Influence of weather on two insectivorous bats in a temperate Pacific Northwest rainforest

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Abstract: Adverse weather conditions frequently have a significant negative influence on survival and reproductive success of insectivorous bats. Low ambient temperatures increase the energetic costs of maintaining euthermia and reduces insect activity, while precipitation likely adds "clutter" making prey more difficult to detect using echolocation. We studied two species of insectivorous bats, *Myotis lucifugus* (LeConte, 1831) and *Myotis keenii* (Merriam, 1895), in the Pacific Northwest of Canada, a region that experiences frequent cool, wet weather during spring and summer. Our study took place during the El Niño – La Niña cycle of 1998–1999, which resulted in contrasting years. The summer of 1998 was unusually warm and dry, while the summer of 1999 was unusually cool and wet. We predicted that both species would be adversely affected by the cool, wet conditions of 1999, resulting in prolonged gestation, late fledging of young, and lower reproductive success. However, this was not the case. *Myotis lucifugus* did experience delays in reproductive timing and lower reproductive success in 1999, as predicted, whereas *M. keenii* experienced much shorter gestations, earlier fledgings, and no difference in reproductive success between years. We hypothesize that the ability of *M. keenii* to glean prey enables it to better cope with cool, wet conditions.

Résumé : Les conditions météorologiques défavorables ont souvent un effet négatif significatif sur la survie et le succès de la reproduction chez les chauves-souris insectivores. Les températures ambiantes basses augmentent le coût énergétique du maintien de l'euthermie et réduisent l'activité des insectes, alors que les précipitations produisent des échos parasites qui rendent la détection des proies par écholocation plus difficile. Nous avons étudié deux espèces de chauves-souris insectivores, *Myotis lucifugus* (LeConte, 1831) et *Myotis keenii* (Merriam, 1895), dans la région pacifique du nord-ouest canadien, une région qui connaît fréquemment des conditions fraîches et humides au printemps et en été. Notre étude s'est déroulée durant le cycle El Niño – La Niña de 1998–1999, ce qui a produit deux années bien différentes. L'été 1998 a été exceptionnellement chaud et sec, et celui de 1999 particulièrement frais et humide. Nous avions prédit que les deux espèces seraient affectées négativement par les conditions fraîches et humides de 1999, ce qui se manifesterait par une gestation prolongée, un envol tardif des jeunes et un succès réduit de la reproduction. Ce ne fut cependant pas le cas. *Myotis lucifugus* a connu, comme prédit, des délais dans le calendrier de sa reproduction et un succès reproductif plus bas en 1999, alors que, chez *M. keenii*, la gestation fut beaucoup plus courte, l'envol précoce et le succès reproductif semblable à l'année précédente. Nous émettons l'hypothèse qui veut que la capacité que possède *M. keenii* de glaner des proies sur les surfaces lui permet de mieux s'accommoder des conditions fraîches et humides.

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Introduction

Variability in weather conditions has long been known to influence survival and reproductive success in animals (Michener 1973; Racey 1981; Burles and Hoefs 1984; Neuhaus et al. 1999; Stokes et al. 2001). Insectivorous bats that occur in temperate regions are particularly vulnerable to weather variation because of their relatively small body size and dependence on ectothermic prey whose activity is influenced by weather (Humphrey et al. 1977; Anthony et al.

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1981; Grindal et al. 1992; Lewis 1993; Hoying and Kunz 1998). For example, low ambient temperatures (T_a) increase the energetic cost of maintaining euthermia. Low T_a, particularly below 10 °C, also reduces activity by flying insects (Anthony et al. 1981), leading to a reduction in available prey for aerially feeding bats (Racey and Swift 1981; Racey and Speakman 1987; Racey et al. 1987; Hickey and Fenton 1996). Prolonged periods of low T_a can delay insect development (Taylor 1963; Nebeker 1971; Flannagan and Cobb 1991), thus making them unavailable to bats during early summer when reproduction leads to the highest energy requirements. Temperature, through its effects on insects, has been proposed to limit the distribution of reproductive bats to lower elevations in mountainous regions (Barclay 1991; Cryan et al. 2000).

Precipitation can influence bat activity and survival directly by wetting a bat's fur, thus reducing its insulating value (Tuttle and Stevenson 1982), and by interfering with the ability to echolocate, thus the ability to detect prey (Griffin 1971; Grindal et al. 1992). Precipitation also deters many insects from flying, making them unavailable to most bats (Anthony et al. 1981).

In many temperate regions bats use torpor to conserve energy to survive periods when foraging is not beneficial, typically as a result of adverse weather (Kurta 1991). For males who have few energetic demands other than survival and mating, torpor is an effective way to overcome adverse conditions (Rambaldini and Brigham 2008). Frequent use of torpor though may delay spermatogenesis, which could interfere with autumn breeding activities (Kurta 1991). For reproductive females, use of torpor is an effective means of reducing costs during adverse weather, but it can delay fetal development, and frequent use can prolong gestation (Racey 1973, 1982; McNab 1982). For most bats living at higher latitudes where summers are short, delayed parturition is perceived as a disadvantage, as it may not leave enough time for young to learn to fly and forage, and to accumulate sufficient fat reserves for migration or winter hibernation. Under certain circumstances, however, torpor has been used to advantage as a mechanism to reduce evaporative water loss (Chruszcz and Barclay 2002), or delay parturition until weather conditions improve (Willis et al. 2006).

The perceived disadvantage to using torpor can potentially be overcome by reproductive bats using heated roosts that buffer individuals against inclement conditions. Maternity roosts commonly occur in heated attics, chimneys, or buildings (Nagorsen and Brigham 1993; Kunz and Lumsden 2003), or in solar-heated tree cavities or rock outcrops (Vonhof and Barclay 1996). In instances where bats roost in caves, clustering by large numbers can actually raise roost temperatures (Betts 1997). In a few instances, geothermal activity provides external heat that maintains high roost temperatures (Bell et al. 1986; West and Swain 1999; Burles 2001). A heated roost is not necessarily beneficial when food is limited, however, because it likely reduces the effectiveness of torpor (Zahn 1999) and increases water loss (Racey 1982).

Given the potential constraints of adverse weather conditions, bats in the Pacific Northwest of Canada, where rain is frequent and low temperatures common, may be particularly affected. We studied a nursery colony of little brown bats (*Myotis lucifugus* (LeConte, 1831)) and Keen's myotis (*Myotis keenii* (Merriam, 1895)) occupying geothermally heated roosts at Gandll K'in Gwaayaay (Hotsprings Island), Haida Gwaii (Queen Charlotte Islands), British Columbia, Canada. We predicted that relatively cool, wet conditions would influence parturition dates and reduce overall reproductive success, especially during summers with adverse weather. We further predicted that the hover-gleaning foraging strategy used by *M. keenii* should make it better suited to the conditions of the Pacific Northwest relative to the aerial hawking strategy used by *M. lucifugus*. Weather conditions during the study were influenced by a strong El Niño Southern Oscillation that resulted in unusually warm, dry conditions in 1998, followed by a La Niña event that brought cooler, wetter conditions in 1999 (National Oceanic and Atmospheric Administration 2008). This provided us with an opportunity to assess the reproductive success by these bats during two contrasting years.

Materials and methods

Our study focused on a nursery colony of *M. lucifugus*

and *M. keenii* on 15 ha Gandll K'in Gwaayaay (GKG) located in the southeastern part of Haida Gwaii. GKG and surrounding islands are located in 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 climate of Haida Gwaii is dominated by an onshore air flow generating a relatively mild, humid climate year-round (Williams 1968). Summers are typically cool (maximum T_a generally <22 °C) and rainfall is moderate (approximately 57 mm/month during summer).

We identified roost locations for both species by observing where bats emerged at dusk and by tracking radiotagged individuals. Visual counts of emerging bats were made as they flew from shoreline roosts across a thermal meadow towards the forest to determine the minimum number of bats using the roosts. We used a bat detector (Mini-2; Ultrasound Advice, London, UK) tuned to 40 kHz to assist with bat detections, and recorded all observations to a hand-held tape recorder to minimize time spent not watching for bats. Counts were carried out on two, and occasionally three, consecutive nights on a weekly basis to assess variation owing to weather.

Bats were caught in 2.6 m high × 6–12 m long nylon mist nets (Avinet®, Inc., Dryden, New York) set perpendicular to emergence flight paths near the roosts. The bottom shelf was set 0.5–1.5 m above ground level to capture low-flying *M. keenii*. In 1999, we also deployed a 1.8 m × 2.0 m harp trap (Tuttle 1974) along trails in the nearby forest. Captured bats were classified to species, gender, age, and reproductive status. 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). Reproductive state of females was determined by palpation of the abdomen and examination of the nipples. The mass of all captured bats was determined to the nearest 0.1 g using a 30 g Pesola spring scale. Bats were released at the site of capture. Radio tags (model LB-2; Holohil Systems Ltd., Carp, Ontario) were glued to the interscapular region of selected bats using Skin Bond cement (Smith and Nephew United, Inc., Largo, Florida) after the fur had been trimmed. Roosting activities were then monitored using a portable radio receiver (Suretrack STR 1000, Lotek Engineering Inc., Newmarket, Ontario, or TRX 2000S, Wildlife Materials Inc., Murphysboro, Illinois) and a two-element directional antenna. All protocols were approved by the University of Victoria Animal Care Committee prior to beginning the study.

We deployed 2–8 Luminoc light traps (Comlab Division, Québec, Quebec) on a regular basis in areas where bats were known to forage on GKG and nearby Ramsay Island in both summers to sample insects. Each trap consisted of a small battery-powered light tube 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 trapped insects. Traps were set to automatically turn on at dusk (at light levels of approximately 400 lx) and turn off after 5 h. Captured insects were identified to family follow-

ing Borror et al. (1989), McAlpine (1981–1989), and Holloway et al. (1987).

Weather conditions (cloud cover, wind speed and direction, temperature, and precipitation) were recorded at approximately 2200 each night we were on GKG. Weather data for 1967–1999 were also obtained for Sandspit, British Columbia, which is the nearest weather station, located 75 km north of the study area.

We compared temperatures recorded at 2200 on GKG in 1998 and 1999 with those recorded on the same date and time at Sandspit using paired *t* tests to determine if Sandspit data were representative of conditions on GKG. Paired *t* tests were also used to compare monthly mean minimum and maximum temperatures between years. Monthly levels and frequency of precipitation between years were compared using Wilcoxon's signed rank tests because the data were not parametric. Both parameters were compared with 30-year means for 1967–1997 (1992 data missing). Independent *t* tests were used to make between-year comparisons of mass for each species, with 1st year being the "standard" against which the 2nd year was compared. All tests were two-tailed and conducted using SPSS version 7.5 employing an α value of 0.05.

Results

Emergence counts conducted in 1998 (N = 34) and 1999 (N = 38) indicated that at least 110 and 111 bats, respectively, used the roosts on GKG during June. We found both species roosting in numerous rock crevices and under boulders along about 50 m of the southwestern shore of GKG. Many of the roosts are geothermally heated by water up to 50 °C that percolates through them (Firman et al. 1993). Radio-tagged *M. keenii* (N = 3 individuals at 4 different locations) were found roosting either solitarily or in low numbers in narrow (1–2 cm wide) crevices, while *M. lucifugus* (N = 5 individuals at 6 different locations) were roosting communally in larger (2–5 cm wide) crevices and under boulders (Burles 2001). Temperatures measured in one 75 cm deep crevice in which *M. lucifugus* frequently roosted ranged from 32–34 °C (equal to the temperature of the water flowing through the crevice) in the inner reaches to 15–24 °C (equal to T_a) at the outer edge (Burles 2001). On cool, overcast days bats using this crevice could not be seen, apparently because they were deep in the crevice. On warm, sunny afternoons bats were frequently seen clustered near the outer edge, potentially taking advantage of solar heating of the crevice. We measured temperatures of 27–33 °C near these clusters, as well as a drop of about 5 °C when the bats moved away, indicating that clustering accounted for some of the heat generated in the crevice.

The temperatures we recorded at GKG were comparable with those recorded at Sandspit ($t_{[40]}$ = –0.67, P < 0.51 for 1998; $t_{[52]}$ = –1.27, P < 0.51 for 1999), so we used data from the latter for all subsequent comparisons of conditions between years because the data set was more complete. Weather during spring and summer of 1998 was unusually warm and dry, owing to a strong El Niño Southern Oscillation event that developed in late 1997 and early 1998. In contrast the spring and summer of 1999 was cooler and wetter, owing to a La Niña event beginning in late 1998 (Na-

Fig. 1. Mean monthly maximum and minimum temperatures for Sandspit, British Columbia, for 1998 and 1999 compared with the mean for the period 1967–1997 (◆, 1998 temperatures; □, 1999 temperatures;▲, 30-year means; 95% confidence intervals are shown on 30-year means).
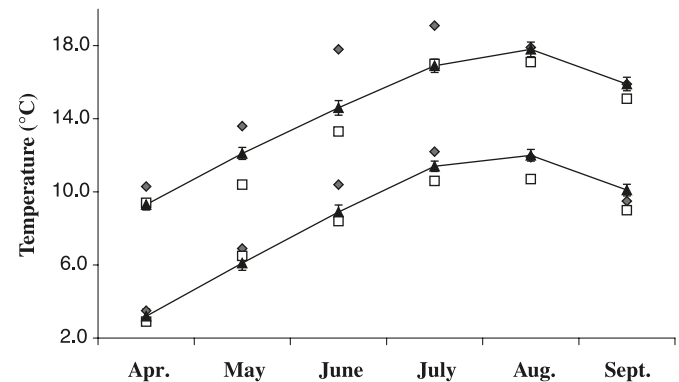
Fig. 2. Monthly precipitation and number of days each month with measurable rain for Sandspit, British Columbia, for 1998 and 1999 compared with the 30-year mean (1967–1997) (◆, 1998 temperatures; □, 1999 temperatures; ▲, 30-year means; 95% confidence intervals are shown on 30-year means).
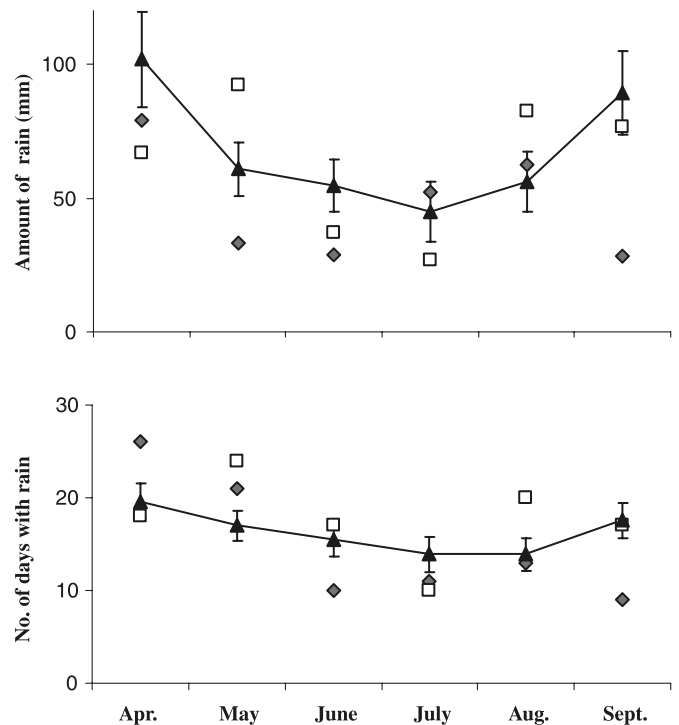
tional Oceanic and Atmospheric Administration 2008). Temperatures in 1998 were higher than 1999 for all months from April through to September (Fig. 1), with mean monthly maxima being significantly greater for April ($t_{[29]}$ = 2.51, P < 0.02), May ($t_{[30]}$ = 6.58, P < 0.01), June ($t_{[29]}$ = 8.35, P < 0.01), and July ($t_{[30]}$ = 2.89, P < 0.01). Differences in minimum temperatures were also significantly higher for June ($t_{[29]}$ = 6.00, P < 0.01), July ($t_{[30]}$ = 3.63, P < 0.01), and August 1998 ($t_{[30]}$ = 2.17, P< 0.04). Minimum T_a of 10 °C or above occurred on 3 nights in May and 19 nights in June 1998, but on only 1 night in May and 5

Fig. 3. Reproductive chronologies of Keen's myotis (*Myotis keenii*) and little brown bats (*Myotis lucifugus*) at G̲andll K'in Gwaayaay, Haida Gwaii, during 1998 and 1999 (F, female; J, juvenile).

	May		June		July		August		September	
Species	15	31	15	30	15	31	15	31	15	30

Myotis keenii
1998 (N=22F): <--?--<------------GESTATION------------------> <----------LACTATION----------> <-FLEDGING ?->

1999 (N=26F + 4J): <--?--<--------GESTATION---------> <-----------LACTATION------------> <--FLEDGING-->

Myotis lucifugus
1998 (N=33F + 4J): <--?--<-------GESTATION-------> <--------LACTATION--------> <---FLEDGING--->

1999 (N=30F + 7J): <--?--<--------------GESTATION----------------> <-----------LACTATION----------> <--FLEDGING-->

nights in June 1999. Temperatures in 1998 were generally above long-term means, while in 1999 they were near or just below (Fig. 1).

We compared monthly levels of precipitation and the number of days each month that received measurable amounts of rain between years and with long-term means (Fig. 2). The spring of 1998 was relatively drier than the spring of 1999, but there were no significant differences between years in either monthly precipitation (Wilcoxon's signed ranks test: $Z = -0.94$, $P > 0.34$) or number of days with rain (Wilcoxon's signed ranks test: $Z = -0.84$, $P > 0.39$). Both years had less precipitation in May, June, and July relative to long-term means.

Mist netting and (or) harp trapping was carried out along emergence corridors within 100 m of the roosts on 28 nights in 1998 and 36 nights in 1999. We caught a total of 56 *M. keenii* and 102 *M. lucifugus*. In both years, only adult females were captured in the vicinity of the roosts before 10 July, but thereafter adult males of both species were occasionally captured. Capture records allowed us to assess reproductive chronology and success (Fig. 3). In 1998, pregnant *M. keenii* were caught as late as 19 July, the same night that the first lactating females were caught. Although 80% (8 of 10) of *M. keenii* captured during July and August were reproductively active, we did not capture any fledged juveniles. For *M. lucifugus*, the last pregnant female was captured on 1 July, while the first lactating female was captured on 10 July, indicating that parturition occurred during late June – early July. The first volant juvenile was captured on 20 July, and we caught 4 in total (2 males, 2 females). Eleven of 15 (73%) female *M. lucifugus* caught during July and August were reproductively active.

In 1999, all *M. keenii* that we captured prior to 5 July were confirmed or likely pregnant. The first lactating female was caught on 12 July, and thereafter all females were either lactating or nonreproductive. Four juveniles (2 males, 2 females) were captured in August. Eighteen of 22 (82%) fe-

Table 1. Summary of masses of bats captured at G̲andll K'in Gwaayaay, Haida Gwaii, by species, age, and sex in 1998 and 1999.

	1998	*N*	1999	*N*
Myotis lucifugus				
Adult females*	6.1	20	6.2	14
Adult males	6.4[†]	9	5.6[†]	17
Juveniles	5.2	4	4.8	7
Myotis keenii				
Adult females*	5.3[†]	17	4.7[†]	22
Adult males	5.5	1	4.8	3
Juveniles	No sample	No sample	4.1	4

*Does not include obviously pregnant females.
[†]Significantly different between years at the $\alpha = 0.01$ level.

male *M. keenii* caught in July and August were reproductively active. In spite of catching 20 female *M. lucifugus* in July, including 3 pregnant females on 20 July, we did not catch a lactating female until 2 August. One small juvenile *M. lucifugus* was seen in a roost on 15 July, however, indicating that at least some pups were born in mid-July. The first volant young was captured on 15 August, and 7 young (6 males, 1 female) were caught in total. Sixty-three percent of female *M. lucifugus* (17 of 27) caught in July and August were reproductively active.

Our capture data also allowed us to compare differences in body mass of bats between years (Table 1). We found that bats captured in 1999 were significantly lighter than those captured in 1998, with the exception of adult female *M. lucifugus*, for which no significant difference was found.

Light traps were operated for a total of 269 and 175 trap-nights between May and August in 1998 and 1999, respectively (Table 2). Dipterans made up the vast majority (86%–96%) of insects caught in all months of both years, most of which had a body length <4 mm (76% in 1998 and 87% in 1999). Lepidopterans were generally the second

Table 2. Summary of total numbers of insects, and numbers of lepidopterans and small dipterans (<4 mm), as well as other dipterans (≥4 mm), captured by month near G̲andll K'in Gwaayaay, Haida Gwaii, during 1998 and 1999.

Year	Month	Mean no. of insects/trap	No. of Lepidoptera	Small Diptera	Other Diptera	Other insects	No. of trap-nights
1998	May	17.3	1.0	14.3	1.8	0.2	39
	June	7.7	0.2	5.8	1.4	0.3	75
	July	15.4	0.8	12.4	1.7	0.5	76
	August	22.1	1.7	16.8	2.6	1.0	79
1999	May	10.7	0.2	9.1	1.3	0.0	40
	June	13.8	0.2	12.5	0.9	0.2	58
	July	34.4	0.7	31.7	1.8	0.1	54
	August	46.8	5.7	31.7	8.6	0.4	23

Table 3. Chi-square analysis of relative frequency of occurrence of insects by order between 1998 and 1999.

Parameter		May	June	July	August	Critical value ($\alpha = 0.05$)
Comparing 1998 and 1999 samples (dipterans split into two categories: small and other)	$\chi^2 =$	2.832	8.103	31.898	65.206	15.5
	$N =$	9	9	9	9	
Comparing 1998 and 1999 samples (excluding small dipterans)	$\chi^2 =$	0.917	0.657	2.007	51.991	14.1
	$N =$	8	8	8	8	

most abundant order in samples, while coleopterans, hemipterans, homopterans, trichopterans, psocopterans, hymenopterans and neuropterans made up the remainder of other insects caught. Capture rates generally increased over the course of both summers, with the exception of June 1998, which was likely the result of an unusually warm, dry spring. Comparing insect abundance by order between years (Table 3), we found that the relative abundance of insect orders was not significantly different in May and June, but that the numbers were significantly higher in July and August 1999, largely due to a dramatic increase in the number of small dipterans. When small dipterans were excluded from the analysis, differences were only significant in August (Table 3). Lepidopterans, a favoured prey item for both species in this study (Burles et al. 2008), were less abundant during May 1999, were equally abundant during June and July, and became more abundant in August 1999.

Discussion

Previous studies have demonstrated that weather plays an important role in reproductive timing and success of insectivorous bats. Frequent low temperatures have been singled out as the primary factor causing prolonged gestation and delayed fledging (Humphrey et al. 1977; Anthony et al. 1981; Audet and Fenton 1988; Lewis 1993; Hoying and Kunz 1998), although precipitation has also been implicated (Grindal et al. 1992). In some of these studies, authors suggest that it was not necessarily the direct impact of weather on the bats themselves, but rather the effect weather had on decreasing insect abundance and (or) activity (Anthony et al. 1981; Hoying and Kunz 1998). In cases where food was abundant and available despite low temperatures and (or) high precipitation, reproduction was not delayed (Racey 1973; Syme et al. 2001).

Given these results, we predicted that both species in our study would be more successful during the warm year (1998) than the cooler one (1999). We found that the repro-

ductive success of *M. lucifugus* was consistent with this prediction. The proportion of reproductive females present at the G̲KG roosts was higher in 1998, parturition appeared to be early and synchronous in late June – early July, and volant young were caught by early August. In contrast, during 1999 parturition was less synchronous and extended into late July, with most young not fledging until mid-August. *Myotis lucifugus* thus appeared to have greater reproductive success in the warmer, drier conditions of 1998.

Myotis keenii reacted differently than *M. lucifugus* to the variable weather between years. The proportion of reproductive female *M. keenii* at G̲KG was similar in both years, but gestation extended into late July 1998, and few, if any, young apparently fledged. In contrast, parturition during 1999 occurred during a relatively short period in early July and young were flying by early August. *Myotis keenii* thus appeared to be more successful during the cooler, wetter conditions of 1999.

The conditions experienced in 1999 undoubtedly increased energetic stress on both species by increasing the amount of energy required to maintain euthermia, as was evidenced by the generally lower body masses recorded in 1999 than in 1998. The seemingly ideal conditions of the geothermally heated roosts at G̲KG likely ameliorated some of this stress, but the benefits of heated maternity roosts may be outweighed if food is limiting (Zahn 1999). When food is limiting, warm roosts may reduce the effectiveness of torpor for conserving energy, which would force reproductive females to either seek alternative, cooler roosts, or to abort or resorb developing embryos. The consistent use of the G̲KG roosts and the lower proportion of reproductive *M. lucifugus* captured in 1999 suggest that some females may have been forced to forego reproduction. On the other hand, the proportion of reproductive female *M. keenii* was similar for both years, suggesting that they were less affected by the adverse conditions of 1999.

The cooler, wetter conditions in 1999 likely limited forag-

ing opportunities for both species. We observed few bats emerging on evenings when T_a was below 10 °C, or when it was raining. Presumably it was more beneficial to remain in the roost rather than forage on nights when conditions were poor. Given that minimum temperatures dropped below this threshold on 90% of nights in May and June 1999, there were likely only a few good nights to forage.

Our light-trap data indicate that the adverse weather in 1999 also had an influence on the availability of insects early in the season. While the relative numbers of insects captured during 1999 was not significantly different from 1998 except in August (Table 3), there were fewer insects of all orders present in May 1999. Of particular note, lepidopterans and larger dipterans, favoured prey items for both *M. keenii* and *M. lucifugus* (Burles et al. 2008), were less common in May 1999 and remained so until July. On the other hand, small dipterans, which neither *M. keenii* nor *M. lucifugus* eat, appeared to thrive in 1999, making up the vast majority of insects caught by July and August. We do not know if the insects were actually less abundant or simply spending less time flying, as one limitation of light traps is that they only collect flying insects. The dramatic increase in abundance of lepidopterans and larger dipterans in August suggests that the cool weather may have delayed their metamorphosis into flying adults. Whatever the case, the reduced availability of food in May and June appears to have influenced reproductive success for *M. lucifugus* in 1999.

In spite of the significantly lower body masses suggesting that female *M. keenii* may have been energetically stressed in 1999, their relatively early and synchronous timing of parturition suggests that neither the weather nor the apparent reduction in flying insects limited reproductive success. On the contrary, and counter to our prediction, they appeared to be more successful in 1999 than in 1998. One likely explanation for this lies in the ability of *M. keenii* to glean prey (Burles et al. 2008), a foraging strategy that is more effective than aerial hawking during cool weather (Barclay 1991). We hypothesize that although insects were less active and spent less time flying when ambient temperatures were low, they were likely still available to *M. keenii*. The ability to glean prey also allowed these bats to exploit other sources of prey (i.e., spiders) that aerial hawking bats such as *M. lucifugus* could not (Burles et al. 2008). Although we were not able to directly quantify it, based on wing morphology, the greater manoeuvrability of *M. keenii* likely allowed them to forage under the canopy of the forest, making feeding possible even on rainy nights. *Myotis keenii* appears to be well adapted to the cool, wet conditions experienced in 1999 and to survival in temperate coastal rain forests.

While the weather during the 2 years of the study starkly contrasted with each other, 1998 was the more unusual year. Comparisons with long-term data indicate that the summer of 1998 experienced temperatures well above and precipitation well below 30-year means, whereas in 1999 both temperatures and precipitation were only marginally different than the 30-year means. Given this, conditions on Haida Gwaii may thus be marginal for bats, and their continued survival may largely be due to the geothermally heated roosts and to their longevity, which enables populations to overcome poor breeding seasons.

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