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Water availability and successful lactation by bats as related to climate change in arid regions of western North America

Rick A. Adams* and Mark A. Hayes

School of Biological Sciences, University of Northern Colorado, Greeley, CO, 80639, USA

Summary

1. Climate change in North America is happening at an accelerated rate, reducing availability of water resources for bats and other wildlife that require it for successful reproduction.

2. We test the water-needy lactation hypotheses directly by tracking the drinking habitats of individual lactating and non-reproductive female fringed myotis at an artificial water source located near a maternity roost.

3. We used a submerged passive integrative transponder (PIT) tag reader system designed to track fish to instead record numbers of water source visitations by tagged bats.

4. Of 24 PIT-tagged adult females, 16 (67%) were detected repeatedly by the plate antenna as they passed to drink between 18 July and 28 August 2006.

5. The total number of drinking passes by lactating females (n = 255) were significantly higher than those of non-reproductive adult females (n = 22). Overall, lactating females visited 13 times more often to drink water than did non-reproductive females. On average, lactating females visited six times more often per night. Drinking bouts occurred most frequently just after evening emergence and at dawn.

6. Drinking patterns of non-reproductive females correlated significantly with fluctuating ambient temperature and relative humidity recorded at the water source, whereas lactating females drank extensively regardless of ambient conditions.

7. We provide a mathematical model to predict the rate of decline in bat populations in the arid West in relation to climate change models for the region.

Key-words: bats, conservation, lactation, *Myotis thysanodes*, water

Introduction

The effects that climate change is having on wildlife populations are of increasing interest to ecologists, as large-scale consequences are being documented for some species (see Walther, Burga & Edwards 2001; Humphries, Umbanhowar & McCann 2004). Climate warming is expected to alter seasonal ambient temperatures, amount of precipitation and levels of snowpack in the western North America. Indeed, current climate models indicate that snowpack in the region is already in significant decline due to warming (Mote *et al.* 2005) and the projected adverse effects on regional hydrology are of serious concern (Hamlet & Lettenmaier 1999; Cayan *et al.* 2001; Mote 2003a, 2003b; McCabe & Clark 2005; Mote *et al.* 2005; Regonoda *et al.* 2005; Knowles *et al.* 2006). For example, timing of stream flow measured from 1948 to 2002 from 302 western North America gauges show coherent trends towards earlier onset of springtime snowmelt (Stewart, Cayan & Dettinger 2005), having significantly negative effects on standing water availability during the warmest summer months.

Data from the Earth Systems Research Laboratory (ERSL) managed by the National Oceanic and Atmospheric Administration (NOAA) show that warming is indeed occurring in Colorado, as is being experienced in other regions of the western United States. Mean January temperature for Denver, Colorado in 2006 was 4·4 °C above average and warming is occurring, perhaps at a higher rate, at highest elevations (> 3000 m), thereby affecting winter snow pack levels seriously. In the upper Colorado River basin, temperatures were 1·3 °C above average between 1999 and 2004 and in 2005 reached 1·8 °C above average. Temperatures in most upper river basins in Colorado showed increases of 2·1 °C above average between 1999 and 2004 and 3·55 °C in 2005 during January. Regional warming involves not only increased ambient temperature,

*Correspondence author: Rick A. Adams.
E-mail: rick.adams@unco.edu

but also has negative effects on precipitation. A recent best-case scenario for the Colorado River basin between the years 2010–39 predicts that 1 °C more heat will result in 24% less snow pack, 3% less precipitation and 36% less water storage (Christensen *et al*. 2004). Such dramatic changes are expected to have profound effects on regional wildlife.

The ability of successful reproductive effort in female insectivorous bats is related directly to roost temperatures and water availability. The females of some bat species living in semidesert habitats are known to form summer maternity colonies in roosts having microclimate temperatures stable within the species' thermo-neutral zones (Vaughan & O'Shea 1976; Adams, unpublished data). In arid environments such as Colorado, high summer temperatures combined with low relative humidity predictably causes high rates of evaporative water loss in reproductive females. Laboratory and field data show that bats roosting under conditions of low relative humidity (RH < 20%) and high temperature (T > 27 °C) may lose as much as 30% body mass over a 12-h period (Studier 1970; Studier, Proctor & Howell 1970; Hattingh 1972; Studier & O'Farrell 1976; Webb 1995; Webb, Speakman & Racey 1995; Baudinette *et al*. 2000). Such large daily losses of body water must be replenished and studies have shown that replenishment of at least 20–22% of losses is accomplished by drinking from water sources (Kurta *et al*. 1989; Kurta, Kunz & Nagy 1990; McLean & Speakman 1999).

Water loss in female bats during roosting is escalated throughout lactation. Milk produced by big brown bats (*Eptesicus fuscus*) was composed of 72–76% water (Kunz, Stack & Jenness 1983; Kunz *et al*. 1994) and body water flux increased significantly during lactation (Wilde *et al*. 1995; Wilde, Knight & Racey 1999). Moreover, some studies have noted the propensity of maternity roost sites to be located, and in some cases clustered, in proximity to permanent water sources (McLean & Speakman 1999; Adams & Thibault 2006).

In this paper, we provide novel data that measured the visitation patterns of lactating vs. non-reproductive females to an artificial water source placed near a maternity roost of fringed myotis (*Myotis thysanodes*) in eastern foothills habitat in Colorado. This species occurs throughout the western United States encompassing a range of habitat types, including desert and semidesert habitats. Studier & O'Farrell (1976) found daily water losses of 14·5–15·8% of body mass in individuals of this species roosting in a building in New Mexico under ambient mean conditions of 26·8 °C and a relative humidity range of 18–31%. Vespertilionid bats can be found in roost sites with relative humidity as low as 5% (Studier & Ewing 1971). Unfortunately, the roost site used by bats in the present study could not be accessed safely for placement of a climate data logger; however, temperature-only data loggers placed in two other *M. thysanodes* maternity roosts ($n = 2$) at our field site ranged between 27·1 and 36·5 °C in July and August (R. A. Adams, unpublished data).

Our overall hypothesis is that reproductive female insectivorous bats living in arid environments require frequent and uninterrupted access to free-standing water during the lactation period. We tested the following predictions – P1: the frequency of visitations to water sources by lactating females will significantly exceed those of non-reproductive females; P2: due to significant dehydration during diurnal roosting, visitations to water sources will be highest directly after evening emergence from the day roost; and P3: numbers of drinking bouts by females will correlate with daily environmental conditions (i.e. ambient temperature and relative humidity).

Materials and methods

SITE DESCRIPTION

Our study site was located in Geer Canyon (40° N, 105° W) at Heil Valley Ranch, a 2000-ha natural area managed by Boulder County Parks and Open Space, Colorado. Major landscape attributes were Ponderosa pine woodlands (*Pinus ponderosa*) with mountain riparian habitat running through the canyon that supports cottonwood trees (*Populus angustifolia*), some aspen stands (*P. tremuloides*) and willows (*Salix* spp.). The orientation of the canyon runs NW–SE, with the south-facing canyon wall having the highest daily solar influence on the maternity roost of *M. thysanodes*.

ROOST SITE AND ARTIFICIAL WATER SOURCE

We located this colony of *M. thysanodes* in 2005 by tracking a radio-tagged, 7·6 g lactating female equipped with a model LB-2, 0·45 g transmitter that equalled 5·9% of its body mass (Aldridge & Brigham 1988; Holohil, Inc., Ontario, Canada) netted at a natural water source below the roost site. We conducted evening emergence counts to determine colony size. In 2006, at a location approximately 0·6 km west of the roost site (Fig. 1), we constructed a 1·5 m-diameter artificial water source using a nylon tarp braced with rocks into which water from the natural drainage flowed.

CAPTURING AND MARKING ANIMALS

In 2006, we trapped bats away from the artificial water source using a mist-net erected at two natural water sources, one just below the maternity roost and the other approximately 1 km north-west of the roost, but in the same drainage (Fig. 1). Between 16 and 21 July 2006 we captured, recorded standard data and inserted passive integrative transponder (PIT)-tags (BioMark, Inc., Boise, Idaho, USA; model TX1440ST, 14 mm sterile PIT-tags) dorsally between the shoulder blades of female *M. thysanodes*, alternating trapping sessions between the two sites (Fig. 1). All capture and handling conformed to the guidelines established by the American Society of Mammalogists. After we had determined that most of the female *M. thysanodes* from the maternity colony (based upon exit counts) were tagged, we placed large, dead tree-branches in the natural water sources where netting occurred to prevent further usage by bats, thereby driving them to the artificial water source to drink. We never mist-netted at, or otherwise disturbed, the artificial water source.

TRACKING INDIVIDUAL VISITATIONS TO ARTIFICIAL WATER SOURCE

On 22 July, after it appeared we had captured and PIT-tagged most individuals in the roost, we placed a plate antenna (BioMark, Inc; model FS2001, designed originally to track PIT-tagged fish) into the artificial water source submerged 1·5 cm below the surface. The plate

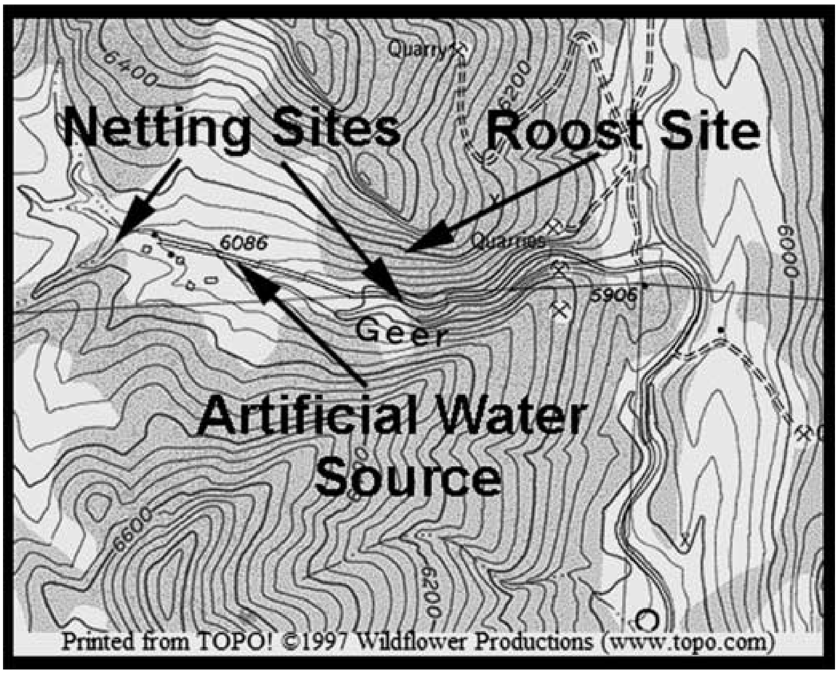

Fig. 1. Map of field site in Geer Canyon, Heil Valley Ranch, Boulder County, Colorado (40° N, 105° W). Shown are locations of *Myotis thysanodes* maternity roost, natural water source netting sites and placement of artificial water source. Approximate distance between roost site and artificial water source was 0·60 km.

antenna was attached to a PIT-tag reader (BioMark, Inc.; model FS2001 ISO) that was charged by a car battery attached to a solar panel. The system was checked daily and each night's data downloaded. On the first few nights we filmed at the artificial water source with a Sony NightShot camcorder (Sony, Inc., New York, NY, USA) fitted with auxiliary infrared lighting (Dalton, Inc., Tucson, AZ, USA), allowing us to observe drinking paths of the bats and to assure that the plate antenna was properly placed to record bats as they passed to drink. Pretests showed that the antenna was capable of detecting passing bats as they skimmed to drink within a range of approximately 8–10 cm above the water line.

MEASURING AMBIENT CONDITIONS

We recorded ambient temperature and humidity in vicinity of the artificial water source using a DataScribe Endurance EN-H Precision Temperature/Humidity data logger (Elucit, Inc., Mendocino, CA, USA) attached under a 7·5 cm-thick limb of a Ponderosa pine (*P. ponderosa*) tree in a position of shade at all times. We let the data logger run continuously throughout the study period, 28 July–18 August 2007.

DATA ANALYSIS

We transcribed visitation times recorded by at the plate antenna into minutes after sunset (MAS) to account for seasonal changes in day-length. Wilcoxon's rank-sum test was used to test for significant differences between drinking passes of lactating and non-reproductive females. Adams & Simmons (2002) used a thermal camera to film bats both above and at the water's surface at similarly sized water sources. They reported that visiting bats show two distinctive flight patterns where foraging passes were distinctively above the water source by a metre or more, had no discernable organization and were multi-directional, whereas drinking passes were orchestrated within a particular flight pathway directly at the water's surface (Adams & Simmons 2002). Filming with night-vision camcorders and infrared lights at our artificial water source showed corroborative patterns of behaviours, as defined in the Adams & Simmons (2002) paper, and that bats using the drinking pathway hit the water's surface 98% of the time. We used Spearman's rank correlation to test the relationship between an index of daily temperature and relative humidity (temperature/humidity) and numbers of passes of lactating and non-reproductive females. Lastly, using Christensen *et al.*'s (2004) estimates for climate warming-induced reductions in water storage in Colorado, we constructed a model that predicts how losses in natural drainages will affect the ability of females to access enough water during the lactation period.

Results

PIT-TAG DATA ACQUISITION AND VISITATION RATES

Among 24 female *M. thysanodes* PIT-tagged at the netting sites, 16 (67%) were detected repeatedly with the plate antenna at the artificial water source between 28 July and 18 August, the peak of the lactation period at our study site. Of these, 10 females were lactating when tagged and six were non-reproductive. Table 1 shows raw data, means and standard deviations of drinking passes of lactating vs. non-reproductive females. The number of visits by lactating females varied nightly but averaged 21·3 per night, whereas non-reproductive females averaged 3·7 visits per night. These data were significantly different (Wilcoxon's rank-sum test, median 18, $Z = 3{\cdot}78$, $P = 0{\cdot}0001$), and thus prediction 1 was supported.

TIMING OF VISITATION FOR LACTATING FEMALES

Lactating females showed a bimodal drinking pattern (Fig. 2) with the majority of drinking visits occurring soon after emergence, with a second drinking pulse at dawn before re-entering the day roost. There were relatively few drinking visits between 120 and 490 min after sunset (MAS), and thus prediction 2 was supported.

Table 1. Numbers of passes of lactating vs. non-reproductive *Myotis thysanodes* females by date. Number of individuals for which data were recorded on that night are in parentheses. Blank cells indicate no passes recorded for that group on that night. There was a significant difference between groups in total number of passes, Wilcoxon's rank-sum test, *P = 0·0001

Date	Lactating (n)	Non-reproductive (n)
7/19–7/20	19 (2)	4 (3)
7/28–7/29	42 (6)	
7/29–7/30	32 (4)	1 (2)
7/30–7/31	18 (3)	8 (3)
7/31–8/1	13 (3)	
8/1–8/2	24 (6)	
8/2–8/3	18 (4)	
8/3–8/4	14 (3)	
8/4–8/5	18 (3)	
8/16–8/17	22 (6)	3 (2)
8/17–8/18	16 (4)	4 (2)
8/22–8/23	19 (4)	2 (1)
Sum	255*	22*
Mean	21·2	3·7
Standard deviation	8·59	2·71

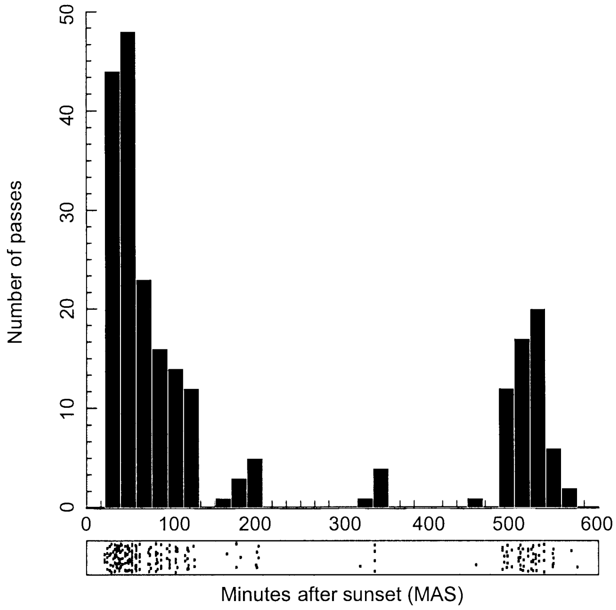

Fig. 2. Histogram of visitation times for lactating *Myotis thysanodes* at an artificial water source. Most visitations occurred directly after evening emergence from the roost and before re-entering the day roost at dawn. Fewest visitations occurred between 120 and 490 min after sunset (MAS).

VISITATION RATES VERSUS TEMPERATURE AND RELATIVE HUMIDITY

Figure 3 shows to what extent three lactating females, for which we had the most individual pass data, corresponded to daily ambient temperature and relative humidity recorded at the water source. An apparent drop in number of drinking passes among the three females was observed when temperature was low and humidity was high. However, among all PIT-tagged lactating females, there was no significant correlation with the temperature/humidity index relative to number of drinking passes (r = 0·51, P = 0·13), whereas with non-reproductive females we found a significant correlation between number of visitations and the temperature/relative humidity index (r = 0·63, P = 0·05). Lactating females drank often independent of ambient temperature and relative humidity (Table 2); prediction 3 was supported partially.

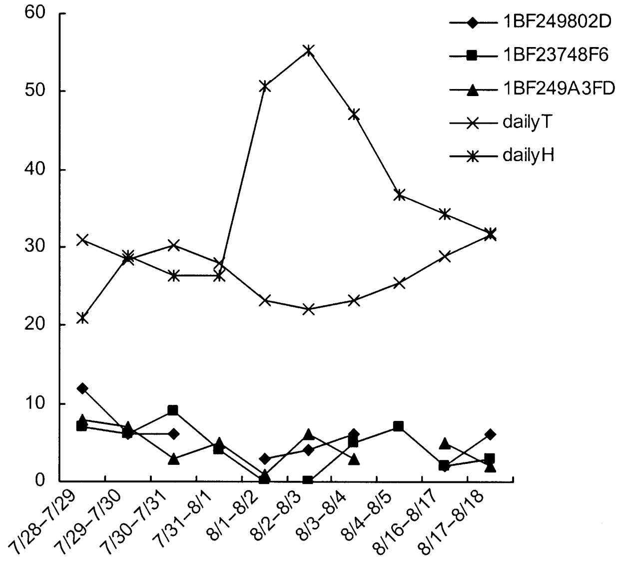

Fig. 3. Line graph showing number of visitations per night for each of three female lactating *Myotis thysanodes* (indicated by passive integrative transponder-tag number) plotted against daily ambient temperature (T) and relative humidity (H). The number of visitations by the three females decreased slightly when temperature was relatively low and humidity was relatively high. However, there was no significant correlation of lactating female visitation patterns with our index of ambient temperature and relative humidity (see Table 2).

Table 2. Temperature/humidity indices (higher index indicates higher temperature, lower humidity) compared to number of drinking visits by lactating and non-reproductive *Myotis thysanodes* by date

TH index	Lactating	Non-reproductive	Date
1·477327	42	4	7/28–7/29
0·9827049	32	1	7/29–7/30
1·1467577	18		7/30–7/31
1·0669456	13	1	7/31–8/1
0·4549744	24		8/1–8/2
0·4011218	18		8/2–8/3
0·4926922	14		8/3–8/4
0·6964091	18		8/4–8/5
0·8456592	22	3	8/16–8/17
0·9943271	16	4	8/17–8/18

Discussion

Use of water sources by bats in arid environments is an under-investigated topic in ecology and behaviour. Previous studies have shown that for bats, water sources may have structuring effects on bat populations and communities. For example, visitation patterns are temporally orchestrated among bat species that congregate at spatially restricted water sources to drink, thereby increasing efficiency of resource use (Commissaris 1961; Cockrum & Cross 1964; Adams & Simmons 2002; Adams & Thibault 2006), and female bats visit water sources higher in dissolved calcium (Adams *et al.* 2003). In the present study we used a novel method to provide unique insight into the visitation patterns of female bats as related to their reproductive status.

The availability of free water to reproductive females has been suggested in previous studies, but none of these studies have measured directly the apparent importance of water sources to bats living in natural populations. With our use of a novel PIT-tag system, we were able to gather data on visitation patterns to an artificial water source of individual bats of known reproductive condition. Our results are consistent with our predictions based on bat ecophysiology concerning evaporative water loss, but we show the added effect of lactation on water-seeking behaviours in reproductive females. Moreover, we mist-netted at all other potentially available water sources ($n = 7$) within 4 km of the Geer Canyon site, and found only one other water source where female *M. thysanodes* were captured consistently and that was at a quarry approximately 3 km and several mountain ridges away. However, none of our PIT-tagged females from Geer Canyon were captured at that quarry and none of the female *M. thysanodes* PIT-tagged at the quarry have been acquired by the reader placed in Geer Canyon. Our telemetry data from radio-tagged *M. thysanodes* captured at the quarry showed that those individuals forage between the water source and their roost site located on a rock wall approximately 1 km due west of the quarry, about 4 km from the Geer Canyon roost site.

Our water visitation data make it possible to formulate a predictive model for bat reproduction in the western United States based upon expected loss of water resources, as projected from current climate-change models. Predicted changes in bat population distributions relative to hibernation and climate change have been modelled previously (Humphries, Thomas & Speakman 2002).

DECAY MODEL ESTIMATING LOSS OF BAT LACTATION RATES WITH CLIMATE WARMING

Bats, marsupials and primates, as a group, have lactation lengths 50% longer (on a $\log_{10}$ scale) than other therians of comparable body masses (Hayssen, van Tienhoven & van Tienhoven 1993). However, the median length of lactation for bats (60 days) is more than twice that of the Insectivora (28 days) (Hayssen, van Tienhoven & van Tienhoven 1993). For vespertilionid bats, the average lactation length is 40·9 days (Barclay & Harder 2003). Combining our data on visits to water sources by lactating female fringed myotis (*M. thysanodes*) with data from the literature, we have derived the following model to predict affects of expected climate-induced changes on water storage capacity at a local level (Christensen *et al.* 2004).

We calculated the average volume (length × width × depth) of water across four natural water sources near roost sties in our study area to be 200 000 cm^3. The volume of 1 L of water is 1000 cm^3, thus on average these water sources held about 200 L. From our calculation above, we estimate that each lactating female will require about 0·113 L of water over a 21-day lactation period. Thus, each water source can support approximately 1770 lactating female *M. thysanodes*. For simplicity, we assume that stream inflow, local precipitation and evaporation are negligible effects during the lactation period.

Using the scenario presented by Christensen *et al.* (2004), where 1 °C climate warming will result in 36% less regional water storage, and beginning with 200 L of available water in support of 1770 female lactating *M. thysanodes* over a 21-day lactation period (O'Farrell & Studier 1973), we generate two decay curves, one that tracks water loss per degree increase in regional climate and the other a decay curve representing predictive declines in lactation ability in female bats (Fig. 4). As it stands, a 1 °C increase in warming would result in reduced water availability, thereby supporting only 1128 of the 1770 (64%) lactating females over the 21-day lactation period. A 2 °C warming results in only 40·8% (722) of females supported during the expected 21-day lactation period. Extrapolating the model to a 5 °C increase in regional average temperature predicts that only 10·7% (189) of the original 1770 lactating females would be supported by water availability (Fig. 4).

Although the anticipated decline in reproductive ability appears to be clearly significant, in reality our model data may be conservative. For example, our estimation of a 21-day lactation period for *M. thysanodes* was based upon data concerning flight ability of juveniles from a single, but detailed, study conducted by O'Farrell & Studier (1973). Tuttle (1976) showed that length of lactation period in *M. grisescens* varied between 58 and 76 days and was dependent upon growth

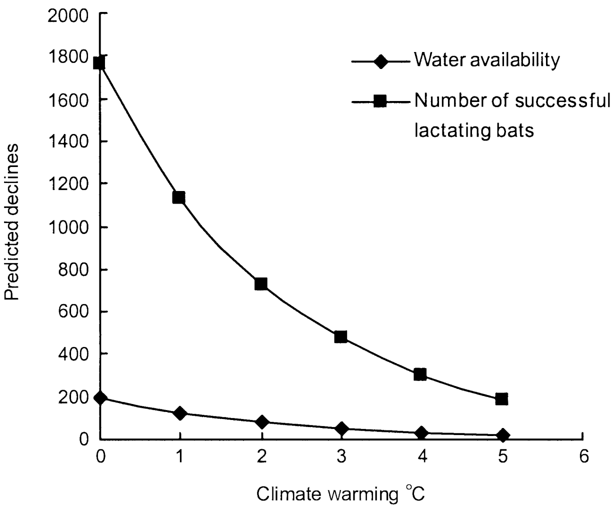

Fig. 4. Mathematical model showing the relationships between climate warming, loss of storage in natural water sources, and declines in bat lactation ability. See text for further explanation.

rates of juveniles which varied by the distance travelled to foraging areas and water sources; thus, the longer lactation period occurred in the most stressed colony. These data suggest that lactation periods may vary widely between populations of a single species (Tuttle & Stevenson 1982). Because of this, unless length of lactation is known for a given population, we suggest that the average lactation length of 40·9 days for *Myotis* species (Barclay & Harder 2003) be used in the model as a conservative measure of water needs for local bat populations. Furthermore, other variables consistent with loss of water from natural systems, such as significant increase in regional human population and its need for more water, may well come into play in determining local resource availability to bats and other wildlife.

To our knowledge, no data exist on consumption of water by free-flying lactating female bats, either in captivity or the wild, but Webb *et al.* (1993) suggested that consumption of drinking water was 1·76 g day^{-1} ± 0·42 g under ambient temperature conditions of 14·9 ± 4·1 °C and a relative humidity of 33·8 ± 11·2 for non-reproductive, free-flying, captive *M. daubentonii*. Hence, the average estimated nightly water consumption of 5·40 mL (g) day^{-1} for free-ranging lactating female *M. thysanodes* used in our model seems reasonable under arid conditions.

One obvious question concerning bats and water availability concerns whether bat species living in arid environments are adapted, or are becoming adapted, to living in water-limited environments. Investigations into urine-concentrating ability and renal structure (Carpenter 1969; Geluso 1978, 1980) showed that many of the bat species living in arid habitats, including *E. fuscus*, *M. lucifugus*, *M. auriculus*, *M. volans*, *M. yumanensis* and *Corynorhinus townsendii*, had no specialized adaptations of the kidney for greater water retention than average. Relative to the present study, *M. thysanodes*, of which many populations are distributed throughout desert and semidesert habitats, had relatively poor urine-concentrating ability (Carpenter 1969; Geluso 1978, 1980). Thus, survival of many of the bat species inhabiting arid environments is conditional on the availability of permanent water sources nearby roost sites (Findley *et al.* 1975; Adams & Thibault 2006), and thus continued residency and/or survival of such populations under conditions of reduced water availability is questionable.

Year-to-year variation in winter snowpack as translated into spring and summer runoff timing and rates, as well as local timing and rates of precipitation, are variables that may decelerate or accelerate predicted declines in local bat population numbers with increased climate warming. However, long-term predictions from our model suggest overall declines in bat populations in the western United States. We emphasize that this model provides a provisional baseline for understanding the complex relationships between predicted climate-induced declines in water availability as being related to foreseeable consequences for bats and other wildlife populations. We encourage more research in this regard. We also anticipate that the PIT-tag system that we describe will be useful in estimating survival rates as well as monitoring the behaviour and movement patterns of forest bats. The implications of our findings on visits to water sources by lactating female *M. thysanodes* has far-reaching implications across many species of bats and for the continued biodiversity of arid regions in the western United States and elsewhere.

Conclusions

Data from our study show, for the first time, patterns of water-seeking behaviour by lactating female vs. non-reproductive female bats in a natural setting. Lactating females visited the water source 13 times more often than did non-reproductive females and sought water at higher rates independent of ambient weather conditions.

When these data are placed into a context of regional climate warming and predicted reduced water storage capacity in the western United States, we can expect serious consequences to local and regional bat populations. The unique natural history traits of bats and their susceptibility to local temperature, humidity and precipitation patterns make them an early warning system for anticipated and cascading effects of climate change in regional ecosystems and the eventual effects on many wildlife species. Another contributing factor to this pattern is the anticipated increased in human population in the western United States, and the Front Range of Colorado in particular, resulting in more pronounced loss of water resources in natural ecosystems.

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