Ectoparasites are an important factor in bat health due to emergent diseases and their associated threats to global public health. The diverse foraging habits of bats expose them to different surfaces which may influence ectoparasite infestations. In spite of these, most studies often overlook dietary specialisations when observing ectoparasite loads. The present paper quantitatively investigates whether foraging strategies as well as other host characteristics (sex, age, trunk and patagial area) influence ectoparasite load (nycteribiids and mites) of bats. Ectoparasite counts and morphometric data were taken from mist net captures of bats. We then developed and compared models for modeling bat ectoparasite abundance under various distributions using generalised linear models. The negative binomial distribution consistently proved to be adequate for modeling mite, nycteribiid and total ectoparasite abundance based on information-theoretic approaches. Generally, females and frugivores had higher ectoparasite loads conditional on bat sex and diet, respectively. Contrary to nycteribiid abundance, mite abundance was positively related to patagial area. Thus, our findings suggest that dietary guild, sex and patagial area (as well as age-nycteribiid abundance) are significant determinants of ectopara- site abundance.

Keywords: mammal, negative binomial, parasitism, Poisson, Zero Inflated Negative Binomial, Zero Inflated Poisson

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to sex-based differences in immunocompetence or home range size (Morand et al. 2004, Krasnov et al. 2005). The immunocompetence hypothesis, which was proposed by Folstad and Karter (1992), suggests that testosterone may have a dual effect. Thus, while increasing investment in sexually selected characters it may simultaneously compromise the immune system.

Despite studies that have investigated the factors explaining the diversity of bat ectoparasites, such as colony size or roosting behaviour (Bordes et al. 2008, Gay et al. 2014), none of them had considered the foraging strategies of bats. Hence, the goal of the present study was to quantitatively investigate the determinants of ectoparasite loads on bats. Specifically, we hypothesised that ectoparasite intensity will vary among bat dietary habits (frugivores and insectivores). Thus diverse foraging strategies of bats expose them to different types of foliage, animals and numbers of conspecifics which may influence ectoparasite infestations. Foraging habits have been shown to influence pathogen transmission risk due to an increased likelihood of vertebrates to ingest contaminated food or infected prey (Bell and Burt 1991, Vitone et al. 2004). Rosenzweig (1995) reported that larger habitats support more individuals (and species) than do smaller habitats. We therefore hypothesised that if host body size is analogous to habitable area, then larger hosts should have a higher prevalence and intensity of ectoparasites than do smaller hosts. Also, we expect that host characteristics such as sex and age would determine the intensity and prevalence of ectoparasites.

**MATERIALS AND METHODS**

**Study area**

The study was conducted at Kosane in the Dormaa West district of the Brong Ahafo Region, Ghana. The district was carved out of Dormaa which lies within longitude 3°–3°30’W and latitude 7°–7°30’N. The vegetation is characterised by unused forests, broken forests, grasslands and extensively cultivable forestlands and forest reserves. It has a bimodal rainfall pattern with a dry spell that spans from November to February. Mean annual rainfall values in the area are between 1,250 mm and 1,750 mm with an average temperature of 26.1°C–30°C (Dormaa Municipal Assembly 2006).

**Capture of bats and collection of ectoparasites**

Bats were captured with the aid of 12 × 2.5 m mist nets set at ground level at identified fly ways in three of each agroecosystem type (citrus farms, mixed farms, fallow lands, teak plantations, oil palm plantations, maize farms) following a reconnaissance survey. Mist nets were monitored periodically from 18:30 hours each day until they were closed at 02:00 hours the following day. Each captured bat was marked to avoid double sampling and then released at the same site of capture. During this period, species identification and morphometric (body mass and forearm length) measurements of chiropterans were carried out. Species were later classified into two foraging guilds based on diet (Hill and Smith 1984, Giannini and Kalko 2004) for analyses. Fruit-eating bats were classified as frugivores while insect-eating bats were classified as insectivores. Sexing of individuals was based on the presence of male external genitalia (Racey 1988). Captured bats were later classified into three age groups namely; juveniles, subadults and adults (Nelson 1965, Vardon and Tidemann 1998, Holmes 2002). In addition, ectoparasites were removed from bats with the aid of forceps and preserved in vials of 70% ethanol for identification. To prevent the possibility of ectoparasite escapes, a cloth was held around the body of each captured bat while removing the parasites. In order to avoid contamination of samples, a cloth bag was used for each bat sampled. These cloth bags were later washed and inspected before re-use.

**Data analysis**

A total of 183 ectoparasites (57 mites and 126 nycteribiids) were identified on 253 captured chiropterans (bats) during the research period. This comprised of 128 frugivorous (Epomops buettikoferi Matschie, Lissonycteris angolensis Bocage, Micropteropus pussilus Peters and Rousettus aegyptiacus Geoffroy St.-Hilaire) and 125 insectivorous bats (Hipposideros aff. ruber Noack, Hipposideros jonesi Hayman and Nycteris spp.) pooled based on diet and or family (with the exception of Nycteris spp.) for the purpose of this study. A preliminary test (nested random-effects analysis of variance) performed to determine the distribution of variance phylogenetically (species within genus within family) based on square root transformed total ectoparasite counts revealed that most of the variation was centred around genera (34%, P < 0.0001) and families (45%, P = 0.0411). Though it was envisaged that genera of higher taxa essentially pooled diverse lineages, we opted to use two species as the unit of analysis due to the small size of the dataset based on species within genera and genera within families. The two species, namely L. angolensis (family Pteropodidae) and H. jonesi (family Hipposideridae), which have distinct dietary specialisations, belong to the same sub-order ‘Pteropodiformes’.

The patagia or trunk of hosts are common areas where many species of ectoparasites are located. Body mass and forearm length were therefore used as alternate measurements of body size. Since these two parameters do not have a linear relationship with surface area, the criteria of Emerson et al. (1994) was adopted for the ectoparasite study. Patagial area and host trunk area were therefore estimated (scaled) using forearm length² and body mass²/3, respectively, for the analysis.

**Generalised linear models**

The minimum and maximum counts of ectoparasite infestations per individual chiropteran ranged from zero (no infestation) to ten (high infestation). Thus, close inspection of the entire body surface of chiropterans for ectoparasite infestation or abundance will generate a non-negative integer or count data which will thus be inappropriate for traditional linear modeling. Insisting on their use may result in the prediction of negative counts, non-normality of errors and the possibility of the variance increasing with the mean (model misspecifications and inconsistent estimators). Generalised Linear Models (GLM) are therefore extensions of Traditional Linear Models (TLM) formulated to accommodate responses with non-normal distributions as well as model functions of the mean (Agresti 2002). Suppose a response variable with independent random observations \( y, y_2, \ldots, y_n \) and expected response \( E(y) = \mu_i \). Then both the TLM and GLM will be defined by the linear component given below:
Nycteribiid abundance

BIC 158.40*
336.18*
log \log 2
355.82*
200.33
309.14*
307.60
392.60
BIC 337.90
309.76
2 \log 2 \phi
173.90
TE abundance

AIC 198.45
182.99
376.70
366.98

parsimony. The model with minimum fit has a minimum number of parameters to ensure simplicity and penalise for the addition of parameters such that the model of best fit has a minimum number of parameters to ensure simplicity and parsimony. The model with minimum AIC, AICc and BIC in the class of competing models is thus considered best. The general computations for the AIC, AICc and BIC are given below:

\[
AIC = \log(\sigma^2) + \frac{2m}{N} \quad (4)
\]

\[
AIC_c = AIC + \frac{2m(m+1)}{N-m-1} \quad (5)
\]

\[
BIC = \log(\sigma^2) + \frac{m\log N}{N} \quad (6)
\]

where;

\( \sigma^2 \) is the maximum likelihood estimate of residual term variance
\( m \) is the number of parameters in the model and
\( N \) is the total number of observations in the dataset

RESULTS

Based on the selection criteria, the Negative Binomial distribution was appropriate for modeling mite, nycteribiid and total ectoparasite abundance of chiropterans. Thus, the Negative Binomial distribution consistently recorded the least BIC values compared to that of the Poisson, Zero Inflated Poisson and Zero Inflated Negative Binomial distributions in terms of the variables modeled (Table 1). The full and reduced models of the ectoparasite analyses are presented in Tables 2 and 3, respectively.

Mite abundance

Though the parameter estimates for juveniles (-6.7064, \( P = 0.8649 \)) and subadults (-0.8376, \( P = 0.1169 \)) were negative, they were not significantly different from adult chiropterans in terms of mite abundance. Also, the insignificant negative parameter estimate for host trunk indicates that for each one unit increase in host trunk area, the expected log count of the number of mites decreases by 0.0372 (Table 2). Due to the statistical insignificance of these two parameters (age and host trunk), a reduced model was fitted with only the significant variables as shown in Table 3. Based on the findings, the difference in the logs of mite counts is expected to be 1.7861 units lower for males compared to females, given that all other variables are held constant in the model. Furthermore, the expected log mite count for \( L. \ angolensis \), which has a frugivorous diet, is 4.6605 higher than the expected log mite count for \( H. \ jonesi \), which has an insectivorous diet. The significant estimate for patagia implies that for a unit increase in patalgial area, the expected log count of the number of mites increases by 0.0020.
Table 2. Parameter estimates of ectoparasite abundance for the comparative analysis between *Lissonycteris angolensis* Bocage (frugivory) and *Hipposideros jonesi* Hayman (insectivory) based on sex, age, diet, host trunk and patagial area – full models employed appropriate distributions based on selection criteria in Table 1.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Std. error</th>
<th>Wald χ²</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mite abundance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-3.9710</td>
<td>1.8398</td>
<td>4.66</td>
<td>0.0309</td>
</tr>
<tr>
<td>Male</td>
<td>-1.6319</td>
<td>0.5335</td>
<td>9.36</td>
<td>0.0020</td>
</tr>
<tr>
<td>Female</td>
<td>0.0000</td>
<td>0.0000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Juvenile</td>
<td>-6.7064</td>
<td>9.4226</td>
<td>0.03</td>
<td>0.8649</td>
</tr>
<tr>
<td>Subadult</td>
<td>-0.8376</td>
<td>0.5342</td>
<td>2.46</td>
<td>0.1169</td>
</tr>
<tr>
<td>Adult</td>
<td>0.0000</td>
<td>0.0000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Frugivory</td>
<td>3.6578</td>
<td>2.0964</td>
<td>4.08</td>
<td>0.0434</td>
</tr>
<tr>
<td>Insectivory</td>
<td>0.0000</td>
<td>0.0000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Host trunk area</td>
<td>-0.0372</td>
<td>0.0889</td>
<td>0.17</td>
<td>0.6760</td>
</tr>
<tr>
<td>Patagial area</td>
<td>0.0019</td>
<td>0.0007</td>
<td>6.56</td>
<td>0.0104</td>
</tr>
</tbody>
</table>

Nycteribiid abundance

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Std. error</th>
<th>Wald χ²</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>2.6391</td>
<td>0.9517</td>
<td>7.69</td>
<td>0.0056</td>
</tr>
<tr>
<td>Male</td>
<td>-0.5565</td>
<td>0.2605</td>
<td>4.57</td>
<td>0.0326</td>
</tr>
<tr>
<td>Female</td>
<td>0.0000</td>
<td>0.0000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Juvenile</td>
<td>0.8046</td>
<td>0.3166</td>
<td>6.46</td>
<td>0.0110</td>
</tr>
<tr>
<td>Subadult</td>
<td>0.1594</td>
<td>0.3945</td>
<td>0.16</td>
<td>0.6862</td>
</tr>
<tr>
<td>Adult</td>
<td>0.0000</td>
<td>0.0000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Frugivory</td>
<td>2.1969</td>
<td>0.8246</td>
<td>7.10</td>
<td>0.0077</td>
</tr>
<tr>
<td>Insectivory</td>
<td>0.0000</td>
<td>0.0000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Host trunk area</td>
<td>-0.0631</td>
<td>0.0401</td>
<td>2.47</td>
<td>0.1159</td>
</tr>
<tr>
<td>Patagial area</td>
<td>-0.0007</td>
<td>0.0003</td>
<td>5.51</td>
<td>0.0189</td>
</tr>
</tbody>
</table>

Total ectoparasite abundance

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Std. error</th>
<th>Wald χ²</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.3284</td>
<td>0.6455</td>
<td>4.23</td>
<td>0.0396</td>
</tr>
<tr>
<td>Male</td>
<td>-0.3653</td>
<td>0.1908</td>
<td>3.66</td>
<td>0.0556</td>
</tr>
<tr>
<td>Female</td>
<td>0.0000</td>
<td>0.0000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Juvenile</td>
<td>0.2045</td>
<td>0.2845</td>
<td>0.52</td>
<td>0.4723</td>
</tr>
<tr>
<td>Subadult</td>
<td>0.4055</td>
<td>0.2754</td>
<td>2.17</td>
<td>0.1408</td>
</tr>
<tr>
<td>Adult</td>
<td>0.0000</td>
<td>0.0000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Frugivory</td>
<td>1.3983</td>
<td>0.5875</td>
<td>5.66</td>
<td>0.0173</td>
</tr>
<tr>
<td>Insectivory</td>
<td>0.0000</td>
<td>0.0000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Host trunk area</td>
<td>-0.0413</td>
<td>0.0342</td>
<td>1.45</td>
<td>0.2278</td>
</tr>
<tr>
<td>Patagial area</td>
<td>-0.0003</td>
<td>0.0002</td>
<td>1.72</td>
<td>0.1897</td>
</tr>
</tbody>
</table>

Nycteribiid abundance

From the results in Table 2, host trunk area was not a significant predictor of nycteribiid abundance. The reduced model in Table 3 shows that the expected log nycteribiid count for males is 0.5256 lower than that of females. Whereas the expected log nycteribiid counts for both juveniles and subadults were 0.9577 (P = 0.0015) and 0.2233 (P = 0.5718) higher than the expected log nycteribiid count for adults, respectively, only that of juveniles was statistically significant. Again, the expected log count for individuals with a frugivorous diet is 1.5739 higher than the expected log count for individuals with an insectivorous diet. Contrary to the chiropteran mite abundance model above, patagial area showed a significant negative relationship in terms of nycteribiid abundance suggesting a decline of the parasite in that ‘area/locality’.

Total ectoparasite abundance

Since age, host trunk and patagial area were not significant predictors of total ectoparasite abundance (Table 2), a reduced model excluding these parameters was fitted (Table 3). The findings reveal that the difference in the logs of expected total ectoparasite abundance is expected to be 0.3827 unit higher for individuals exhibiting frugivory (*L. angolensis*) compared to those exhibiting insectivory (*H. jonesi*). Also, the expected log total ectoparasite count for males is 0.3576 lower than the expected log count for females while holding the other variables constant in the model.

**DISCUSSION**

The present study explicitly revealed fundamental differences in foraging behaviour of bats based on ectoparasite loads. This suggests that ectoparasite prevalence is related to chiropteran diet. Insectivorous bats are noted to be rich in nitrogen (Whitaker 1988) whereas frugivores are poor in nitrogen (Korine et al. 1996, Kam et al. 1997). There is a large array of evidence suggesting that lack of protein inhibits the proper functioning of the immune system (Lochmiller et al. 1993, Vestey et al. 1993, Saino et al. 1997). It was therefore expected that frugivores would have higher ectoparasite loads than insectivores due to suppressed immune system functioning and notable risk of infestation through contaminated plant matter contact (Fogarty et al. 2008). Thus insectivores will have lower loads of ectoparasites (mite, nycteribiid and total ectoparasite abundance) since they mostly catch their prey while in flight minimising contact with contaminated surfaces. Some bat ectoparasite studies support female-biased parasitism (Christe et al. 2007, Presley and Willig 2008) as was the case in our findings. However, this finding contrasts those of many other mammalian ectoparasite studies. Male
mammalian species are widely known to harbour more ectoparasites than do females (Moore and Wilson 2002) due to sex-related differences in immunocompetence or home-range size (Morand et al. 2004, Krasnov et al. 2005). Generally the immune system of males is suppressed due to higher levels of androgen (Foldstad and Karter 1992) resulting in greater parasitic loads than those of females. In spite of this, other ecological factors may greatly influence sex-biased parasitism (Krasnov et al. 2005), such as differential roost-site selection (based on sex) and colony-size effects. For instance, more bats are attracted to roosts of high quality selected by females, which makes females more susceptible to infestations (Zahn and Rupp 2004). Also, transmission of ectoparasites is encouraged when females tend to roost in dense maternity colonies for the maintenance of high body temperatures required to promote rapid juvenile growth (McCracken 1984).

When age is taken into account, ectoparasitic loads will differ markedly among chiropterans based on mite, nycteribiid and total ectoparasite abundance. Evidence for horizontal transfers of ectoparasites (encounters between infested and non-infested) through offspring adoption and/or social interactions, which are common among colonial organisms, has been documented (Altizer et al. 2003, Bize et al. 2003). This mechanism is especially true for both nycteribiids and mites, which are wingless and not highly mobile. Hence, they mostly depend on colonial hosts for their survival and population maintenance rather than solitary hosts that provide limited substrates. Other life history traits or strategies of both hosts and parasites may also influence the intensity and prevalence of bat ectoparasites. For instance, bat flies are holometabolous with pupation having to take place off the host specifically, in the bat’s roost (Fritz 1983). In order to feed after eclosion, nycteribiids must immediately locate and colonise a host (Caire 1983). In order to feed after eclosion, nycteribiids must immediately locate and colonise a host (Caire 1983), thus making the young of bats ‘vulnerable’. This could have led to significantly higher nycteribiid loads among juveniles compared to adults. Though subadults had higher nycteribiid loads, they were not statistically different from adult bats. Furthermore, the restricted energy budget of young bats, especially juveniles, may have accounted for such higher nycteribiid abundance due to the high cost of self-grooming. Most mites such as spinturnicid mites are exclusive ectoparasites of bats, which spend their entire life cycle on the host’s patagium (Dolving 2006). They therefore adjust their reproductive cycle to that of the host in order to infest neonates (Christe et al. 2000). Thus, we can argue that adult chiropterans will temporarily have higher mite intensities compared to juveniles and subadults, as was the case in our findings (hence, the statistical insignificance) in lieu of horizontal transfers and restricted energy budgets.

Contrary to evidence that larger habitats (host body size) support more individuals than do smaller habitats (Rosenzweig 1995), host trunk area, which is a surrogate of body size, did not influence mite, nycteribiid and total ectoparasite abundance of chiropterans. This suggests that larger-sized chiropterans will not necessarily have higher ectoparasite loads in a predictable way. If grooming reduces ectoparasite prevalence (Clayton 1991, Cotgreave and Clayton 1994, Mooring 1995, Poiani et al. 2000), juveniles should also have reduced ectoparasite loads because grooming is a common practice among vertebrates.

A study of de Fanis and Jones (1995) study of a captive colony of long-eared bats (Plecotus auritus Linnaeus) revealed the presence of mother-juvenile and adult-adult allogrooming but no evidence of juvenile-juvenile allogrooming. As such, grooming can reduce ectoparasite loads not only in adults but across all age groups of chiropterans. The intensity and period spent grooming may also cause ectoparasites to be spatially localised (Reiczigel and Rózsa 1998). This could have led to the insignificant (negative relationship for all analyses) contribution of host trunk area to mite, nycteribiid and total ectoparasite abundance since the area is readily exposed to grooming. Contrary to host trunk area, patagium has a significant effect on mite and nycteribiid abundance probably due to less grooming accessibility. The significance of patagial area could also be attributed to morphological adaptations and preferences of ectoparasites for resource partitioning, thus restricting them to chiropteropatagium. This may have accounted for the significantly positive relationship between patagia and mite and nycteribiid abundance contrary to the significantly negative relationship between patagia and nycteribiid abundance since the former (mite) spends its entire life cycle on the host (specifically the patagium).

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Page 5 of 7


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