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Drivers of variation in nocturnal insect prey mass and quality

Alexandria E. Cosby

acosby@uoguelph.ca

University of Guelph https://orcid.org/0009-0005-8750-0992

Genevieve B. Kleefisch

University of Guelph

Andrew D. Young

University of Guelph

Liam P. McGuire

University of Waterloo

Quinn M.R. Webber

University of Guelph

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Abstract

Global declines in aerial insectivores highlight the need to understand their foraging landscape. Aerial predators face unique biomechanical and aerodynamic constraints; therefore, prey profitability must be evaluated through the combined lens of nutritional value and handling costs. To address this gap, we evaluated the body mass and lipid content of nocturnal insects to determine how intrinsic (i.e. taxonomy and adult feeding strategy) and extrinsic traits (i.e. larval developmental habitat) traits of the sampled insect groups influence profitability of this group of prey. Our results demonstrate that prey quality is driven by three factors. First, taxonomy influenced nutritional profiles. Relative to their body mass, mayfly's lipid content scaled hypo-allometrically whereas the other sampled taxa scaled isometrically. Second, intrinsic feeding strategies predicted energy stores of insects. Larval-feeders had higher body mass and lipid content than life-time-feeders. Third, developmental habitat influenced total body mass but not proportional lipid content. Terrestrial insects were heavier than aquatic-emergent insects, yet total lipid content did not differ between terrestrial and aquatic-emergent insects. While these traits define potential energetic payload for insectivores, actual profitability is strictly bounded by the handling capacity of foraging predators, particularly with regards to gape limitations. Energy-dense prey are only ecologically valuable within an optimal size range for size-selective predators. By quantifying multiple drivers of prey quality, our study provides a nuanced view of the nocturnal prey landscape, demonstrating that the nutritional ecology of aerial predators is highly context-dependent on the composition of the prey community.

Introduction

Optimal foraging theory predicts that animals select prey to maximize profitability. Foragers can optimize net energy intake by reducing search time (i.e., selecting prey with high encounter rates) or reducing handling time (i.e., selecting easily consumable prey) (Macarthur and Pianka 1966). Under assumptions of optimality, simplistic models of optimal foraging assume profitability is the outcome of the relationship between energy gained and energy expended (Stephens and Krebs 1986). Models of optimality also assume that diet breadth is driven by prey availability (Schoener 1971; Stephens and Krebs 1986), even though most models of optimality assume all prey are nutritionally equivalent. However, in practice profitability can be maximized if consumers select prey with high digestible energy (Charnov 1976). Under a Type II functional response curve (see Holling, 1959), handling time is a fixed constraint; therefore, processing abundant but low-quality prey incurs a substantial opportunity cost by dampening the rate of caloric intake per unit of foraging time (Stephens and Krebs 1986). Because optimal foraging is driven by the net rate of energy gain, absolute prey density does not always dictate profitability; rather, consumers should select prey by balancing nutritional density against the time cost of both searching and handling (Raubenheimer and Simpson 2018).

The trade-off between selecting abundant (quantity) relative to nutritionally dense (quality) prey is particularly acute for aerial predators (Speakman and Thomas 2005). Powered flight is the most metabolically expensive form of vertebrate locomotion per unit time, even though it is highly efficient

when considering energetic cost per unit distance (Schmidt-Nielsen 1972; McGuire and Boyles 2024). Compared to terrestrial predators, aerial predators face strict volumetric and mass limitations due to the payload constraints inherent to flight (Norberg and Rayner 1987). Wing loading—the ratio of body mass to wing surface area—is a fundamental biomechanical constraint that dictates flight efficiency and power requirements for a volant organism at a given total mass (Hughes and Rayner 1991). In an experiment with the temperate, insectivorous brown long-eared bats (*Plecotus auritus*), artificially increasing body mass resulted in decreased flight speeds and increased wing-beat frequencies, representing a significant decline in transport efficiency as the energetic cost per unit of distance increased (Hughes and Rayner 1991). The high metabolic cost of flight necessitates a substantial fuel source (Voigt et al. 2010), yet aerial predators, including birds and bats, are frequently faced with the physiological limitation of a limited gut capacity relative to their daily energetic needs (Barry 1976). To navigate the volume constraint, many bats exhibit reduced gastrointestinal tract size and relatively short gut retention times (Staliński 1994; Caviedes-Vidal et al. 2007). Lower gut retention times enable bats to repeatedly fill and empty their stomachs as they forage throughout the night, thereby increasing total caloric intake during foraging bouts while managing fluctuations in body mass and flight efficiency (Roswag et al. 2012). A fast-transit digestive strategy is particularly advantageous when consuming insect prey, as their high proportion of indigestible mass represents a significant physical liability (McGuire and Boyles 2024). However, bats can mitigate locomotive and metabolic costs through prey selection and handling. For example, discarding indigestible chitinous appendages before ingestion reduces the unnecessary energy expenditure and processing time associated with non-nutritive material (Barclay et al. 1991). Bats therefore operate at an energetic ceiling, making it crucial to select prey that provide energy required for flight and not increase dead weight in their gut that could hinder flight efficiency (McGuire and Boyles 2024).

Insects are among the most taxonomically diverse animal groups globally and are the primary prey source for many vertebrate predators (Mooney et al. 2010; Stork 2018). Despite their hyper-variable ecology and life history (Stork 2018), insects are often aggregated at higher taxonomic levels (i.e., phylum, class, order) when described as prey due to research constraints of time and limited taxonomic expertise. Moreover, most studies rely on abundance or biomass as a proxy for energetic value, rather than explicitly measuring the specific nutritional composition of the insect (Sih and Christensen 2001; Ausden and Drake 2006; Didham et al. 2020). Insects differ substantially in morphology and body composition related to their ecology and life history across orders and between species, which should influence their nutritional value as prey items (Haavik and Stephen 2023). Two potentially important life-history factors proposed to dictate insect nutritional value are the environment of larval development (i.e. aquatic-emergent taxa vs strictly terrestrial) (Twining et al. 2019) and whether they feed during the adult stage (Davis et al. 2016). For example, mayflies (Ephemeroptera) have a long larval feeding stage, but a comparatively short adult life span. The primary function of their adult phase is to reproduce and, as a result, mayflies do not feed during their adult stage, with many species surviving only a few days (Brittain 1982). An insect's nutritional value may also be a product of the environment where it developed (Twining et al. 2019). Insects that develop as larvae in aquatic environments before emerging as

terrestrial adults are exposed to a different suite of resources than insects that develop as larvae in a terrestrial environment, which may influence their nutritional value as adults (Shipley et al. 2022). Ultimately, accounting for diverse insect ecology and life history based on functional traits will provide a more nuanced lens through which to evaluate insects as prey.

Nocturnal insects represent a vast and ecologically critical prey base that sustains a diverse array of aerial insectivores, providing the primary energetic fuel for high-metabolism predators like bats (Mooney et al. 2010; Wong and Didham 2024). However, as global insect biodiversity faces unprecedented declines, the stability of nocturnal food webs is increasingly at risk (Owens and Lewis 2018; Didham et al. 2020). Digestive capacity prevents predators from simply consuming more food to offset a poor diet, meaning they are fundamentally dependent on the nutritional value of their prey (Barclay et al. 1991). Consequently, shifts in insect community composition can trigger cascading effects where even subtle changes in available energy may compromise predator survival or reproductive success (Hunter and Price 1992). To predict possible trophic cascades in nocturnal food webs, we must move beyond simple abundance metrics and instead characterize the underlying drivers of the nocturnal foodscape.

Our primary objective was to describe broad patterns in insect body mass and composition (i.e., nutritional value) across taxonomic orders and families, as these innate baseline differences are fundamentally shaped by evolutionary lineage. We did not explicitly test *a priori* hypotheses regarding how mass or lipid content vary among specific orders, given the large number of possible pairwise comparisons. While statistically controlling for taxonomic differences, we tested the hypothesis that the nutritional value of insect prey—as measured by individual body mass and proportional lipid content—is driven by the combined influence of insect feeding strategy and developmental habitat, because habitat dictates the baseline nutrient availability to larvae, while adult feeding strategy determines whether insects must rely entirely on stored larval lipids or can actively supplement their nutritional profile throughout adulthood.

Prediction 1: Insects that only feed as larvae will have higher body mass and higher proportional lipid content relative to insects that feed throughout their lifetime because larval feeders sequester all energy as larvae to fuel the metabolic costs of their dispersal and reproduction as non-feeding adults.

Prediction 2: Aquatic-emergent insects will have higher body mass and higher proportional lipid content than strictly terrestrial insects, as nutrient-dense aquatic larval habitats provide higher concentrations of metabolizable energy than comparatively nutrient-dilute terrestrial habitats.

Methods

Study System and Insect Sampling

We sampled insects from May to September 2025 on Manitoulin Island, Ontario (~ 45.7° N, 82.0° W). Manitoulin Island is located on the northern shore of Lake Huron and features a landscape of limestone alvars, numerous inland lakes, and expansive, shallow-soiled grasslands and is considered one of

Canada's top biodiversity hotspots in crisis (Camaclang et al. 2025). We sampled insects at 15 sites on Manitoulin Island nested within three broader townships (western, central, and eastern) across the study area. Within each township, we established five sampling sites, one in each of five habitat classes: anthropogenic, aquatic, grassland, agriculture, and forest. We used a Esri Landsat layer to identify habitat classes (Esri 2024) with subsequent visual *in situ* ground-truthing performed at each site to ensure classification accuracy. We sampled insects every 10 to 15 days on a rotating basis across the three townships over the course of 11 sampling nights. On each night, we deployed one trap in each of the five habitats, yielding a total of 55 insect samples.

We collected insects using UV light bucket traps (BYOB Weather Resistant Moth Trap, Miller Moth) equipped with an LED light strip tower suspended above a plastic funnel. The funnel led into a five-gallon pail lined with egg cartons to provide refuge and minimize predation or escape within the trap. To further limit insect activity post-capture, we fitted buckets with a vial of 91% ethanol featuring a perforated lid to allow for slow evaporation. While light bucket traps exhibit a known sampling bias toward photo-attractant taxa like moths, they still provide effective coverage for groups such as caddisflies, and capture a wide diversity of incidental taxa through passive interception as insects fly into the structure or are blown by the wind (Yi et al. 2012; Montgomery et al. 2021). However, due to this inherent sampling bias, our collections likely do not represent the complete assemblage of nocturnal prey available in this region. We deployed traps sequentially at sunset, with all light bucket traps deployed within 30 minutes of each other. We collected buckets following the same sequential order four hours post-deployment. We euthanized insects by placing an ethanol-soaked paper towel (91%) in the sealed bucket at room temperature for a minimum of five hours. To prevent desiccation and preserve accurate body mass, we then immediately transferred samples to an airtight container in a -20°C freezer. We sorted and prepared insects for lipid extraction within seven days of collection.

Taxonomic Identification of Insects

We sorted samples to the family level (and suborder for true flies [Diptera]; hereafter just referred to as family) using established taxonomic keys (Beadle and Leckie 2012; Marshall 2017, 2018). Various small and taxonomically difficult moths were also grouped into an informal "Microlepidoptera" category. For families with substantial variation in size among specimens, we separated individual insects into > 1 cm and < 1 cm bins to offset our inability to identify them to species solely using visual keys. Following sorting, we counted individuals, and the aggregate wet mass of each family and size bin was recorded per sample night (± 0.0001; analytical balance Model FX-120i; A&D Company, Ltd., Tokyo, Japan). We assigned feeding strategy (larval-only feeding [hereinafter "larval feeding"] vs. lifetime feeding) and larval habitat use (aquatic-emergent vs. terrestrial) at the family level based on published literature, and we included a 'mixed' category for a small number of families that exhibit split designations (see Table S1 in appendix for categorization, sample sizes, and references). To prevent ambiguous classifications from confounding the results, families exhibiting mixed larval habitat use (n = 3) or mixed feeding strategies (n = 3) were excluded from their respective analyses. While sex has been shown to impact macronutrient

profiles in many insects (Wigglesworth 1960; Boggs 2009), sex could not be determined for our specimens; consequently, sex was not included as a covariate in the statistical models.

Lipid Extraction and Quantification

To ensure sufficient material for lipid extraction, we pooled insects of the same family (and size if applicable) across habitats and aggregated the sampling periods into calendar months. We then selected families that yielded a combined total biomass > 0.1 g per month. We selected target families for lipid extraction based on commonly sampled families and dietary items of Ontario bats (Thomas et al. 2012; Clare et al. 2014; Deeley et al. 2023) which resulted in the inclusion of taxa from five orders: beetles, true flies, mayflies, moths, and caddisflies. We placed insects (pooled or individual, depending on body mass) in pre-weighed cellulose filter paper envelopes (Whatman #1) and weighed to calculate wet mass, with highly prevalent or heavy families allowing for up to five replicate samples per month. We stored prepared samples at -20^{O}C in an airtight container in the field and stored them for up to eight months prior to laboratory processing.

We dried samples to constant mass (< 5% mass change between consecutive weights) in a drying oven (Despatch, Model LBB2-18-1) at 50^{O}C for a minimum of 48 hours until the dry mass stabilized allowing for subsequent weighing of the sample (± 0.0001 g). We gravimetrically determined total lipid mass via Soxhlet extraction using petroleum ether (35–60°C boiling point), with each extraction cycle running for 6–7 hours. Following extraction, we dried samples again to remove residual solvent, and the lipid-free mass of the samples were recorded (± 0.0001 g).

We calculated the proportion lipid content by dividing the total lipid mass of the pooled sample by the initial fresh wet mass. While wet mass can be susceptible to minor desiccation, we used this metric because it best represents the true biological payload available to a foraging predator. To minimize water loss prior to this measurement, we conducted sample preparation and wet mass (hereinafter “body mass”) recording in the field. We assume that subsequent freezer storage did not impact this ratio because all samples were fully dehydrated prior to extraction. By taking this approach, we were able to assess the proportion of lipids relative to the total captured biomass available to predators.

Statistical Analysis

We conducted statistical analyses using R (version 2026.01.1) within the RStudio integrated development environment (version 2026.05.1 + 225). To validate model assumptions, we assessed the distribution of the model residuals using quantile-quantile (Q-Q) plots and standard residual diagnostics. Upon visual inspection of diagnostic Q-Q plots, we determined that the untransformed distributions for insect body mass, lipid mass, and proportional lipid content exhibited pronounced right-skew and deviated from normality. We therefore natural log-transformed insect body mass lipid mass, and proportional lipid content for all subsequent analyses.

We recorded insect collection month to account for both phenological turnover and insect senescence. However, the insect community was highly dynamic; many families exhibited ephemeral life histories, appearing only within a temporally narrow sampling window. The insect community turnover resulted in uneven dispersion of insect families through time, which resulted in a risk of over-parameterizing models and confounding taxonomic variation with seasonal variation. Given that the primary objective of the study was to evaluate broad-scale taxonomic and functional drivers, we did not include a temporal variable (e.g., sampling month) in the hypothesis-driven models to maintain a more parsimonious and stable analytical framework.

To examine the scaling relationship between body mass and lipid content across different taxonomic groups, we fitted a linear model with natural log-transformed total lipid content as the response variable, and the interaction between natural log-transformed body mass and insect order as the predictors using the lme4 package (Bates et al. 2015). This interaction allowed us to estimate a distinct scaling slope for each of the five insect orders (beetle, moth, fly, caddisfly, and mayfly). To determine how lipid content scales within each group, we extracted the estimated marginal trends (slopes) for each order using the emmeans package (Lenth 2025). We then tested each order-specific slope against a null hypothesis of isometry (slope of 1.0) to evaluate whether lipid reserves scale proportionally or allometrically with body size within each order.

The Variance Inflation Factor (car package (Fox and Weisberg 2019)) was high given that the majority of families within an order fell into the same binary feeding type and habitat use categories; consequently, we tested our hypotheses using three separate linear models: taxonomic (family nested within order), feeding type, larval habitat type. To ensure a robust comparison between feeding type and habitat use, we filtered the dataset prior to analysis to remove insect families categorized as “mixed” for either feeding strategy or habitat type. For both feeding and habitat analyses, we modeled our transformed nutritional metrics (body mass and proportion lipid content) as response variables, incorporating taxonomic order and the respective trait categories as independent fixed predictors. This approach allowed us to isolate the independent contribution of ecological traits (feeding type or habitat type) while controlling for the broad evolutionary constraints associated with insect phylogeny. All data visualizations were generated using the ggplot2 package (Wickham 2016).

Results

Between May and September 2025, we collected > 34,000 insect specimens. From this pool, we selected 8,418 individual specimens from five orders (26 families) that met our taxonomic and body mass requirements (n = 153 samples, with each sample representing a single extraction envelope of pooled or individual insects; see Table S1 for full taxonomic breakdown). Across all sampled taxa, untransformed individual body mass ranged from $2.50e^{-4}$ to 0.392 g (median = 0.0173 g), and lipid content ranged from $1.70e^{-5}$ to 0.0321 g (median = 0.00100 g). The median relative lipid content across all sampled insects was 6.63% of their total body mass (Table 1).

Table 1
Summary statistics of body mass and lipid content across five sampled insect orders. Data include sample size (N), median individual body mass (g), median lipid content (g), and median relative lipid content (%). Values in brackets denote the minimum and maximum observed ranges for mass and lipid measurements within each taxonomic group.

Order	N	Median Body Mass (g) [Min – Max]	Median Lipid Content (g) [Min – Max]	Median Relative Lipid (%)
Beetles (Coleoptera)	22	0.0431 [0.00135–0.392]	0.00190 [0.0000618–0.0230]	6.69
True Flies (Diptera)	10	0.000633 [0.000310–0.00623]	0.0000277 [0.0000170–0.000155]	3.84
Mayflies (Ephemeroptera)	9	0.00394 [0.000250–0.0464]	0.000127 [0.0000192–0.000944]	3.23
Moths (Lepidoptera)	95	0.0181 [0.000572–0.261]	0.00116 [0.0000552–0.0320]	7.45
Caddisflies (Trichoptera)	17	0.0155 [0.000678–0.0732]	0.000786 [0.0000446–0.00356]	4.87

Taxonomy & Isometric Comparisons

Across all samples (n = 153), lipid content was strongly and positively correlated with body mass (Adjusted R^2 = 0.94, $F_{9,143}$) = 288.6, $p < 0.001$; Fig. 1). However, our interaction model revealed that the scaling relationship between lipid content and body size varied significantly by taxonomic order ($F_{4, 143}$ = 4.55, $p = 0.002$). When testing order-specific scaling exponents against a null hypothesis of isometry, lipid content scaled proportionally with body mass for beetles (slope = 0.91 ± 0.05 SE, $p = 0.068$), flies (0.83 ± 0.16 SE, $p = 0.27$), moths (1.05 ± 0.03 SE, $p = 0.13$), and caddisflies (0.91 ± 0.08 SE, $p = 0.24$). In contrast, mayflies exhibited significant hypo-allometric scaling (slope = 0.73 ± 0.08 SE, $p < 0.001$), indicating that larger mayflies accumulate proportionally less lipid relative to their body mass than smaller individuals.

Figure 1. Order-specific scaling relationships between lipid reserves and body mass. Natural log-transformed total lipid content (g) plotted against natural log-transformed body mass (g) across five insect orders: beetles (n = 22 samples), flies (n = 10 samples), mayflies (n = 9 samples), moths (n = 95 samples), and caddisflies (n = 17 samples). Solid colored lines represent the estimated marginal trends for each order derived from the interaction model. The dashed black line represents the theoretical null hypothesis of isometric scaling (slope = 1.0). While beetles, flies, moths, and caddisflies accumulated lipids isometrically, mayflies exhibited significant hypo-allometric scaling (slope = 0.73, $p < 0.001$), indicating disproportionately lower lipid reserves at larger body masses.

Further analysis revealed that body mass was significantly driven by broad-scale order ($F_{4,120}$ = 143.49, $p < 0.001$; Fig. 2a) and the nested effect of family ($F_{28,120}$ = 44.36, $p < 0.001$), with the combined

taxonomic model explaining a substantial proportion of the variance in body size (Overall model: $F_{32,120}$ = 56.75, p < 0.001, Adjusted R^2 = 0.92). Similarly, relative lipid content was also significantly constrained by taxonomy at both the order ($F_{4,120}$ = 19.97, p < 0.001; Fig. 2b) and nested family levels ($F_{28,120}$ = 6.59, p < 0.001), with the full model explaining a significant proportion of the variance in relative lipid content (Overall model: $F_{32,120}$ = 8.26, p < 0.001, Adjusted R^2 = 0.60; Fig. 2b).

Figure 2. Taxonomic pairwise comparisons of (A) insect natural log body mass (g) and (B) natural log proportional lipid content. Comparisons are shown in rank order between five taxonomic orders: beetle (n = 22), fly (n = 10), mayfly (n = 9), moth (n = 95), and caddisfly (n = 17). Brackets with stars indicate significant pairwise differences.

Feeding Type

Consistent with our first prediction, we found insects that only feed as larva to have a significantly higher body mass (β = -1.82, p < 0.001; Fig. 3a) and percent lipid content (β = -0.70, p < 0.001; Fig. 3b) compared to lifetime feeders. Functional feeding traits independently predicted both size ($F_{5,115}$ = 16.88, Adjusted R^2 = 0.40, p < 0.001) and lipid content ($F_{5,115}$ = 14.50, Adjusted R^2 = 0.36, p < 0.001; Fig. 3b).

Figure 3. Comparisons of insect body mass and proportional lipid content across feeding strategies. Distributions of (A) natural log-transformed body mass (g) and (B) natural log-transformed proportional lipid content for larval feeders (n = 25) and lifetime feeders (n = 96). Insects that feed exclusively as larvae exhibited significantly higher overall body mass and proportional lipid content compared to lifetime feeders.

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Habitat Type

In contrast to our second prediction, we found that terrestrial insects had significantly higher body mass than aquatic-emergent insects (β = 2.95, variable p = 0.006; Overall model: $F_{5,115}$ = 12.79, Adjusted R^2 = 0.33, p < 0.001; Fig. 4a). However, we found no differences in proportional lipid content between aquatic-emergent and terrestrial insects (β = 0.33, variable p = 0.34; Overall model: $F_{5,115}$ = 6.09, Adjusted R^2 = 0.18, p < 0.001; Fig. 4b).

Figure 4. Comparisons of insect body mass and proportional lipid content across larval habitats. Distributions of (A) natural log-transformed body mass (g) and (B) natural log-transformed proportion lipid content for aquatic-emergent taxa (n = 34) and terrestrial (n = 87). Insects with terrestrial larvae had significantly higher body mass, whereas habitat type did not influence proportion lipid content.

Discussion

Consumers face quality-quantity trade-offs during foraging, yet most models of consumer-resource dynamics focus primarily on resource quantity, such as biomass or abundance, often overlooking the possibility of variance in nutritional value of prey items. To address this gap, we tested hypotheses related to the life-history and environmental drivers of nocturnal insect nutritional value, while we also characterized how taxonomy influences variation in nutritional value of insects. Our results indicate that taxonomy fundamentally constrains both body mass and lipid content. Furthermore, we demonstrated that the scaling relationship between lipid content and body mass varies significantly among orders (Fig. 1). While four of the orders we measured (i.e., beetles, flies, moths, and caddisflies) accumulate lipids proportionally with size, mayflies exhibited hypo-allometric scaling, accumulating disproportionately less lipid content at larger body masses. Furthermore, we found that feeding strategy and larval habitat were important predictors of prey value, such that larval feeders have higher body mass and percent lipid content than lifetime feeders, and terrestrial insects were larger than aquatic-emergent insects. Taken together, our results provide evidence for a highly variable prey base for nocturnal insectivores, highlighting the necessity of integrating taxonomic and functional traits into broader models of energy flow within food webs.

Phylogeny explained a significant proportion of the variation in the nutritional value of nocturnal insect prey, but body mass did not universally scale proportionally with lipid content. Pairwise comparisons revealed that while beetles had a significantly higher body mass than caddisflies, they did not have significantly higher relative proportion of lipids (Fig. 2). The heavily sclerotized cuticle and elytra of beetles contribute significant indigestible mass to the total body mass without increasing lipid storage (Reeves et al. 2021), which likely limits their maximum relative fat concentration compared to highly lipid-dense, soft-bodied taxa like caddisflies or moths. However, structural morphology alone does not universally dictate energy density across the community, as soft-bodied flies had lower relative lipid percentages than beetles. Lipid content is essentially a fixed proportion of body mass across most taxonomic groups. Notably, mayflies deviated significantly from this community-wide isometry, exhibiting hypo-allometric scaling. This difference in the scalar relationship likely reflects the distinct morphology required for dispersal in mayflies, which necessitates expansive wing surface areas that contribute to total weight without increasing lipid stores (Jacobus et al. 2019). Together, our results demonstrate that while body size is a proxy for energy content across much of the prey landscape, taxonomic-specific scaling deviations mean predators must still balance prey selection to optimize nutritional value.

After controlling for phylogeny, larval feeders had higher body mass and lipid content compared to lifetime feeders (Fig. 3). These groups are akin to capital (larval-only) or income (lifetime) feeders based on when they accumulate energy (Boggs 2009; Davis et al. 2016). Maintaining a functional feeding apparatus into adulthood imposes an energetic and morphological constraint (Huberty and Denno 2006). Insects that invest heavily in flight muscles frequently sacrifice the development of feeding structures into adulthood due to finite metabolic budgets (Huberty and Denno 2006). While both strategies necessitate an enlarged abdomen, strict capital breeders dedicate this space entirely to fat reserves, whereas income breeders maintain a functional digestive tract (Davis et al. 2016). In the case

of our results, the significantly higher lipid content and body mass observed in larval feeders directly reflects this morphological trade-off. Active insect flight muscle maintains the highest metabolic rate of any known animal tissue (Marden 2000). To ensure sufficient lifetime energy stores, larval feeders must sequester sufficient energy to fuel their entire, albeit short, adult lifespan, primarily as lipids because lipids offer the highest density energy and the most efficient means of storage (Downer and Matthews 1976; Arrese and Soulages 2010). Obligatory lipid accumulation in insects likely explains why the absence of adult feeding is associated with the greatest lipid content across our sampled community. Although we only compared larval to life-time feeders as binary categories, lifetime-feeding insects can be further differentiated by their adult diets and associated mouthparts, for example, proboscis for liquids compared to mandibles for solids (Boggs 2009). Moths accumulate functionally all of their protein and lipid stores as larvae, and as adults, they either forgo feeding entirely or are morphologically restricted by a proboscis to supplemental liquid carbohydrates like nectar (Wigglesworth 1960). The trend of larval feeders having higher lipid content was particularly evident in families such as Lasiocampidae (a clade of moths including tent caterpillars), where high larval consumption rates sequester the total lipid budget required for adult reproduction (Colasurdo et al. 2009). Because larval feeders are both physically larger and significantly more lipid-dense, they offer a highly efficient energetic return, emphasizing the need for future research to determine if insectivores actively select for these high-yield larval feeders during critical foraging periods.

The environment where larval insects develop contributes to shaping the body composition of the adult (Pechenik 2006). Counter to our initial prediction, insects whose larval and adult stages are exclusively terrestrial had higher body mass than insects whose larval stage is in an aquatic environment, but their adult stage is terrestrial (Fig. 4a). Mechanistically, our initial predictions were related to nutrient acquisition and low-level trophic interactions in aquatic environments; however, environmental variables may be the primary drivers of the differences in body composition between terrestrial and emergent aquatic insects. Insect tracheal systems impose a strict surface-area-to-volume constraint (Harrison et al. 2010). As body size increases, oxygen demand outpaces diffusion capacity, restricting insects' maximum body mass in lower-oxygen aquatic environments (Harrison et al. 2010). Oxygen limitations are compounded by the thermal properties. The high specific heat capacity of aquatic habitats acts as a thermal buffer, creating highly stable developmental conditions that resist extreme temperature fluctuations (Gilbert and Raworth 1996). Conversely, terrestrial environments exhibit much greater thermal variability. Although such variability exposes terrestrial larvae to broader daily extremes, it also allows them to actively exploit warm microclimates to achieve optimal internal temperatures for enhanced digestive efficiency and faster growth (Casey 1976). The combination of aquatic hypoxia and cooler water temperatures restricts aquatic-emergent larvae to slower metabolic rates and a lower maximum body mass compared to terrestrial taxa (Gilbert and Raworth 1996; Harrison et al. 2010), which provides a physiological mechanism for our finding that exclusively terrestrial insects achieved significantly greater overall body mass than aquatic-emergent taxa

Although terrestrial and aquatic-emergent insects had similar proportional lipid content (Fig. 4b), our results may obscure nuanced nutritional differences between insects with different developmental

stages. Because petroleum ether extracts all non-polar fats, our methods could not distinguish between specific classes of essential fatty acids. Crucially, many polyunsaturated fatty acids, such as omega-3 and omega-6, are considered 'essential' because consumers cannot synthesize them *de novo* and must acquire them strictly through their diet (Hulbert and Abbott 2012). Terrestrial insects contain high amounts of omega-6 fatty acids (Zhao et al. 2021). In contrast, aquatic-emergent insects accumulate high concentrations of terrestrially scarce omega-3 polyunsaturated fatty acids by feeding on algae during their larval stage, which are not interchangeable with omega-6 for predators (Hixson et al. 2015; Twining et al. 2019; Scharnweber et al. 2020). Ultimately, the nutritional value of these two prey groups is highly complementary. Terrestrial insects provide the omega-6s critical for initiating immune and inflammatory responses, while emergent aquatic prey supply the terrestrially rare omega-3s necessary to resolve this inflammation and maintain neural and cardiovascular function (Hulbert and Abbott 2012; Twining et al. 2018).

While the biochemical and elemental profiles of insect prey define their potential nutritional value, the foraging landscape of nocturnal aerial insectivores must be evaluated through the constraints of predators. Aerial insectivores face unique biomechanical challenges, as they must capture prey primarily during flight (Norberg 1986). Unlike terrestrial carnivores, which can anchor, manipulate, and sequentially process disproportionately large prey (Vézina 1985), many aerial predators are constrained by the necessity of subduing prey in mid-air or quickly returning to a perch to complete consumption, limiting the time available for complex prey manipulation (Norberg 1986). Aerial predators are highly gape-limited and sensitive to aerodynamic handling costs due to the strict morphological limitations imposed by these foraging behaviours (Barclay and Brigham 1991). Consequently, while certain taxa may offer above-average nutritional payloads, their actual profitability is strictly bound by their physical size. If a large, lipid-dense moth exceeds the handling capacity or gape width of a foraging bat or bird, the energetic cost of processing it in flight renders its nutritional value ecologically inaccessible. Therefore, when evaluating dietary quality within aerial food webs, prey value must be defined not only by maximum nutrient density, but by morphological accessibility.

While the accumulation of lipid reserves is a physiological necessity for maximizing reproductive output in larval feeding insect taxa, this life-history strategy carries an ecological cost. In the context of optimal foraging theory, lipid-dense adult insects that are within an optimal size range for on-the-wing consumption offer significant energetic returns, though their realized value to a predator is mediated by anti-predatory traits. To mitigate the intense selective pressure exerted by aerial insectivores on aerial prey, many prey have evolved divergent defensive strategies (Sugiura 2020). For many nocturnal insects, including some families of moths, survival relies on active evasion (ter Hofstede and Ratcliffe 2016; Sugiura 2020). Many insects have evolved tympanal organs to detect bat echolocation, and some species of moths possess additional sound-producing structures to jam these signals (Fenton and Fullard 1979; ter Hofstede and Ratcliffe 2016). Such an auditory advantage allows moths to initiate erratic flight maneuvers or manipulate returning echoes, reducing a predator's capture success despite their high nutritional reward (Nakano and Mason 2018). Conversely, taxa such as mayflies and true flies that lack the aerodynamic agility or auditory adaptations for active evasion often rely on phenological

defenses. By condensing their adult reproductive phase into highly synchronized emergence events, mayflies typically employ a predator satiation defence, sometimes referred to as predator swamping (Sweeney and Vannote 1982; Ims 1990), which decreases the per capita risk of being predated (Lima and Dill 1990). From the perspective of prey, overwhelming the aerial landscape and swamping predators will ensure that, although predators are likely to feed to maximum capacity, a sufficient proportion of the breeding prey population will survive to successfully reproduce.

Phenological defenses dictate that some prey have limited temporal availability. As a result, another dimension of the nutritional landscape becomes important: functional redundancy (Rosenfeld 2002). Although capturing the fine-scale, short-term turnover of specific insect assemblages remains logistically challenging in field sampling taxonomic shifts do not necessarily equate to shifts in actual dietary availability. Instead, diverse insect taxa may act as functionally redundant nutrient sources. Consequently, as individual species or families rapidly cycle through emergence and decline, the broader landscape may maintain a relatively stable, continuous pool of nutritionally equivalent prey (McCann et al. 1998). For example, within our pool of sampled insects, families Geometridae (moths) and Limnephilidae (caddisflies) represent divergent evolutionary lineages and life histories, yet they act as functionally equivalent prey items; both families offer highly comparable mean body masses (0.019 g and 0.017 g, respectively) and relative lipid proportions (5.75% and 5.04%, respectively). For an aerial insectivore, the specific taxonomic identity of a captured insect is likely secondary to its functional capacity to deliver a required lipid payload (Machovsky-Capuska et al. 2016). However, individual prey quality represents only one dimension of this dynamic foodscape. To fully resolve the true availability of these functionally redundant resources, it is necessary to integrate complementary data on absolute prey abundance and spatial density, ensuring nutritional targets are encountered frequently enough to offset foraging costs (Stephens and Krebs 1986).

Furthermore, the morphological constraints of handling time frequently drive selective consumption behaviours. To maximize profitability, many aerial insectivores systematically remove low-value indigestible appendages (e.g. wings or legs), either during flight or during night roosting bouts (O'Shea and Vaughan 1977; Barclay et al. 1991; Hickey et al. 1996). It is important to note that our nutritional analyses were conducted on intact, whole-body specimens, which inherently include the mass of these indigestible structures. Consequently, for taxa characterized by substantial wing areas or heavy exoskeletons, the selective removal of these parts by a predator would drastically inflate the proportional lipid content of the ingested portion, fundamentally altering the insect's effective value as prey and possibly bypassing gape-limiting constraints. While our whole-body metrics provide a baseline for community-level lipid availability, future studies quantifying the specific nutritional profiles of culled prey would offer a highly valuable complementary perspective, further refining our understanding of the realized energetic yield extracted by aerial predators.

Conclusion

Nocturnal insects are an important prey group for numerous vertebrate predators, many of which, alongside insectivores, are experiencing severe global declines (Nebel et al. 2010; Didham et al. 2020; Adams et al. 2024). The constraints surrounding aerial foraging necessitate a finer-scale view of the profitability of different prey taxa beyond simple metrics of abundance or net biomass. Our findings indicate that distinct insect groups provide complementary energetic and nutritional profiles, serving as diverse resource pools for insectivorous predators. Within the context of aerial predators, we consider the unique foraging constraints, hunting trade-offs, and the counterstrategies of their prey. Ultimately, by estimating the drivers of prey value, we provide a nuanced view of the nocturnal prey landscape and suggest that results from studies focused on the foraging behaviour, prey selection, and nutritional ecology of nocturnal aerial predators are context dependent.

Declarations

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Conflicts of Interest

The authors declare there are no conflicts of interest.

Ethics Approval

Ethics approval was not required for this study according to local legislation, as the research focused exclusively on invertebrate subjects, which are exempt from institutional animal care committee review.

Consent to Participate

Not applicable

Consent for Publication

All authors are aware of this submission and consent to its publication.

Highlighted Student Paper Justification

Linking insect life-history to nutritional profiles provides a framework for assessing prey profitability beyond abundance. Foundational to my bat PhD, it broadly aids modeling predator conservation.

Author's Contributions

AEC and QMRW formulated the idea, and AEC, QMRW, LPM, and ADY developed the methodology. AEC and GBK conducted the fieldwork. AEC, ADY, and GBK identified and classified specimens. AEC and LPM performed the laboratory methodology. AEC analyzed the data and wrote the manuscript; QMRW, LPM, ADY, and GBK provided editorial feedback. QMRW provided funding for the study

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Availability of Data and Material

Data will be made available upon reasonable request after the acceptance of manuscript.

Code Availability

Code will be made available upon acceptance of manuscript.

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Figures

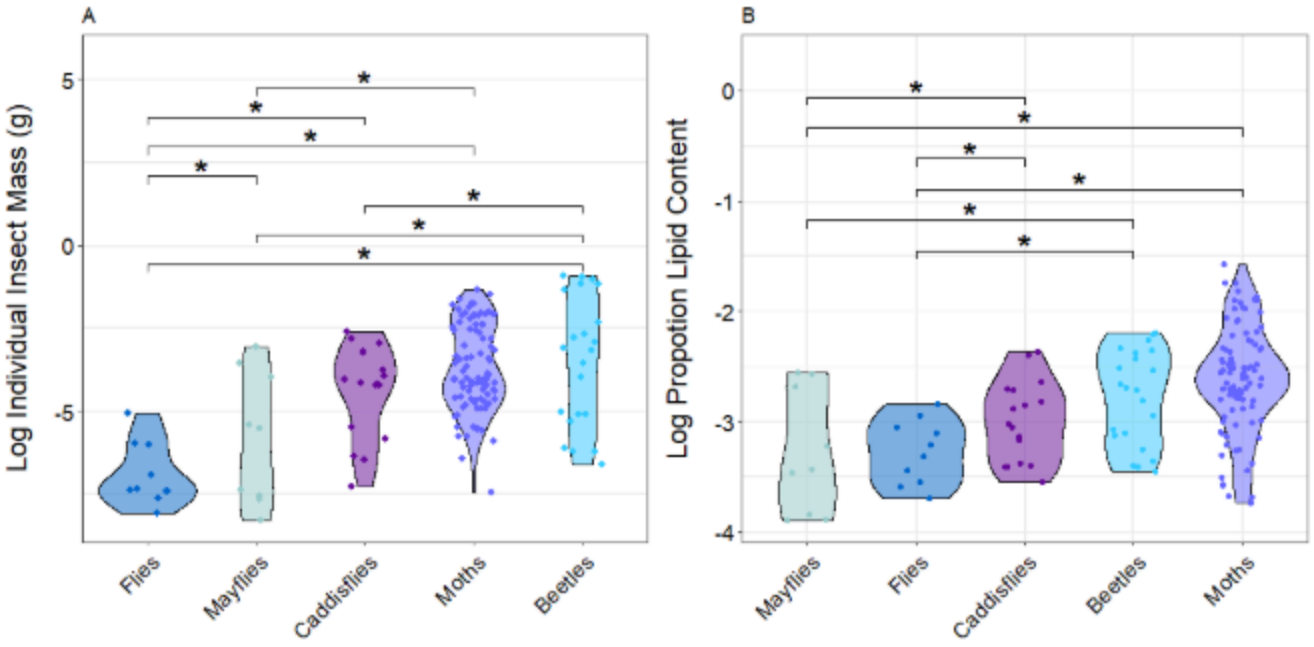

Figure 2

Taxonomic pairwise comparisons of (A) insect natural log body mass (g) and (B) natural log proportional lipid content. Comparisons are shown in rank order between five taxonomic orders: beetle (n =22), fly (n = 10), mayfly (n = 9), moth (n = 95), and caddisfly (n = 17). Brackets with stars indicate significant pairwise differences.

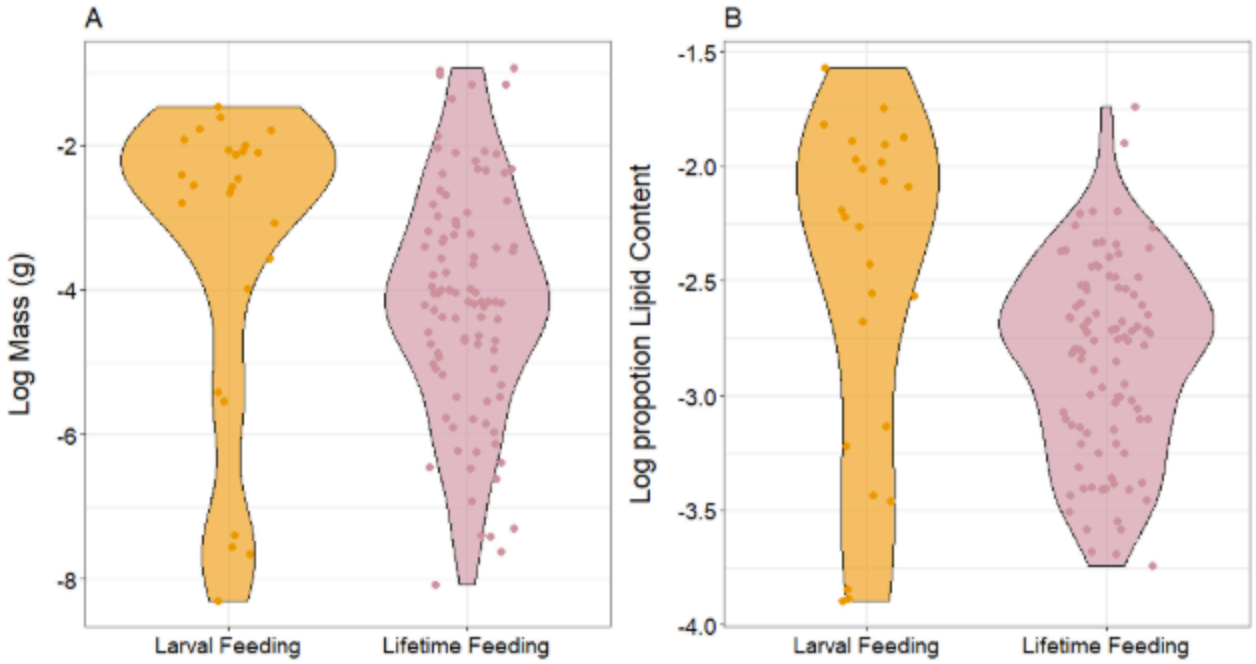

Figure 3

Comparisons of insect body mass and proportional lipid content across feeding strategies. Distributions of (A) natural log-transformed body mass (g) and (B) natural log-transformed proportional lipid content for larval feeders (n = 25) and lifetime feeders (n = 96). Insects that feed exclusively as larvae exhibited significantly higher overall body mass and proportional lipid content compared to lifetime feeders.

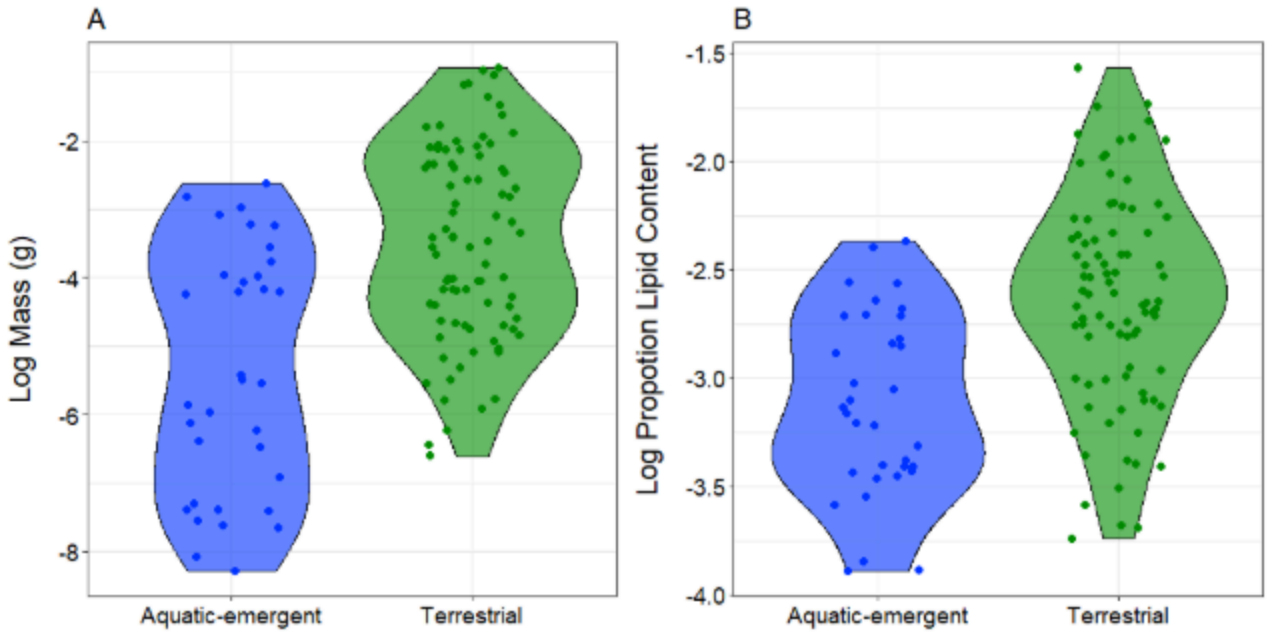

Figure 4

Comparisons of insect body mass and proportional lipid content across larval habitats. Distributions of (A) natural log-transformed body mass (g) and (B) natural log-transformed proportion lipid content for aquatic-emergent taxa (n = 34) and terrestrial (n = 87). Insects with terrestrial larvae had significantly higher body mass, whereas habitat type did not influence proportion lipid content.

Supplementary Files

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