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Complete List of Authors:	Wetzler, Gabrielle; Southern Illinois University, Department of Zoology Boyles, Justin; Southern Illinois University, Cooperative Wildlife Research Lab
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The Energetics of Mosquito Feeding by Insectivorous Bats

Gabrielle C. Wetzler¹ and Justin G. Boyles^{2*}

¹Department of Zoology, Southern Illinois University, Carbondale IL 62901

²Cooperative Wildlife Research Laboratory, Department of Zoology, Southern Illinois
University, Carbondale IL 62901

Corresponding Author: jgboyles@siu.edu

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Abstract

Dietary studies have long shown that insectivorous bats do not often consume mosquitoes, despite cosmopolitan distribution and occasional ubiquity of mosquitoes. The apparent avoidance of mosquitoes relative to availability may relate to their small size, as bats may have difficulties detecting and capturing mosquitoes or they may not return sufficient energy per unit effort of capture. We used bomb calorimetry to determine the energetic content of mosquitoes from Alaska and Illinois, USA, and compared resulting estimates to daily energy expenditure of several bat species. On a per gram basis, mosquitoes were energetically comparable to other insects (26.82 ± 2.40 kJ/g dry mass); however, an individual mosquito contains little energy. Some small insectivorous bats could theoretically meet daily energy needs by foraging exclusively on mosquitoes for <2 h, assuming maximal estimates of the rate of successful capture of mosquitoes. Larger, omnivorous bats may require >25 h of foraging on mosquitoes to meet daily energy needs. Wet mass of the mosquitoes required to balance energy budgets represent 18-92% of body mass of bats, and tends to be higher for smaller species. Thus, it appears that a mosquito-based diet may be constrained by different factors in small and large bat species.

Keywords: bats, Chiroptera, Culicidae, energy budgets, foraging, mosquitoes

Introduction

Energy balance is essential, and all organisms must trade off metabolic functions, thermoregulation, reproduction, predator avoidance, foraging, and other functions to remain in a positive energy state. In all but rare situations of energy abundance, it is crucial for organisms to forage in such a way as to maximize energy intake while minimizing energy expenditure. One of the easiest ways for an animal to do this is through selective foraging on prey that provide high energy per unit effort. Among mammals, bats (Order Chiroptera) exemplify the importance of efficient foraging because, in addition to high reproductive and thermoregulatory costs typical of most mammals, they also use an costly mode of locomotion (Winter and von Helversen 1998). Further, bats are constrained by the biophysical realities of flight (Aldridge and Brigham 1988), so there are limitations in how much food they can consume and how much flexibility they can have in foraging decisions. To meet energetic needs within these constraints, bats display among the widest array of food preferences of any mammalian order, including nectar, fruit, blood, insects, and vertebrates (Altringham 1996).

Among bats, there are no species that specialize on one the most cosmopolitan and occasionally ubiquitous potential prey items: mosquitoes (Culicidae). Numerous studies provide evidence that bats do occasionally consume mosquitoes (e.g., Anthony and Kunz 1977; Kunz and Whitaker 1983; Kurta and Whitaker 1998; Rydell 1992*b*; Whitaker 1972, 2004), and mosquitoes might influence foraging behavior of some bats (Gonsalves et al. 2013*c*). Public sentiment and popular press would further lead you to believe bats are major predators of mosquitoes (Tuttle 1997). However, mosquitoes are almost universally a minor component of the diets of bats. Reported volume of mosquitoes in bat feces is usually under 10% except for some high latitude bat species (Rydell 1992*a, b*). Reproductive state, season, and gender may also play

a role in the likelihood of individual bats consuming mosquitoes, as Indiana bats (*Myotis sodalis*) consume more mosquitoes during pregnancy (Kurta and Whitaker 1998), while male parti-coloured bats (*Vespertilio murinus* L., 1758) consume more mosquitoes than females (Rydell 1992a). Importantly, there is no evidence that any bat species depredates mosquitoes heavily enough to reduce adult mosquito populations, but there is evidence that bats may reduce the number of eggs laid by adult females in experimental conditions (Reiskind and Wund 2009).

There are several hypotheses to explain why bats do not readily consume mosquitoes. The two most common explanations relate to the small size of mosquitoes. First, the small size of mosquitoes may make them difficult for bats to detect and capture (Barclay and Brigham 1991). If this hypothesis is correct, highly maneuverable bats with high echolocation frequencies should consume more mosquitoes than large, low-frequency echolocators. Gonsalves et al. (2013a) report exactly this pattern in an Australian bat community. A second explanation may be that mosquitoes do not provide sufficient energy for most bats, especially larger species, to meet their energy requirements. Early work suggests mosquitoes are not unusually low in mass-adjusted energy content compared to other insects (Kunz 1988 and references therein), but to our knowledge, there are few energy budget calculations of mosquito feeding by bats. Herein, we further test the hypothesis that mosquitoes are unlikely to satisfy the energy needs of insectivorous bats by measuring the energy content of mosquitoes from two geographically disparate areas in North America and comparing resulting values to estimates of daily energy expenditure of representative bats around the world.

Materials and Methods

We collected most of the analyzed mosquitoes from a commercial “bug zapper” trap in June 2012 at a residence in the McCarthy Community within the boundaries of Wrangell-St. Elias National Park, Alaska, USA and froze them at -80°C . We further captured mosquitoes in Illinois, USA between June-July 2016 and froze them at -20°C . In Illinois, we collected mosquitoes using an electric mosquito fan trap (Mini Mosquito Trap, Viatek Consumer Products Group, Chattanooga, TN, USA) set up near a forest pond ($37^{\circ}42' \text{ N}$, $89^{\circ}14' \text{ W}$) on the edge of a suburban/agricultural interface.

We identified a subset of mosquitoes to genus using a web resource (<http://www.utep.edu/leb/mosquito/id.htm>; accessed 18 April, 2017). Mosquitoes from Alaska were all identified as *Aedes* spp. Most mosquitoes from Illinois were identified as *Aedes* spp. or *Culex* spp., but there were also some *Orthopodomyia* spp. To make pellets, we compacted 30-40 mosquitoes using a standard drinking straw. We measured energy content of pellets using a semi-micro bomb calorimeter (Model 6725; Parr Instrument Company, Moline, IL, USA) following all standard correction factors suggested by the manufacturer. Incomplete combustion was accounted for in energy calculations by approximating how many mosquitoes were left after combustion and subtracting mean mass of a single mosquito (taking into account location and size class) from the original mass of the pellet. We omitted trials in which more than six mosquitos did not combust; in total, 34 mosquito combustions were successful. We did not dry mosquitoes before analysis because it was difficult to form pellets of fully dry mosquitoes and they did not combust well when not formed into a tight pellet. Instead, we measured moisture content of a subsample of mosquitoes from each location by comparing the mass before and after a week of oven drying.

Our goal was to determine if mosquitoes were a viable energy source for insectivorous bats. Therefore, we estimated the number of mosquitoes several bat species would need to consume to balance their daily energy budget. We conducted a non-exhaustive literature search to find daily energy expenditure (DEE) estimates for insectivorous bats. We started with data collected by Kunz (1980), and added data from newer studies (Table 1). To convert our energy measurements to number of mosquitoes required for a given DEE, we assumed a 70% digestion efficiency (Barclay et al. 1991) and that live mosquitoes are 70% water mass (Benoit and Denlinger 2007). We used two-way *t*-tests to compare energetic values from mosquitoes sampled in Illinois and Alaska. All results are presented as mean $\pm$ SD.

Results

We calculated water content in seven samples from each location. The average wet mass of a single mosquito (at the time of analysis) was $7.18^{-4} \pm 9.17^{-5}$ g and $1.087^{-3} \pm 3.61^{-4}$ g, from Alaska and Illinois, respectively. Dry mass per individual mosquito was $6.47^{-4} \pm 5.96^{-5}$ g and $6.02^{-4} \pm 2.86^{-4}$ g, from Alaska and Illinois, respectively. The mosquitoes from Illinois were analyzed sooner after capture than those from Alaska, so they had slightly higher water content. Still, water content was relatively consistent at each site ($20.2 \pm 1.4\%$ for Alaska and $25.0 \pm 3.7\%$ for Illinois), so we used mean values to account for water mass in energy calculations.

We analyzed 29 samples of mosquitoes from Alaska and five samples from Illinois. Mosquitoes from Alaska contained 20.19 ± 1.85 kJ/g or $1.46^{-2} \pm 2.7^{-3}$ kJ individual⁻¹; whereas mosquitoes collected in Illinois contained 19.73 ± 1.54 kJ/g or $1.55^{-2} \pm 4.3^{-3}$ kJ individual⁻¹. The per gram energy content of mosquitoes was not different between the two sampling locations ($t = 0.52$, d.f. = 32, $p = 0.60$). Across both locations, mosquitoes contained 20.12 ± 1.80 kJ/g or 1.47^{-2}

2 ± 2.9^{-3} kJ individual $^{-1}$. After adjusting for water remaining at the time of measurement, mosquitoes contained 26.82 ± 2.40 kJ/g or $1.97^{-2} \pm 3.9^{-3}$ kJ and dry mass of these mosquitoes was $5.64^{-4} \pm 1.47^{-4}$ g. We use these combined estimates of dry mass and energy per unit dry mass to calculate the number of mosquitoes bats would need to consume to balance their energy budgets.

Daily energy expenditure of insectivorous bats (or species that occasionally eat insects) ranged from 14.23 to 159.7 KJ/ day (Table 1). Assuming an average energy content, the fewest number of mosquitoes needed to meet DEE was 1,344 (*Myotis velifer* Allen, 1890 - adult male; Table 1), whereas the greatest number of mosquitoes needed to meet DEE was 15,087 (*Phyllostomus hastatus* Pallas, 1767 - adult male). The dry mass of mosquitoes needed to meet these DEE values ranged from 0.76 to 8.51 g. The live mass of mosquitoes, assuming 70% water, to meet these energetic needs varied from 2.53 to 28.4 g.

Discussion

Our per gram estimates of energy content of mosquitoes are slightly greater than previously reported values (20.7-23.0 kJ/g), but comparable with estimates of other insects commonly consumed by bats (19-30 kJ/g; Kunz 1988). We extended our calculations to estimate energy content of individual mosquitoes, which was low because of their small mass. For that reason alone, mosquitoes may represent an inefficient prey item for bats under most circumstances. To satisfy the lowest estimates of DEE we found in the literature (both from small myotiline bats; Table 1) at least 1,300 mosquitoes per night would need to be consumed. Largely anecdotal estimates of maximum consumption rates of mosquitoes range between 10 (Griffin et al. 1960) and 20 mosquitoes min $^{-1}$ (Rydell 1990). Based on these estimates, a bat could consume 1,300 mosquitoes in approximately 1-2 h. Even at high latitudes with few hours

of midsummer darkness, bats often forage for at least two hours (Boyles et al. 2016). However, foraging rates likely do not approach the maximum reported rates under most natural conditions. For example, Rydell et al. (2002) observed 100 predation attempts (with a 92% capture rate) in 2 h of opportunistic observations of 3 or more little brown bats (*Myotis lucifugus* Le Conte, 1831) feeding on mosquitoes inside a building roost. While it is unlikely they observed every attempt and there were likely more than three bats, the reported capture success equates to ~ 15 captures h^{-1} , or 87 h of foraging to consume 1300 mosquitoes. Under most conditions where bats are feeding on mosquitoes, the consumption rate probably falls between these two extremes (0.25 and 20 mosquitoes min^{-1}), and foraging time might be restrictive.

Size of bats likely plays a fundamental role in the value of foraging on mosquitoes. The above calculations demonstrate that for small bats, feeding exclusively on mosquitoes is at least within the realm of possibility, but may still require an exceptional set of conditions for a bat to balance its energy budget with mosquitoes alone. Conversely, the largest bat in our sample, the greater spear-nosed bat, an omnivorous species that feeds largely on fruit, would require > 25 h to meet its energy needs with mosquitoes alone (Table 1). Community-level study of the relationship between mosquito density and bat foraging activity supports the conclusion that foraging activity is related to mosquito density for only small bats (Gonsalves et al. 2013b).

The biophysical limitations of flight might also restrict the ability of bats to consume a mosquito-rich diet if the wet mass of the required mosquitoes impairs flight ability. Assuming mosquitoes are 70% water (Benoit and Denlinger 2007), bats in our sample would need to consume 18-92% of body mass to meet DEE. Although our sample (seven species) is too small to quantify the relationship between body mass and water content of mosquitoes necessary to balance DEE, it qualitatively appears smaller bats may be more constrained in this sense than

larger bats. There is also considerable interspecific variation in these estimates. For example, a 7.5 g little brown bat remaining euthermic in Alaska (Boyles et al. 2016) would require 4.7 g of mosquitoes (63% of body mass) over the course of a night. The mass of necessary mosquitoes might explain why little brown bats in Alaska, where mosquitoes are found in high densities, eat few mosquitoes (mosquitoes generally represent less than 3% of diet by volume; Boyles et al. 2016; Whitaker and Lawhead 1992). Given the short foraging periods available around summer solstice, the bats appear to forage non-stop for a couple of hours, and may not be able to evacuate the water in mosquitoes quickly enough to avoid issues with flight maneuverability. For comparison, a 7.9 g lactating little brown bat in the northeastern United States would require 7.3 g of mosquitoes (92% of body mass). Spread out over the course of a longer night of foraging and night roosting (8 h or more), this might be feasible (Kurta et al. 1989). Thus, it appears the constraints on mosquito-feeding might be different in small and large bats and different among populations of the same species.

Bats are not unique in their avoidance of adult mosquitoes. While there are numerous endotherms for which mosquito feeding has been recorded (e.g. Song Sparrows [*Melospiza melodia* Wilson, 1810] and Purple Martins [*Progne subis* L., 1758]) (Reisen and Fang 2007; Kale 1968), like bats, it appears that adult mosquitoes do not make up a substantial portion of the diet of any endotherm in which diet has been studied in depth. For example, in one study, only 1 of 34 Purple Martins consumed mosquitoes, and mosquitoes comprised just 3% of its stomach contents (Johnston, 1967). This suggests that foraging for adult mosquitoes is not energetically effective for endothermic organisms with large energy budgets. Conversely, many ectothermic vertebrates, including fish and amphibians (Billman et al. 2007; DuRant and Hopkins 2008), have been recorded feeding on larval mosquitoes. Some smaller ectothermic organisms may

consume adult mosquitoes or even specialize on them; for example, some spiders (e.g., *Paracyrba wanlessi* Zabka and Kovac, 1996 and *Evarcha culicivora*, Wesółowska and Jackson, 2003) were found to prefer mosquitoes as prey (Jackson and Cross 2015).

Bats are portrayed in the popular literature and occasionally by scientists to readily eat mosquitoes, thereby providing another vital ecosystem service through the control of mosquito-borne illnesses. This undoubtedly aids in promoting a positive image and public acceptance of bats. However, there is little evidence that most bats eat mosquitoes in large numbers. Our results further support the idea that bats do not specialize on mosquitoes because they do not provide sufficient energy per unit effort capture. Other, better supported, benefits of bats to humans (e.g., pollination and consumption of crop pests) should be emphasized in support of conservation efforts for bats.

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References

- Aldridge, H.D.J.N., and Brigham, R.M. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. *J. Mammal.* **69**: 379-382.
- Altringham, J.D. 1996. *Bats: Biology and Behaviour*. Oxford University Press, London.
- Anthony, E.L.P., and Kunz, T.H. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, **58**: 775-786.
- Barclay, R.M.R., and Brigham, R.M. 1991. Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? *Am. Nat.* **137**(5): 693-703.
- Barclay, R.M.R., Dolan, M.-A., and Dyck, A. 1991. The digestive efficiency of insectivorous bats. *Can. J. Zool.* **69**: 1853-1856.
- Benoit, J.B., and Denlinger, D.L. 2007. Suppression of water loss during adult diapause in the northern house mosquito, *Culex pipiens*. *J. Exp. Biol.* **210**: 217-226.
- Billman, E.J., Wagner, E.J., and Arndt, R.E. 2007. A comparison of mosquito consumption and prey selection between least chub (*Notichthys phlegethontis*) and western mosquitofish (*Gambusia affinis*). *W. N. Am. Nat.* **67**: 71-78.
- Boyles, J.G., McGuire, L.P., Boyles, E., Reimer, J.P., Brooks, C.A.C., Rutherford, R.W., Rutherford, T.A., Whitaker, J.O., Jr., and McCracken, G.F. 2016. Physiological and behavioral adaptations in bats living at high latitudes. *Physiol. Behav.* **165**: 322-327.
- DuRant, S.E., and Hopkins, W.A. 2008. Amphibian predation on larval mosquitoes. *Can. J. Zool.* **86**: 1159-1164.
- Gonsalves, L., Bicknell, B., Law, B., Webb, C., and Monamy, V. 2013a. Mosquito consumption by insectivorous bats: does size matter? *PLoS ONE*: e77183.

- Gonsalves, L., Lamb, S., Webb, C., Law, B., and Monamy, V. 2013*b*. Do mosquitoes influence bat activity in coastal habitats? *Wildl. Res.* **40**: 10-24.
- Gonsalves, L., Law, B., Webb, C., and Monamy, V. 2013*c*. Foraging ranges of insectivorous bats shift relative to changes in mosquito abundance. *PLoS ONE*, **8**: e64081.
- Griffin, D.R., Webster, F.A., and Michael, C.R. 1960. The echolocation of flying insects by bats. *Anim. Behav.* **8**: 141-154.
- Jackson, R.R., and Cross, F.R. 2015. Mosquito-terminator spiders and the meaning of predatory specialization. *J. Arachnol.* **43**: 123-142.
- Kunz, T.H. 1980. Daily energy budgets of free-living bats. *In* Proceedings of the Fifth International Bat Research Conference. Texas Tech University, Lubbock. pp. 369-392.
- Kunz, T.H. 1988. Methods of assessing the availability of prey to insectivorous bats. *In* Ecological and behavioral methods for the study of bats. *Edited by* T.H. Kunz. Smithsonian Institution Press, Washington, D.C. pp. 191-210.
- Kunz, T.H., and Whitaker, J.O., Jr. 1983. An evaluation of fecal analysis for determining food habits of insectivorous bats. *Can. J. Zool.* **61**: 1317-1321.
- Kurta, A., Bell, G.P., Nagy, K.A., and Kunz, T.H. 1989. Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). *Physiol. Zool.* **62**: 804-818.
- Kurta, A., and Whitaker, J.O., Jr. 1998. Diet of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *Am. Midl. Nat.* **140**(2): 280-286.
- Reiskind, M.H., and Wund, M.A. 2009. Experimental assessment of the impacts of northern long-eared bats on ovipositing *Culex* (Diptera: Culicidae) mosquitoes. *J. Med. Entomol.* **46**: 1037-1044.

- Rydell, J. 1990. The northern bat of Sweden: taking advantage of a human environment. *Bats* (Austin), **8**: 8-11.
- Rydell, J. 1992a. Diet of the parti-coloured bat *Vespertilio murinus* in Sweden. *Ecography*, **15**: 195-198.
- Rydell, J. 1992b. Occurrence of bats in northernmost Sweden (65° N) and their feeding ecology in summer. *J. Zool. (Lond.)* **227**: 517-529.
- Rydell, J., Parker McNeill, D., and Eklök, J. 2002. Capture success of little brown bats (*Myotis lucifugus*) feeding on mosquitoes. *J. Zool. (Lond.)* **256**: 379-381.
- Tuttle, M.D. 1997. *America's Neighborhood Bats*. 2nd ed. University of Texas Press, Austin, TX. pp. 112.
- Whitaker, J.O., Jr. 1972. Food habits of bats from Indiana. *Can. J. Zool.* **50**: 877-883.
- Whitaker, J.O., Jr. 2004. Prey selection in a temperate zone insectivorous bat community. *J. Mammal.* **85**(3): 460-469.
- Whitaker, J.O., Jr., and Lawhead, B. 1992. Foods of *Myotis lucifugus* in a maternity colony in central Alaska. *J. Mammal.* **73**: 646-648.
- Winter, Y., and von Helversen, O. 1998. The energy cost of flight: do small bats fly more cheaply than birds. *J. Comp. Physiol. B* **168**: 105-111.

Table 1. Representative daily energy expenditure of bats and the approximate number of mosquitoes needed to meet their energy needs.

Species	Gender	Repro. State	Location	Body Mass (g)	DEE (kJ/animal)	Mosquitos needed to meet DEE	Foraging time to meet DEE (h) ¹	Wet Mass Mosquitoes (g)	Reference ²
<i>Antrozous pallidus</i>	F	N/A	Various	~25.3	55.9	5284	4.4-8.8	9.93	Kunz 1980
<i>Macrotus californicus</i>	N/A	N/A	California, USA	12.9	22.8	2153	1.8-3.6	4.05	Bell 1986
<i>Myotis lucifugus</i>	F	N/A	Alaska, USA	~7.5	26.4	2494	2.1-4.2	4.69	Boyles et al. 2016
	F	P (early)	New Hampshire, USA	7.3	14.6	1383	1.2-2.3	2.60	Kunz 1980
	F	P (late)	New Hampshire, USA	8.5	20.5	1937	1.6-3.2	3.64	Kunz 1980
	F	L	New Hampshire, USA	7.6	28.5	2688	2.2-4.5	5.05	Kunz 1980
	F	P	New Hampshire, USA	9	33.7	3183	2.7-5.3	5.98	Kurta et al. 1989
	F	L	New Hampshire, USA	7.9	41.3	3902	3.3-6.5	7.33	Kurta et al. 1989
<i>Myotis velifer</i>	F	P	Kansas, USA	13.2	19.3	1818	1.5-3.0	3.42	Kunz 1980
	F	L	Kansas, USA	12	25.9	2451	2.0-4.1	4.61	Kunz 1980
	M	A	Kansas, USA	12.2	14.2	1344	1.2-2.2	2.53	Kunz 1980
<i>Phyllostomus hastatus</i>	F	M	Trinidad, West Indies	74.4	132.2	12489	10.4-20.8	23.47	Kunz 1998
	M	M	Trinidad, West Indies	87.1	159.7	15087	12.6-25.1	28.35	Kunz 1998
	M	I	Trinidad, West Indies	74.5	79.7	7529	6.3-12.5	14.15	Kunz 1998

<i>Plecotus auritus</i>	F	L	Scotland	9.7	21.3	2012	1.7-3.4	3.78	McClellan and Speakman 1999
	F	NL	Scotland	8.7	23.6	2230	1.9-3.7	4.19	McClellan and Speakman 1999
<i>Rhinolophus ferrumequinum</i>	F	P(early) and L(late)	Gloucestershire, UK	22	67.8	6403	5.3-10.7	12.03	Kunz 1980
	F	P(late)	Gloucestershire, UK	26	45.2	4269	3.6-7.1	8.02	Kunz 1980

L= lactating, NL= non lactating; M= Mature/ adult, I= immature

¹Based on the maximum consumption of 10-20 mosquitoes minute⁻¹ (Griffin et al. 1960; Rydell 1990)

²Kunz 1980 refers to Table 2 in that paper and references therein.

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