lives off the host did not significantly affect roost-switching frequency of *M. sodalis* (Figure 2). This prediction was tested using a linear regression ($r^2=0.059$; d.f.=1,17; $P=0.318$).

There was no significant difference in average total foraging area between reproductive classes (ANOVA $F=1.87$; d.f.=3, 22; $P=0.164$; Figure 3). Juvenile *M. sodalis* had the lowest mean foraging area at $1.9\text{km}^2 (\pm 0.2)$ followed by lactating females ($2.6\text{km}^2, \pm 0.5$), post-lactating females ($3.5\text{km}^2, \pm 0.6$), and pregnant females ($3.6\text{km}^2, \pm 0.8$). Lactating females foraged for the longest period of time with a mean of 104.6 minutes (± 8.5) followed by post-lactating females (97.0 minutes, ± 20.3), volant juveniles (96.4 minutes, ± 4.2), and pregnant females (93.4 minutes, ± 8.5 ; Figure 4). Despite this variation, no significant difference was found in average foraging duration between reproductive classes (ANOVA $F=0.213$; d.f.=3,21; $P=0.886$).

Volant juvenile *M. sodalis* had the highest average nightly foraging area ($2.2 \text{ km}^2 \pm 1.7$) followed by lactating females ($2.1 \text{ km}^2 \pm 1.0$), post-lactating females ($1.9 \text{ km}^2 \pm 0.1$), and pregnant females ($1.8 \text{ km}^2 \pm 0.4$; Figure 5). However, I found no significant difference in average nightly foraging areas between reproductive classes (ANOVA $F=.031$; d.f.=3, 9; $P=0.992$).

I was only able to compare foraging areas and ectoparasite volumes of *M. sodalis* for 17 individuals. There was no significant relationship between ectoparasite volume and total

foraging area when a linear regression was performed ($r^2=0.179$; d.f.=1, 15; $P=0.091$; Figure 6), average nightly foraging durations ($r^2=0.065$; d.f.=1,14; $P=0.783$; Figure 7), or average nightly foraging area ($r^2=0.220$; d.f.=1,10; $P=0.124$; Figure 8).

Discussion

I did not find ectoparasite load to be a significant factor in roost-switching or foraging behavior of *M. sodalis*, but these results should be interpreted carefully because of the small sample size. The lack of a significant relationship between reproductive class and foraging behavior may also be due to a small sample. Significant results may be found through further research with higher samples of *M. sodalis*, but the bats in this study may have maintained moderate loads of ectoparasites, which would not affect their roost-switching or foraging behavior.

There are advantages and disadvantages of using the volume of a host's ectoparasites when measuring parasite load. One bat may host a variety of ectoparasite species, and these may vary drastically in size than others, and there may also be variation in size between sexes and life cycle periods of individuals from the same species. Calculating the volume of ectoparasites instead of number allows ectoparasites of different sizes to be combined into a more accurate measurement of ectoparasites. It also allows for assumptions to be made about the relative effect to the host caused by differently sized ectoparasites.

The major difficulty in obtaining the volume of an individual parasitic mite is the size of the animal, and the measurements of individuals must be calculated in μm . Once the volumes are calculated, inferences concerning the relative effect various ectoparasite species have may be drawn. Given the volumes of individual female *S. globosus* ($72.586 \mu\text{m}^3$) and *M. crosbyi* (0.947

μm^3), for example, one female *S. globosus* can be assumed to be able to consume the same amount of resources from a bat as approximately 77 female *M. crosbyi*.

However, using using the relative volumes of ectoparasites to compare their effects on hosts may be problematic. When calculating the ratio between ectoparasite species, one only considers the size of the ectoparasites and potential volume of resources potentially consumed. Not taken into account are the actual resources preferred by a given species nor the location on the host's body the parasite is found. The physical irritation experienced by the host also is not accounted for as 77 *M. crosbyi* could be more of a nuisance than one *S. globosus*.

The variation in abundance of the ectoparasites of *M. sodalis* observed between reproductive classes is similar to data of Ritzi (2004), who found that ectoparasitic mites increase in abundance during the pregnancy and lactation periods of *E. fuscus* and *N. humeralis*. It is reasonable to expect *M. sodalis* to display the same seasonal variation in ectoparasite abundances as seen with *N. humeralis* and *E. fuscus* described by Ritzi (2004) when larger samples are studied, and the variation may be statistically significant, considering trend of ectoparasites increasing in abundance during the pregnancy period.

The reproductive classes of *M. sodalis* (pregnant, lactating, post-lactating, and volant juveniles) had significantly different roost-switching frequencies. Lactating females had the lowest roost-switching frequency of the four reproductive classes examined in this study. A lactating female has offspring that remain in the roost during nightly foraging, and because it is energetically costly to transport non-volant young between roosts, the females are more likely to show higher fidelity to roosts when lactating. During this period, females form maternity colonies averaging about 80 individuals (Whitaker & Brack 2002), possibly for thermoregulatory benefits.

Pregnant females had a higher roost-switching frequency than lactating females but were still burdened by the weight of their offspring. However, considering the overlap of standard errors between pregnant and lactating females (Figure 1), the difference in roost-switching frequency between these two reproductive classes is likely not significant. Although they would seemingly have more freedom to move between roosts than lactating females, the extra weight of growing embryos creates more of an energy drain than was the case for post-lactating females. Post-lactating females are no longer burdened by their young in that they no longer carry the extra weight nor are they obligated to return to roosts to feed their offspring.

Juvenile *M. sodalis* had the highest roost-switching frequency of the four reproductive classes. Juveniles became volant in late June to mid-July, and their high roost-switching frequency may be in part due to a lower need for a group to help thermoregulatory needs. Another reason for higher roost-switching could be parasite avoidance. Ritzi (2004) found that ectoparasite intensities increase during the pregnancy and lactation periods of *Eptesicus fuscus* and *Nycticeius humeralis*, which also form maternity colonies during summer. *Spinturnix myoti* has been found to increase on juveniles after timing their reproductive period with that of their host bat *M. myotis* (Christe et al. 2000). If an increase in ectoparasites occurs in a maternity roost of *M. sodalis*, as seen with *E. fuscus*, *N. humeralis*, and *M. myotis* (Christe et al. 2000; Ritzi 2004), then individuals may seek alternate roosts once juveniles become volant.

Many Indiana bats often used artificial bat boxes as roosts in this study area, and this behavior has been observed for several years (Ritzi et al. 2005). Reckardt and Kerth (2007) found that *Myotis bechsteinii*, which also roost in artificial bat boxes, switched roosts to avoid parasitic flies. Their study, however, used a much larger sample of bats than the 18 individuals of *M. sodalis* I was able to track. However, *M. bechsteinii* switches roosts to avoid a parasitic fly

that is a much larger parasite than even the largest mites that afflict *M. sodalis*. Following the roost-switching of a larger sample of *M. sodalis* and comparing it to ectoparasite data may demonstrate similar behavior, but it may be unreasonable to expect ectoparasites such as *S. globosus* or *M. crosbyi* to have as much of an effect on roost-switching as larger insect ectoparasites like bat flies.

The sample size used in this study may also not have provided enough statistical power to demonstrate relationships between foraging behavior and reproductive class or between foraging behavior and ectoparasite load. Neither reproductive condition nor ectoparasite volume significantly affected total foraging area, average nightly foraging duration, or average nightly foraging area.

Although a significant difference between the total foraging areas of reproductive classes was not found, it was reasonable to expect post-lactating and pregnant females to have larger foraging areas than lactating females and volant juveniles. Switching between roosts may increase a bat's foraging range if the roosts are in different areas, and lactating bats have been known to switch roosts less frequently than pregnant females (Kurta et al. 2002). Increasing the sample size may provide enough data to demonstrate a significant difference in foraging area between reproductive classes.

No significant difference was found between the mean foraging durations of the reproductive classes of Indiana bats, but lactating females had the largest mean duration. Increasing the sample size or tracking the foraging of other species may provide a better understanding of the relationship between reproductive class and foraging behavior of bats.

It is reasonable to assume that lactating females would have longer nightly foraging bouts because they periodically return to roosts to feed their offspring and should compensate by

obtaining more resources. Bats of other reproductive classes are free from this burden and thus are able to exhibit uninterrupted foraging. The apparent fidelity to roosts is likely due to the energetic cost accrued by transporting juveniles between roosts and the preference to remain in a large maternity roost.

Obtaining foraging data may help to formulate management plans for *M. sodalis* as well as other species. Future work that should be considered includes examining land classes that are preferred foraging areas by *M. sodalis*. Given that *M. sodalis* in this study forages in total areas no greater than 4km², land management plans should not only include roosting habitat but also adequate proximal foraging habitat. This study demonstrates that ectoparasite load does not significantly affect foraging behavior, but perhaps with ample roosting options, *M. sodalis* is able to avoid problematic burdens of ectoparasites, which have been shown in other bats (Bartonicka and Gaisler 2007; Reckardt and Kerth 2006, 2007).

Although ectoparasites of bats have been extensively studied in Indiana, collecting additional data may yield new information about associations between host and parasite species (Ritzi 2004). Future work with *M. sodalis* as well as other bat species should involve the collection and documentation of ectoparasites whenever possible. Further research may be conducted on the endoparasites of *M. sodalis* as well. Combining these data would yield more information on habits of bats that help to compensate for heavier parasite burdens.

The Indiana bats in this study may have been burdened with moderate levels of ectoparasites, the result of co-evolution between host and parasite species (Price 1980). The immune response that is developed by the host is likely the selection factor that is acting on the ectoparasite population. More harmful to hosts would be newly invasive ectoparasites to which a defense has not been developed (Ritzi 2002). An example of this could be the fungus

Geomyces destructans growing on hibernating *M. sodalis* as well as other bat species afflicted with White Nose Syndrome in the eastern United States and Canada. Continuing to collect and study ectoparasites of *M. sodalis* as well as other bat species will aid in our understanding of the evolutionary responses of bats to ectoparasites.

Table 1. Total ectoparasites recovered and abundances of ectoparasites from different reproductive classes of *Myotis sodalis* at the Indianapolis International Airport habitat restoration lands.

Reproductive Period (Total Examined)	Total Ectoparasites Recovered	Abundance of Ectoparasites
Pregnant (10)	65	6.50
Lactating (6)	22	3.67
Post-Lactating (8)	31	3.88
Volant Juvenile (10)	7	0.70

Table 2. Ectoparasites recorded from *Myotis sodalis* at the Indianapolis International Airport habitat restoration lands.

Ectoparasite Species	Prevalence	Abundance	Mean Intensity	Total Recorded
<i>Macronyssus crosbyi</i>	0.45	2.92	6.53	111
<i>Spinturnix globosus</i>	0.70	1.51	2.16	80
<i>Myodopsylla insignis</i>	0.05	0.08	1.5	3
<i>Cimex adjunctus</i>	0.05	0.05	1.0	2

Table 3. Volumes of ectoparasites found on Indiana bats (*Myotis sodalis*).

Ectoparasite Species	Volume		
	Male	Female	Nymph
<i>Macronyssus crosbyi</i>	0.44 μm^3 (± 0.24)	0.95 μm^3 (± 0.46)	0.19 μm^3 (± 0.10)
<i>Spinturnix globosus</i>	23.44 μm^3 (± 2.65)	72.59 μm^3 (± 8.52)	23.44 μm^3 (± 2.41)
<i>Myodopsylla insignis</i>	553.10 μm^3 (± 118.70)	NA	NA

Table 4. Ectoparasite volumes for each reproductive class of Indiana bats (*Myotis sodalis*).

Reproductive Class (N)	Mean Ectoparasite Volume	Standard Error
Pregnant Females (10)	119.43 μm^3	24.33
Lactating Females (6)	121.45 μm^3	20.27
Post-Lactating Females (8)	154.24 μm^3	4.22
Juveniles (10)	24.18 μm^3	16.50

Figure 1: Mean roost switching frequencies for reproductive periods of *M. sodalis*: pregnant = 0.426, lactating = 0.345; post-lactating = 0.601; juvenile = 0.727. Error bars represent standard error of the mean.

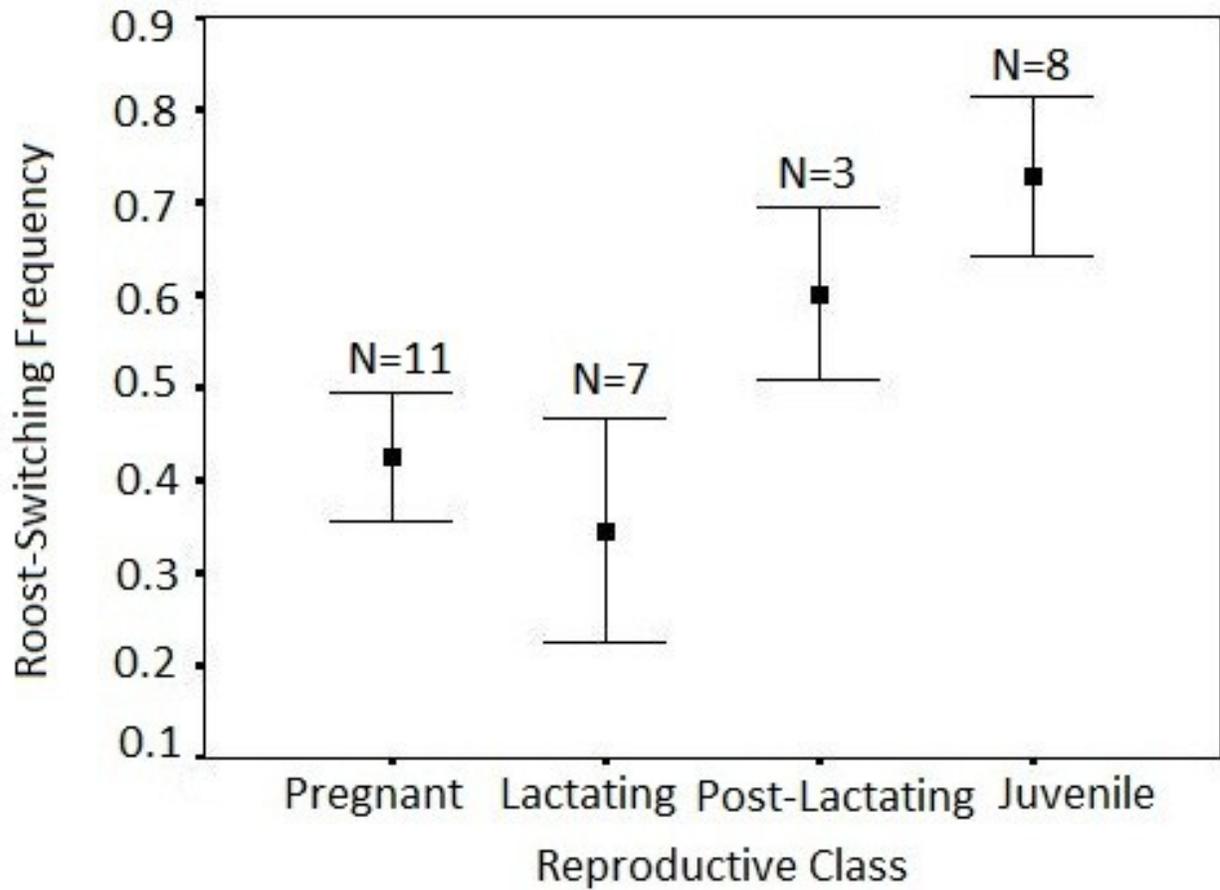


Figure 2: Roost-switching as a function of volume of ectoparasites that spend time off the host.

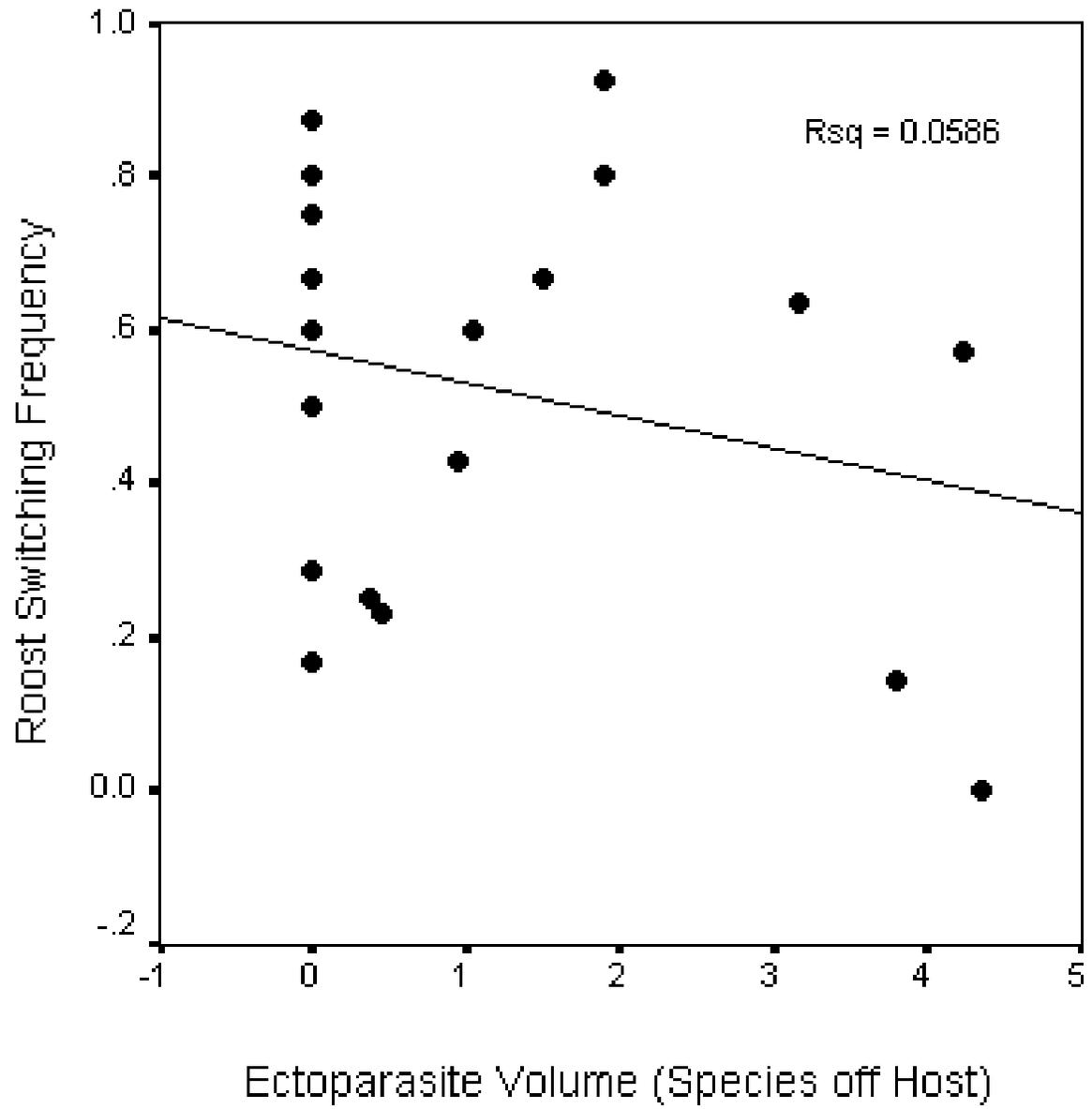


Figure 3: Average total foraging area (km^2) for each reproductive period of *M. sodalis*. Error bars represent standard error of the mean.

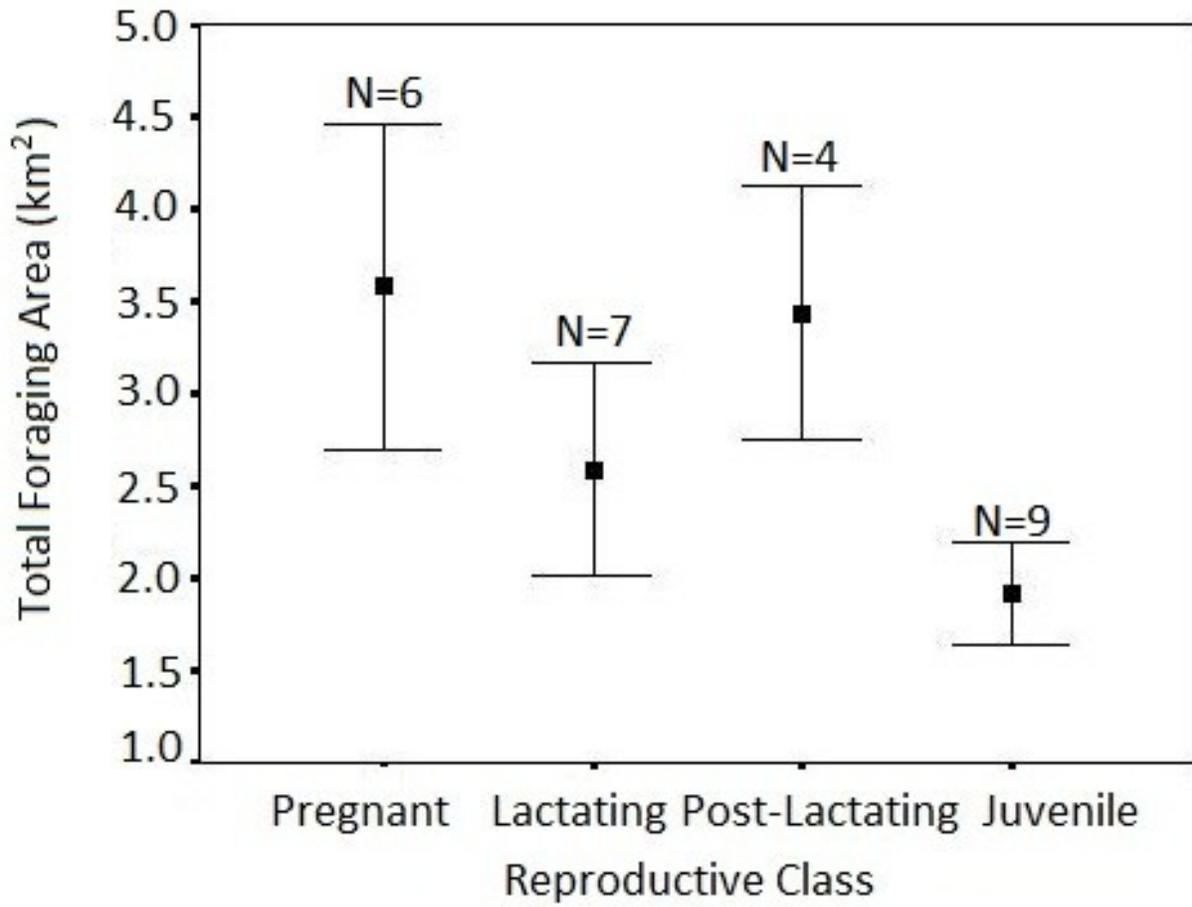


Figure 4: Average foraging duration (minutes) for reproductive classes of *M. sodalis*. Error bars represent standard error of the mean.

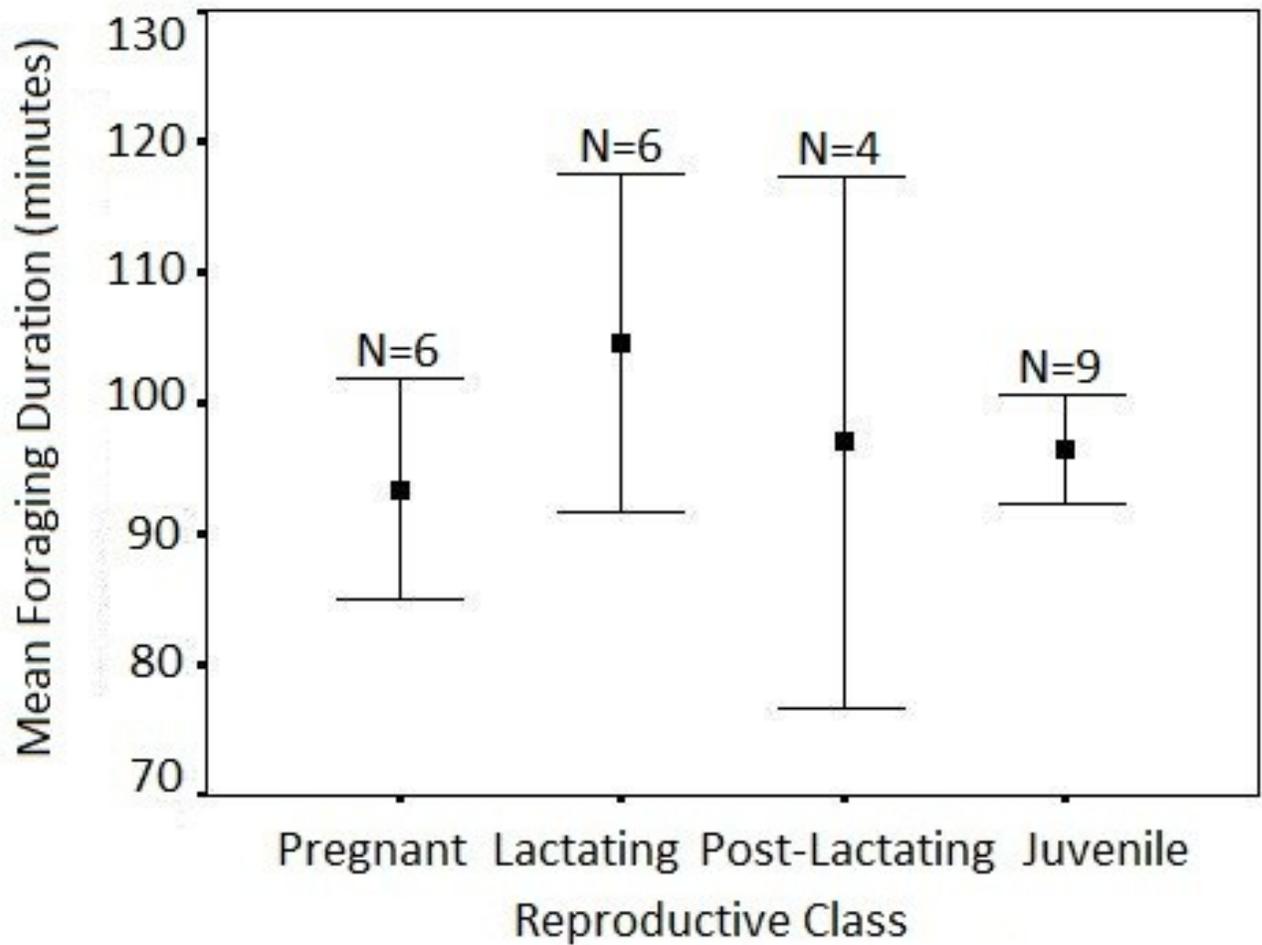


Figure 5: Average nightly foraging area (km^2) for reproductive classes of *M. sodalis*. Error bars represent standard error of the mean.

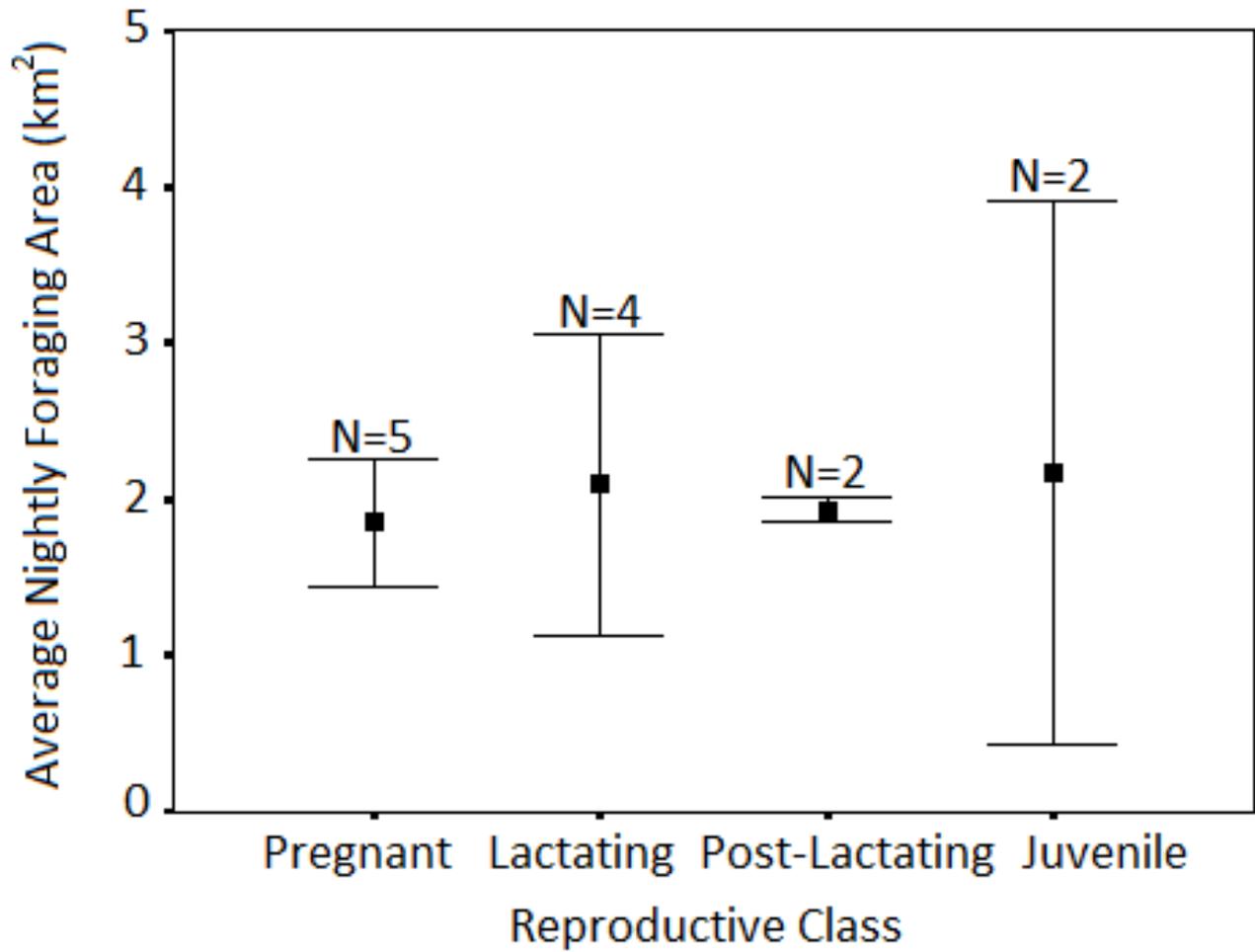


Figure 6: Total foraging area as a function of total ectoparasite volume. Data have been log-transformed for normality.

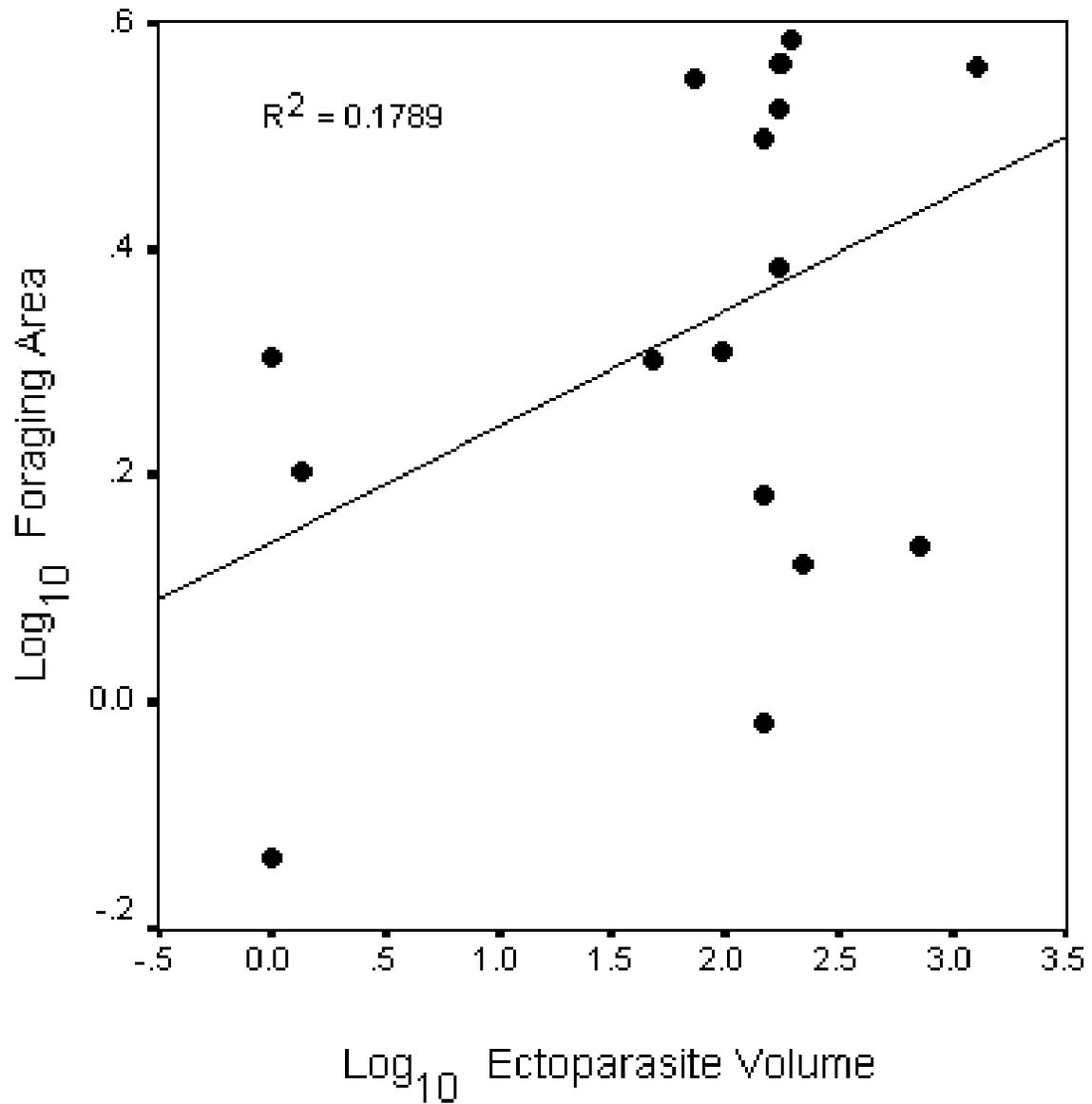


Figure 7: Scatterplot of Average foraging duration as a function of total ectoparasite volume. Ectoparasite volume has been log transformed for normality.

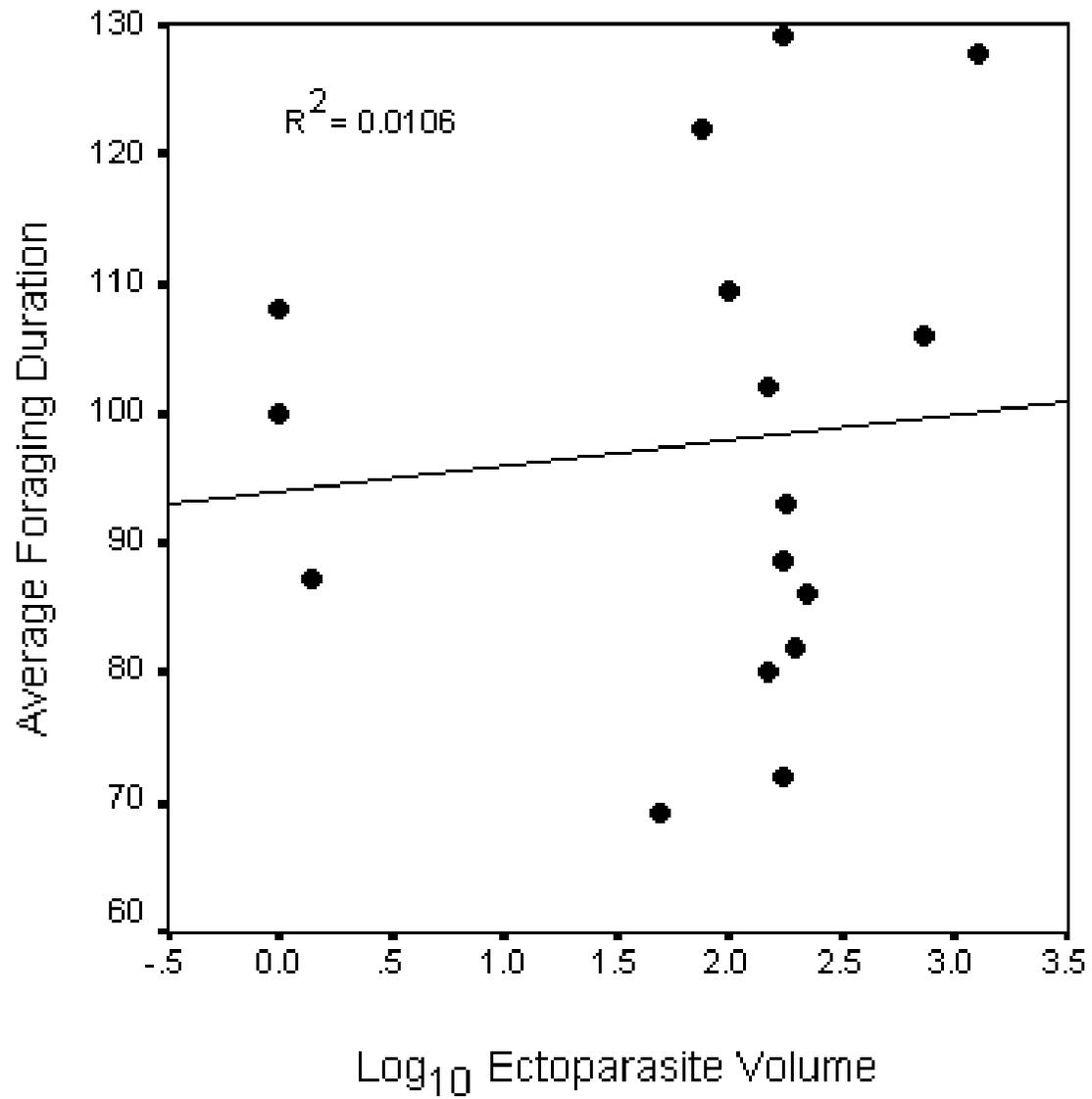
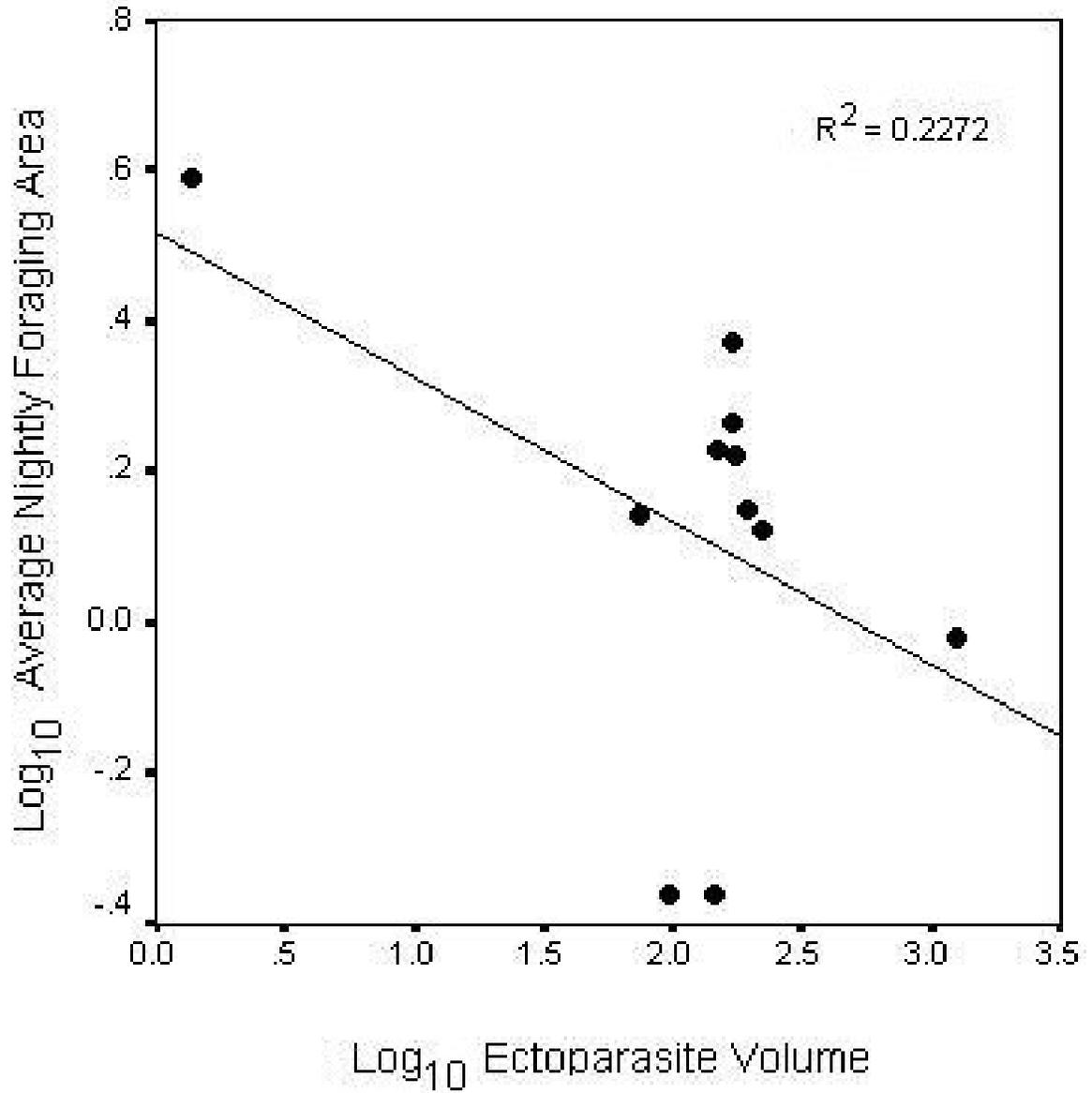


Figure 8: Average nightly foraging area as a function of total ectoparasite volume. Data have been log-transformed for normality.



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