

Diet of two insectivorous bats, *Myotis lucifugus* and *Myotis keenii*, in relation to arthropod abundance in a temperate Pacific Northwest rainforest environment

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Abstract: We assessed the diet of two morphologically similar bats (*Myotis lucifugus* (LeConte, 1831) and *Myotis keenii* (Merriam, 1895)), which both used hydrothermally heated nursery roosts at Gandll K'in Gwaayaay (Hotspring Island), Haida Gwaii (Queen Charlotte Islands), British Columbia, in 1998 and 1999. Our purpose was to determine if they fed opportunistically or actively selected prey, and whether they partitioned prey resources. We determined diet by analyzing feces collected from captured bats and compared it with the relative abundance of insects captured in light traps. *Myotis lucifugus* fed mainly on lepidopterans, medium-sized to large dipterans, neuropterans, and hymenopterans, while *M. keenii* fed on lepidopterans, arachnids, medium-sized to large dipterans, and neuropterans. We found that both species were selecting prey, although selection may have been more a function of prey size than particular taxa. Arachnids occurred in feces of both species, implying that both were capable of gleaning prey from surfaces, although only *M. keenii* regularly fed on spiders. We concluded from the preponderance of flying insects in the diet of *M. lucifugus* that it was primarily aerial hawking prey, while we took the frequent occurrence of both flying insects and spiders in the diet of *M. keenii* to indicate that it was both aerial hawking and gleaning prey. Weather conditions between years affected relative abundance of insects and bat diet, with species diversity being lower in light-trap samples and diet of *M. lucifugus* in 1999, which was cooler and wetter than in 1998. Species diversity in the diet of *M. keenii* was higher in 1999. Similarities in diet indicated that some interspecific competition was occurring, although this competition was likely minimized by their different foraging strategies.

Résumé : Nous avons analysé le régime alimentaire de deux chauves-souris morphologiquement semblables (*Myotis lucifugus* (LeConte, 1831) et *Myotis keenii* (Merriam, 1895)), qui utilisent toutes deux des perchoirs de nourricerie chauffées par hydrothermie à Gandll K'in Gwaayaay (Île Hotsprings), Haida Gwaii (îles de la Reine-Charlotte), Colombie-Britannique, en 1998 et 1999. Notre objectif était de déterminer si les chauves-souris se nourrissent de façon opportuniste ou sélectionnent leurs proies, de même si elles font une partition des ressources qui leur servent de proies. Nous avons précisé les régimes alimentaire par l'analyse des fèces recueillies chez des chauves-souris capturées et les avons comparés à l'abondance relative des insectes récoltés dans des pièges lumineux. *Myotis lucifugus* se nourrit surtout de lépidoptères, de diptères moyens à grands, de neuroptères et d'hyménoptères, alors que *M. keenii* mange des lépidoptères, des arachnides, des diptères moyens à grands et des neuroptères. Les deux espèces font une sélection des proies, bien que la sélection puisse être plus fonction de la taille des proies que des taxons particuliers. Des arachnides se retrouvent dans les fèces des deux espèces, ce qui indique que toutes deux sont capables de glaner des proies sur des surfaces; cependant, seul *M. keenii* se nourrit régulièrement d'araignées. À cause de la prépondérance d'insectes aériens dans le régime de *M. lucifugus*, nous concluons que l'espèce chasse ses proies surtout en vol; par ailleurs, la présence fréquente à la fois d'insectes aériens et d'araignées dans le régime de *M. keenii* nous amène à penser que l'espèce attrape ses proies autant par chasse aérienne que par écumage des surfaces. Les conditions météorologiques différentes entre les années affectent l'abondance relative des insectes et les régimes alimentaires des chauves-souris; la diversité spécifique est plus faible dans les échantillons aux pièges lumineux et dans le régime de *M. lucifugus* en 1999, une année plus fraîche et plus humide que 1998. En 1999, la diversité spécifique du régime de *M. keenii* est plus élevée. La similarité des régimes alimentaires indique qu'il y a de la compétition interspécifique, bien que cette compétition soit vraisemblablement minimisée par les différences de stratégies de recherche de nourriture.

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Introduction

The ability of animals to forage successfully is influenced by prey abundance and availability. For insect-eating bats, prey abundance (frequency and distribution in the environment) can vary between seasons, years, and habitats for reasons that include weather, prey availability, rearing habitat, life history, and population cycles. Unusually cool temperatures or dry conditions often delay reproduction in some insect groups (Flannagan and Cobb 1991; Perry et al. 1987). Cool, rainy weather deters many insects from flying (Taylor 1963; Johnson 1969), while wind can also limit flight behaviour: some insects cease flying altogether, while others congregate in areas sheltered from the wind (Verboom and Spoelstra 1999).

Even when insects are abundant, however, they may not necessarily be “available” to bats (i.e., detectable and could be caught by bats). Many insects are diurnal and do not fly during the night when bats are active. Others occupy habitats that are too cluttered for bats to fly in. Some insects, with moths being the best known, have evolved ears that enable them to detect bat echolocation calls and avoid capture (Fullard 1987; Faure et al. 1993). Small insects, on the order of 4 mm long or less, are not commonly eaten, possibly because they are not readily detected by bat echolocation (Anthony and Kunz 1977, although see Rydell et al. 2002). Furthermore, not all bats can perform the rapid aerial maneuvers necessary to capture small insects detected at short range (Barclay 1985; Brigham et al. 1997; Sleep and Brigham 2003).

Several studies have assessed whether insectivorous bats feed opportunistically on prey they encounter or actively select certain items (Belwood and Fenton 1976; Anthony and Kunz 1977; Belwood and Fullard 1984; Barclay 1985; Swift et al. 1985). To forage optimally and maximize energy intake, they may feed opportunistically on whatever prey they encounter unless a concentration of a particular species is encountered. The approach usually taken in “prey selection” studies has been to compare a measure of prey available (expected distribution) to what was actually eaten (observed distribution). The conclusions of these studies have varied between active selection (Black 1974; Buchler 1976; Anthony and Kunz 1977; Belwood and Fullard 1984; Brigham 1990) and opportunistic foraging (Belwood and Fenton 1976; Barclay 1985; Swift et al. 1985; Rydell 1986; Saunders 1989).

We studied a nursery colony of little brown bats (*Myotis lucifugus* (LeConte, 1831)) and Keen’s myotis (*Myotis keenii* (Merriam, 1895)), which both occupied geothermally heated roosts at Gandll K’ in Gwaayaay (Hotsprings Island), Haida Gwaii (Queen Charlotte Islands), British Columbia, Canada. Our sampling was carried out in 1998, an El Niño year that brought unusually warm, dry conditions, and in 1999, a La Niña year that produced atypically cool, wet conditions (Burles 2001). These weather patterns afforded us the opportunity to compare bat diets and prey availability in two contrasting years. We compared diets of each species assessed by analyzing feces from captured individuals with the relative abundance of insects in light-trap samples to determine whether bats foraged selectively or opportunistically. We predicted that with prey size taken into account,

M. lucifugus, a species thought to forage primarily on flying insects (Belwood and Fenton 1976; Anthony and Kunz 1977; Fenton and Bell 1979; Barclay 1991), would prey opportunistically on the insects available. In contrast, we predicted that *M. keenii*, a long-eared bat potentially able to glean prey, would be more selective in the prey eaten. We expected that the predicted differences in foraging strategy would result in resources being partitioned.

Study species

Myotis lucifugus is a common and widely distributed North American species weighing 5–11 g, with medium-length ears. It is described as a relatively fast flyer that captures flying prey in open areas, especially over water (Saunders and Barclay 1992; Fenton and Bogdanowicz 2002). *Myotis keenii* on the other hand has one of the most restricted distributions of any North American bat. First collected near Massett, Haida Gwaii (Merriam 1895), it has subsequently been found only in coastal regions of British Columbia, Washington, and southeastern Alaska (Parker and Cook 1996; COSEWIC 2003). Adults weigh 4–6 g and have relatively longer ears than *M. lucifugus*. Fenton and Bogdanowicz (2002) predicted, based on external morphology, that *M. keenii* likely captures both flying prey in the air and by gleaning prey from surfaces. Its’ similarity to long-eared myotis (*Myotis evotis* (H. Allen, 1864)) and northern long-eared bats (*Myotis septentrionalis* (Trouessart, 1897)) (van Zyll de Jong 1979; van Zyll de Jong and Nagsorsen 1994), both of which have been shown to glean prey in laboratory conditions (Faure and Barclay 1992; Faure et al. 1993), provides further support that it likely gleans prey. The nursery colony we studied is one of only two known for *M. keenii*.

Materials and methods

Study area

Our study focused on the nursery colony of *M. lucifugus* and *M. keenii* located on 15 ha Gandll K’ in Gwaayaay (GKG), and on 4557 ha Ramsay Island located in the southeastern portion of Haida Gwaii. Both are situated within the Coastal Western Hemlock Wet Hypermaritime Biogeoclimatic Zone (Pojar et al. 1987), which is dominated by mature forests of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and western red cedar (*Thuja plicata* Donn ex D. Don). The maternity colonies are located in a rock outcrop on GKG from which hot water (~35–40 °C) percolates (Firman et al. 1993).

Haida Gwaii is dominated by an onshore air flow that generates a relatively mild, humid climate year-round (Williams 1968). Summers are typically cool (maximum air temperatures generally <22 °C) and rainfall is moderate (e.g., 55–60 mm per month).

We caught bats in 2.6 m high × 6–12 m long nylon mist nets (Avinet[®], Inc., Dryden, New York) set across flight paths of bats emerging from the GKG nursery colony, or in adjacent forest areas. Nets were set with the bottom shelf 0.5–1.5 m aboveground to capture low-flying *M. keenii*. We also deployed a 1.8 m × 2.0 m harp trap (Tuttle 1974) along trails on GKG in 1999.

Captured bats were held in a cotton bag for ~1 h to col-

lect fecal pellets before being released at the site of capture. Bats were classified by gender and we took standard wing, ear, and mass measurements. We determined relative wing shape between the two species by comparing forearm length and a ratio of the length of metacarpal bones of the third (MC 3) and fifth (MC 5) digits, and compared ear size using ratios of pinna:forearm and tragus:forearm to standardize differences in body size, as per Fenton (1972). Measurements for males and females were analyzed separately, owing to sexual dimorphism found in both species. Age was assessed as either adult or juvenile (young of the current year) based on the degree of ossification of the finger joints and pelage colour (Anthony 1988). Female reproductive state was assessed by gentle palpation of the abdomen and examination of the nipples.

We deployed four Luminoc light traps (Comlab Division, Québec, Quebec) on a regular basis during both summers to sample insects. The traps we used consisted of a small battery powered light tube, each with a different wavelength (white, green, blue, and ultraviolet), located in the centre of clear baffles situated above a collection container. We put a 1 g piece of Vapona No-Pest Strip® (Fisons Horticulture Inc., Mississauga, Ontario) into the collection container to kill the insects collected. Traps were set to automatically turn on at dusk (at light levels of ~400 lx) and turn off 5 h later.

We deployed 2–4 light traps on GKG at locations where bats were detected foraging (automated bat detectors were periodically used near insect sampling sites to confirm that bats foraged in these areas). Four traps were deployed on Ramsay Island in both years because we regularly tracked radio-tagged *M. lucifugus*, which roosted on GKG, to foraging areas over Ramsay Island. Traps were set ~2 m above-ground, 100–400 m inland, and 200–500 m apart. They were operated for up to 10 consecutive nights during the early or latter part of each month. Traps were emptied as early each morning as possible to minimize contamination by diurnal insects. Captured insects were identified to family following McAlpine (1981–1989), Holloway et al. (1987), and Borror et al. (1989). We measured body length of all Diptera and classified them by size (small < 4 mm, medium-sized = 4–8 mm, large > 8 mm).

The feces we collected were stored in 95% ethanol until analysis, which involved carefully teasing apart pellets under a 6× to 50× dissecting scope. Invertebrate remains were identified to order, and where possible to family, using a number of keys (Holloway et al. 1987; Whitaker 1988; McAney et al. 1991; Borror et al. 1989) and by comparing parts to whole specimens. We ascertained the minimum number of prey in each pellet based on the number of legs, etc., present. The importance of each order relative to the total number of individual prey items was estimated following Whitaker (1988). The proportion of fecal pellets that contained a particular prey item was also calculated to assess the relative importance of various orders in the diet. We did not estimate the relative volume of each order in samples because there was a high proportion of unidentifiable material.

We used SPSS version 7.5 (SPSS Inc., Chicago, Illinois) and Microsoft Excel 2000 to conduct all statistical tests. Spearman's rank correlations (r_s) were used to compare ra-

tios of invertebrates caught in light traps on GKG and Ramsay Island. Chi-square analyses of contingency tables were used to assess the relationship between the diets of *M. lucifugus* and *M. keenii* and the relative abundance of insect orders in light traps. We did not include Araneae in these comparisons because light traps do not effectively sample these arthropods. Independent *t* tests were used to compare forearm lengths and the ratios of pinna:forearm, tragus:forearm, and MC 3 : MC 5 measurements between species. Levene's test of equality of variances was used to assess whether variances were equal. All tests for significance were two-tailed and employed an α value of 0.05.

Results

Analysis of physical measurements of bats captured in this study revealed that the pinna of *M. keenii* was significantly longer ($t = 25.1$, $df = 106$, $P < 0.001$) than those of *M. lucifugus* (Table 1), a difference that was even more significant when corrected for body size as per Fenton (1972). Tragus length was significantly longer in female *M. keenii* ($t = 21.4$, $df = 53$, $P < 0.001$), but not males ($t = 3.3$, $df = 2.11$, $P = 0.073$), likely because we only caught three male *M. keenii*. Forearm length was longer and MC 3 : MC 5 ratio was higher in *M. lucifugus* (Table 1), indicating that they had longer, narrower wings than *M. keenii*.

Insect abundance

Overall capture rate of insects in light traps were similar on both islands during 1999. In 1998, the capture rate on Ramsay Island was lower. This was because fewer small dipterans were caught, likely owing to the relatively warm, dry spring in 1998. We collected insects from 8 orders and 46 families in 1998, compared with 5 orders and 29 families in 1999. There was greater richness in the samples from Ramsay Island than from GKG in both years (8 orders, 38 families vs. 7 orders, 33 families, respectively), consistent with Ramsay being a much larger island with more fresh water. Dipterans were by far the most common insects caught on both islands in both years, making up 86%–96% of trap samples. Small dipterans made up 76%–87% of samples.

Diet

Based on our analysis of fecal pellets, the most common prey of *M. lucifugus* in both years were lepidopterans and dipterans (Table 2). Hymenopterans were consistently eaten in both years, albeit in small numbers. Prey items identified to family were mostly medium-sized and large dipterans (Mycetophilidae, Empididae, Culicidae, Chaoboridae, Tipulidae, and Trichoceridae), medium-sized neuropterans (Hemerobiidae and Chrysopidae), and large trichopterans (family unknown). Only two small dipterans (1 Ceratopogonidae and 1 Phoridae) were recorded.

Lepidopterans were also the most common prey in the diet of *M. keenii* in both years, although spiders (Arachnida: Araneae) were almost as common (Table 3). Spiders made up almost half of prey items identified in *M. keenii* pellets in 1999. Arachnids could not be identified below order, but the sizes of tarsi in feces were indicative of medium-sized spiders (body length 4–8 mm, overall length 8–14 mm) col-

Table 1. Comparison of physical measurements of Keen's myotis (*Myotis keenii*) and little brown bats (*Myotis lucifugus*) captured at Gandll K' in Gwaayaay, Haida Gwaii, during 1999.

	Males		Females	
	<i>M. keenii</i>	<i>M. lucifugus</i>	<i>M. keenii</i>	<i>M. lucifugus</i>
Ear length (mm)	14.8 (3)*	11.1 (17)*	15.5 (25)*	11.2 (30)*
Tragus length (mm)	6.7 (3)	4.4 (17)	7.3 (25)*	4.4 (30)*
Forearm (mm)	35.6 (3)	36.2 (17)	36.5 (25)*	37.2 (30)*
Metacarpal 3 (mm)	31.7 (3)*	33.1 (17)*	33.0 (25)*	34.1 (28)*
Metacarpal 5 (mm)	31.1 (3)	31.3 (17)	31.8 (25)	32.0 (28)
Mass (g)	4.8 (3)	5.6 (17)	4.7 (22)	6.2 (14)
Pinna:forearm ratio	0.42 (3) [†]	0.31 (17) [†]	0.42 (25) [†]	0.30 (30) [†]
Tragus:forearm ratio	0.19 (3)	0.12 (17)	0.20 (25) [†]	0.12 (30) [†]
MC 3 : MC 5 ratio	1.02 (3)	1.06 (17)	1.04 (25)*	1.07 (28)*

Note: Sample sizes are in parentheses.

*Difference is significant ($\alpha = 0.05$).

[†]Difference is significant ($\alpha = 0.01$).

lected on GKG. *Myotis keenii* ate a few larger dipterans, neuropterans, and hymenopterans, but no small dipterans were recorded.

Prey selection vs. availability

We compared prey availability (light-trap data) with the prey eaten (both the relative number of occurrences of a particular order and the relative number of pellets containing a particular order) by both bat species to assess the degree of selection. Radiotelemetry data for *M. lucifugus* confirmed that individuals foraged on both islands. We were unable to determine where *M. keenii* foraged because they are too small to carry radio transmitters. The ratios of orders of arthropods caught in light traps from both islands were similar for both years (Spearman's correlation coefficient; 1998 data: $r_s = 0.846$, $P = 0.004$; 1999 data: $r_s = 0.862$, $P = 0.003$), so we combined the samples for our comparison with diet. We compared diet to the relative abundance of all insects caught in traps, as well as the abundance of only medium-sized and large insects, for each year of the study. The diet of *M. lucifugus* was not significantly correlated with the relative proportions of insects sampled in either year, indicating that it was selecting prey (Table 4). In both years, it fed more frequently on lepidopterans, medium-sized to large dipterans, and hymenopterans than expected, while small dipterans, the most abundant group, and coleopterans were not consumed. Neuropterans were an important prey only in 1998, when they were abundant. All correlations between diet and insect abundance were stronger when small insects were excluded, suggesting that size was an important factor in selection of prey.

Likewise we found no significant correlation between the diet of *M. keenii* and the relative abundance of insects sampled in either year even though we excluded Araneae, which the light traps did not adequately sample (Table 4). We found lepidopterans, neuropterans, and medium-sized to large dipterans appeared in greater proportions than expected in both years. It was not possible to determine if these insects were caught in flight or gleaned from surfaces.

Discussion

At the outset of this study, we postulated that because of its' aerial hawking foraging strategy, *M. lucifugus* would likely forage opportunistically on medium-sized to large flying insects. Our data indicate, however, that it actively selects prey, particularly lepidopterans, medium-sized to large dipterans, neuropterans, and hymenopterans. When small dipterans were removed from the analysis, the correlations between diet and prey abundance become stronger (i.e., prey capture is more opportunistic), although still not statistically significant. The occurrence of small dipterans in its' diet in 1999 provides evidence that *M. lucifugus* can capture small prey but may only do so when it has less choice.

We also postulated that because of its potential capability to glean, *M. keenii* would select prey, a prediction that our data supports. The high frequency of occurrence of spiders in the diet and the absence of other nonflying prey suggests that it was actively selecting for spiders. Lepidopterans and medium-sized to large dipterans also made up more of the diet than expected in both years. As with *M. lucifugus*, correlations were stronger when small dipterans were removed from the analysis, indicating that selection may be due, in large part, to prey size. Thus, it may be much as Siemers and Güttinger (2006) found for *M. myotis* in that the bats are selecting for larger prey which are more easily detected, rather than for any particular taxa.

Our findings show that both *M. lucifugus* and *M. keenii* feed on lepidopterans, neuropterans, and medium-sized to large dipterans (Tables 2, 3), indicating that some interspecific competition is occurring. This competition is likely minimized to some extent by their different foraging strategies, which allows them to forage in different habitats and thus partition resources. Their different foraging strategies may also influence their ability to cope with years of adverse weather (D.W. Burles et al., submitted for publication),² and the resulting variable reproductive success may be the factor that ultimately preserves the dynamic balance between the two populations.

²D.W. Burles, R.M. Brigham, R.A. Ring, and T.E. Reimchen. Influence of weather on two insectivorous bats in a temperate Pacific rain-forest environment. Submitted for publication.

Table 2. Summary of the diet of little brown bats (*Myotis lucifugus*) and the relative abundance of arthropods in the area where they foraged during 1998 and 1999.

	Diptera											Sample size (N)
	Psocoptera	Hemiptera	Homoptera	Neuroptera	Coleoptera	Small	Other	Trichoptera	Lepidoptera	Hymenoptera	Araneae	
1998												
Percent identified items ^a	0	3	0	16	0	0	28	0	41	9	3	66
Percentage of fecal samples containing order ^b	0	8	0	35	0	0	38	0	100	23	8	26
Percent occurrence in light traps ^c	1	<1	<1	<1	1	76	14	0	6	1	<1	4165
Percent occurrence in light traps (excluding small insects) ^d	4	<1	0	1	4	0	60	0	27	5	<1	923
1999												
Percent identified items ^a	0	0	0	0	0	2	30	6	50	12	0	51
Percentage of fecal samples containing order ^b	0	0	0	0	0	4	32	11	93	21	0	28
Percent occurrence in light traps ^c	0	0	0	0	<1	87	9	<1	4	<1	0	4138
Percent occurrence in light traps (excluding small insects) ^d	0	0	0	0	3	0	64	2	30	2	0	577

^aPercent occurrence of all individuals identified in feces.

^bPercentage of fecal samples in which an individual of that order was found.

^cPercent occurrence of orders when all insects captured were considered.

^dPercent occurrence of orders when only medium-sized and large insects were considered.

Table 3. Summary of the diet of Keen's myotis (*Myotis keenii*) and the relative abundance of arthropods in the area where they foraged during 1998 and 1999.

	Diptera											Sample size (N)
	Psocoptera	Hemiptera	Homoptera	Neuroptera	Coleoptera	Small	Other	Trichoptera	Lepidoptera	Hymenoptera	Araneae	
1998												
Percent identified items ^a	0	5	0	14	0	0	10	0	38	0	33	21
Percentage of fecal samples containing order ^b	0	10	0	30	0	0	20	0	80	0	70	10
Percent occurrence in light traps ^c	1	<1	<1	<1	1	76	14	0	6	1	<1	4165
Percent occurrence in light traps (excluding small insects) ^d	4	<1	0	1	4	0	60	0	27	5	<1	923
1999												
Percent identified items ^a	3	0	0	3	0	0	9	0	34	3	47	32
Percentage of fecal samples containing order ^b	8	0	0	8	0	0	23	0	85	8	85	13
Percent occurrence in light traps ^c	0	0	0	0	<1	87	9	<1	4	<1	0	4138
Percent occurrence in light traps (excluding small insects) ^d	0	0	0	0	3	0	64	2	30	2	0	577

^aPercent occurrence of all individuals identified in feces.^bPercentage of fecal samples in which an individual of that order was found.^cPercent occurrence of orders when all insects captured were considered.^dPercent occurrence of orders when only medium-sized and large insects were considered.

Table 4. Results of χ^2 contingency table analyses between diets of little brown bats (*Myotis lucifugus*) and Keen's myotis (*Myotis keenii*) with relative abundance of arthropods in light-trap samples during 1998 and 1999.

Parameter	<i>Myotis lucifugus</i>		<i>Myotis keenii</i>	
	Relative occurrence in diet	Frequency of occurrence in diet	Relative occurrence in diet	Frequency of occurrence in diet
1998				
Light-trap samples	14 319 (9)	2 972 (9)	10 914 (9)	2 422 (9)
Light-trap samples (excluding microinsects)	1 453 (8)	272 (8)	1 164 (8)	267 (8)
1999				
Light-trap samples	46 759 (9)	15 205 (9)	20 901 (9)	2 994 (9)
Light-trap samples (excluding microinsects)	373 (8)	93 (8)	96 (8)	139 (8)

Note: Critical value = 18.31, $\alpha = 0.05$. The number of insect orders compared, which excludes the Araneae, are in parentheses after the χ^2 values.

Both our diet and morphological data support the finding that *M. lucifugus* in this study uses an aerial hawking foraging strategy, as previously described for this species (Fenton 1972; Barclay 1991; Rydell et al. 2002). The lower diversity of prey in the diet in 1999 (Table 2) we take as another indication that *M. lucifugus* was feeding primarily on flying insects. In that year we observed lower species richness in light-trap samples, likely owing to cooler temperatures that reduced insect flight activity (Burles 2001), which resulted in less prey for an aerial hawking bat. The remains of two spiders in fecal samples collected in 1998 suggests that *M. lucifugus* may also glean prey from vegetation, although we cannot rule out that these spiders were caught at a roost, or in flight in a web, or while the spider was ballooning (i.e., drifting on a breeze while suspended from web material). Gleaning by this species has been reported by Fenton and Bell (1979) and Ratcliffe and Dawson (2003). Exploitation of spiders by *M. lucifugus* has also been recorded (Whitaker and Lawhead 1992; Lee and McCracken 2004; Kellner and Harestad 2005), suggesting that gleaning by this species is more widespread than previously thought.

We interpret the predominance of spiders in the diet of *M. keenii* to mean that it frequently gleans prey, as has been previously predicted (Fenton and Bogdanowicz 2002); a finding that is also supported by our morphological data. The greater diversity in diet in 1999 (Table 3) also implies an ability to glean; although insects were flying less frequently owing to the cooler temperatures, they were still available to bats that could glean. It is possible that *M. keenii* caught some of these spiders in day roosts, but if this were the case, we would have expected *M. lucifugus*, which occupies the same roosts, to exploit this food source as well. We also found no evidence that spiders were being taken by aerial hawking, as no web material was ever found on captured bats or in their feces, and ballooning spiders were rarely observed. If spiders were commonly caught in flight, we would have expected both bats to regularly feed on them. The prevalence of flying insects in the diet of *M. keenii* indicates that it probably also captures prey by aerial hawking, much as Fenton and Bogdanowicz (2002) had predicted, although we cannot rule out that these too were gleaned from vegetation. The ability of *M. keenii* to both glean and aerial hawk prey is not unexpected, given its' morphological similarity to *M. evotis*, a bat that is known to forage using both strategies (Faure and Barclay 1994).

Few "insectivorous" bats commonly eat spiders even though these arthropods are abundant in coastal rainforests, and exploited by few other predators (N. Winchester, personal communication (1999)). Those bats that do eat spiders typically glean them from surfaces (Whitaker et al. 1977, 1981; Warner 1985; Swift 1998; Whitaker 2004), either in rainforests (Whitaker et al. 1977; Schulz 2000; Kellner and Harestad 2005) or other locations where conditions make foraging opportunities limited (Whitaker and Lawhead 1992). Only the golden-tipped bat (*Kerivoula papuensis* (Dobson, 1878)) has previously been reported to specialize on spiders. It is similar to *M. keenii* in having relatively low wing loading, and slow, fluttery flight, and it occurs only in rainforest environments (Schulz and Wainer 1997; Schulz 2000). It is noteworthy that five of six species of *Myotis* occurring in the wet, western part of Oregon feed on spiders, while only two of their counterparts do in the dry, eastern part of the state (Whitaker et al. 1977, 1981). Similarly, on Vancouver Island, four of five *Myotis* species, including *M. lucifugus*, feed on spiders (Kellner and Harestad 2005). In both of the Oregon studies, *M. lucifugus* did not eat spiders, while *M. evotis*, which is morphologically very similar to *M. keenii* (van Zyll de Jong and Nagorsen 1994), feeds on spiders at both locations. These authors did not identify whether this was due to spiders being more abundant in western Oregon, or whether the bats were exploiting this food resource in otherwise unfavourable habitat. In central Alaska, Whitaker and Lawhead (1992) reported the occurrence of spiders in the diet of *M. lucifugus*. Whitaker (2004) speculated that this was because 24 h daylight during summer forced bats to forage by gleaning in the forest to avoid avian predators.

The importance of spiders in the diet of *M. keenii* highlights a problem inherent in sampling arthropods to assess prey abundance that has been referred to in a number of studies, i.e., there is a difference between prey abundance and what is actually available to the predator (Buchler 1976; Faure and Barclay 1992; Whitaker 1994; Siemers and Güttinger 2006). The light traps we used were designed to sample flying insects, not terrestrial arthropods, so there was a separate nonflying prey base available to *M. keenii* that our light traps did not sample.

On Haida Gwaii, where rain and cool temperatures are frequent, it is adaptive for bats to be able to glean prey and to forage under the protective canopy of the forest. The rare occurrence of spiders in the diet of *M. lucifugus* reflects the

occasional use of gleaning as a foraging strategy, but evidence of low reproductive success in cool, rainy years suggests that individuals often forego reproduction (Burles 2001; D.W. Burles et al., submitted for publication²). The higher reproductive success in *M. keenii*, even in cool, rainy years (Burles 2001; D.W. Burles et al., submitted for publication²), imply that its' foraging strategy makes it well adapted to the cool, wet coastal environment of the Pacific Northwest.

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