

Bat reproduction declines when conditions mimic climate change projections for western North America

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Abstract. Climate change models predict that much of western North America is becoming significantly warmer and drier, resulting in overall reductions in availability of water for ecosystems. Herein, I demonstrate that significant declines in the reproductive success of female insectivorous bats occur in years when annual environmental conditions mimic the long-term predictions of regional climate change models. Using a data set gathered on bat populations from 1996 through 2008 along the Front Range of Colorado, I compare trends in population numbers and reproductive outcomes of six species of vespertilionid bats with data on mean annual high temperature, precipitation, snow pack, and stream discharge rates. I show that levels of precipitation and flow rates of small streams near maternity colonies is fundamentally tied to successful reproduction in female bats, particularly during the lactation phase. Across years that experienced greater than average mean temperatures with less than average precipitation and stream flow, bat populations responded by slight to profound reductions in reproductive output depending on the severity of drought conditions. In particular, reproductive outputs showed profound declines (32–51%) when discharge rates of the largest stream in the field area dropped below 7 m³/s, indicating a threshold response. Such sensitivity to environmental change portends severe impacts to regional bat populations if current scenarios for climate change in western North America are accurate. In addition, bats act as early-warning indicators of large-scale ecological effects resulting from further regional warming and drying trends currently at play in western North America.

Key words: bats; climate change; hydrology; lactation; reproduction; water.

INTRODUCTION

The Earth's surface has warmed ~0.6°C over the past century, whereas regional warming in the western United States has increased 0.9°C over the same time period (Saunders et al. 2008). Further global warming of 1.1°–6.4°C over the next century is expected, and some regions in the western United States are already approaching this threshold (Parry et al. 2007, Saunders et al. 2008). Climate models predict that some mountainous areas in western North America will be epicenters of significant heat waves and drought in the future (Parry et al. 2007).

The timing of snowmelt-derived stream flow measured from 1948 to 2002 and based on 302 western North America gauges shows coherent trends towards earlier spring onset of snowmelt by one to four weeks (Stewart et al. 2005). The widespread effects of hydrological shifts in both timing and intensity are already detectable, particularly across western mountain ranges where rising mean temperatures are affecting annual precipitation, snowpack, and stream discharge rates (Cayan et al. 2001, Christensen et al. 2004, McCabe and Clark

2005, Mote et al. 2005, Regonda et al. 2005, Stewart et al. 2005, Knowles et al. 2006).

Changes in the timing of and amounts of water flow in drainages will radically alter regional ecologies, food webs, and biodiversity. Recent estimates of the ecological consequences when global warming trends exceed 2°C or 3°C forecast rising extinction risks for 20% to 30% of plant and animal species world-wide (Bates et al. 2008). The Intergovernmental Panel on Climate Change expects that increases in global temperatures and modifications to the Earth's water cycle will influence biodiversity on every continent (Bates et al. 2008), and such impacts are already being measured (Walther et al. 2001, Parmesan and Yohe 2003). For example, in sub-Saharan Africa, climate change reductions in water resources have already altered density feedback mechanisms in breeding elephant populations, thereby restricting population growth (Chamaillé-Jammes et al. 2007). Closer to home, drought conditions caused a 97% reduction in arid-land bird populations in California in 2002, illustrating the destructive, and sometimes, disproportional effects of water loss on particular species (Bolger et al. 2005).

This paper concerns the effects of climate change in the southern Rocky Mountain region of North America, where warming is occurring predominately during the winter months at the highest elevations, thereby

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affecting winter snowpack depth, critical for sustaining water availability at lower elevations during the summer months (Stewart et al. 2005). In addition, models predict increasing years of higher mean temperatures and reduced precipitation during summer months, the major reproductive season for many organisms (Saunders et al. 2008). Already, the mean temperature measured for the Colorado River Basin has increased by 1.2°C as compared to 20th-century averages, leading to less snowfall, and thus reduced snowpack throughout the highest reaches of the Southern Rocky Mountains (Christensen et al. 2004). Reductions in winter snowpack affect water availability for populations of organisms living at lower elevations throughout the spring, summer, and autumn, the prime reproductive season. In addition, reduced precipitation during the summer months further limits availability of water to wildlife (Stewart et al. 2005) and will have cascading effects on the structure and complexity of forest food webs across terrestrial ecosystems (Nakano et al. 1999, Nakano and Murakami 2001, Bastow et al. 2002, Fausch et al. 2002, Power and Dietrich 2002, Sabo and Power 2002, Lowe et al. 2006, Knight et al. 2007), especially in arid environments (Polis and Hurd 1996, Polis et al. 1997, 2004).

Because bats constitute ~20% of all living mammal species (Wilson and Reeder 2005), their diverse ecologies are distributed across all terrestrial biomes, with the exception of Antarctica (Patterson et al. 2003), making them profoundly important components of food webs world-wide (Patterson et al. 2003, Jones et al. 2009). Thus, declines in bat populations are of obvious concern in regards to ecosystem health and sustainability (Jones et al. 2009). Due to their small size and large surface area to volume (exacerbated by having uninsulated wings) bats are highly prone to losing large amounts of water through evaporative loss and therefore may be disproportionately affected by climate warming leading to higher incidence of drought across some ecosystems. In laboratory and field tests, individuals lost as much as 31% of their body mass during 12-hour roosting bouts under moderate temperature (27°C) and relative humidity (20%) (Studier 1970, Studier et al. 1970, Studier and O'Farrell 1976, Webb 1995, Webb et al. 1995). Evaporative water losses are expected to be further magnified significantly during the lactation period when females are producing milk consisting of 76% water (Kunz et al. 1983, 1994, Kurta et al. 1989, Wilde et al. 1995, 1999). A field experiment conducted by Adams and Hayes (2008) underscored the increase need of water by lactating female fringed myotis (*Myotis thysanodes*) that visited to drink at a nearby water source 13 times more often than did nonreproductive adult females over an 11-day period.

In this paper, I compare 13 years of capture data gathered on bat populations living in the Front Range of Colorado with data on annual temperatures, precipitation, snow pack, and stream discharge rates recorded

over the same time frame to examine how variation in yearly weather conditions affected female reproductive patterns. My results show a striking interrelatedness between yearly weather conditions and the reproductive outcomes for six species of vespertilionid bats. These data portend significant consequences for regional insectivorous bat populations in response to climate change in western North America.

METHODS

Site and species descriptions

The study area was located on the eastern slope of the Rocky Mountains, encompassing 178 km² of foothills environments ranging in elevation from 1650 m to 2250 m and housing a habitat mosaic of montane meadow, shrubland, and ponderosa pine woodlands (*Pinus ponderosa*) in the lower elevations, and mixed-coniferous forest habitat, dominated by Douglas fir (*Pseudotsuga menziesii*) and mountain juniper (*Sabina scopulorum*) at the higher elevations. Several small- to medium-sized drainages support mountain riparian woodlands where cottonwood trees (*Populus angustifolia*) and willows (*Salix* spp.) dominate. There are nine species of bats that occur in the area, five of which are most common: the little brown myotis (*Myotis lucifugus*), small-footed myotis (*M. ciliolabrum*), long-eared myotis (*M. evotis*), fringed myotis (*M. thysanodes*), and the big brown bat (*Eptesicus fuscus*).

Capturing bats

The protocol for netting bats was consistent across sites and across years. I erected American-made mist nets (Avinet, Dryden, New York, USA) at small water holes and occasionally in forest flyways to capture bats from mid-May through June, July, and August during the reproductive season from 1996 to 2008 (Adams et al. 2003, Adams and Thibault 2006, Adams and Hayes 2008). To standardize sampling efforts, variable-sized mist nets were used to afford similar coverage across water sources of different size (Adams and Thibault 2006). Two nets per site were used with one positioned to centrally bisect the water hole, and the other was extended perpendicular to it along the water's edge. For flyways, nets were used of proper length to span the entire width of the flyway. Nets were set ~30 min before published sunset, and were dismantled and removed at ~200 min past published sunset.

For all captures, individuals were identified to species, sexed, weighed, and reproductive condition recorded. From 1996 to 2008, each captured individual was marked with a split-ring, numbered, plastic forearm band (Hughes, Hampton Mill, Middlesex, UK) before release. To minimize disturbance, sites were netted no closer than three weeks apart and sampled usually three times per season. In order to accurately assess reproductive conditions in adult females, captured individuals were placed in cloth capture sacs where they remained for a minimum of 30 min and a maximum of 90 min, to

allow defecation of ingested food (Coultts et al. 1973). This permitted accurate assessment of pregnancy by palpation of the abdomen for gestating young.

Because early pregnancies can be difficult to detect due to the small size of the fetus, if an individual was of uncertain status, the bat was categorized as unknown and these data were not used in the analysis. In very few cases (<0.2%) was assessment of pregnancy not possible. Generally, these were individuals captured very early in the season (mid-May); 98% of captures were later in the reproductive season (June through August) when pregnancy was readily detectable by palpation of the abdomen. Lactating females were considered to be those where milk could be expressed from the nipple. Post-lactating females were considered those in which milk could not be expressed, but showed obvious tissue transformations such as enlargement of mammary glands and nipples and loss of fur surrounding the nipple. Juveniles were distinguished from adults by checking for any nonfused epiphyses of the metacarpal and phalangeal joints of digits 3 through 5. Late-season juveniles were distinguished from adults by series of characters (very sharp and pointed canine teeth, lighter than average weight, and grayer pelage). Over the 13-year period, the relative age and reproductive condition of individuals was assessed by me, even when students were helping with the field work.

Weather data and stream discharge rates

Data on mean monthly weather variables per year were gathered from the Earth Systems Research Laboratory (ESRL) of the National Oceanic and Atmospheric Administration (NOAA) for Boulder, Colorado, USA. I used monthly mean precipitation (millimeters) and high temperature data (degrees Celsius) for June, July, and August, overlapping with the bat sampling period; mean monthly snow pack data (millimeters) were used for January through April for each year. I used mean monthly stream discharge rate (cubic meters per second [cms]) data for Boulder Creek, the only monitored stream within the study area, for the months of June, July, and August as provided by Division of Water Resources for Boulder Creek at Orodell station (BOCOROCO: latitude 40°00'23" N, longitude 105°19'49" W, in NE¼SW¼ sec. 34, T.1 N., R.71 W., Boulder County, Hydrologic Unit 10190005).

Data analysis

I ran principal components analysis (PCA) on mean monthly data for precipitation, high temperature, stream discharge rates (June, July, and August), and snow pack (January through April) from 1996 through 2008 to determine which variable(s) were most interrelated for delineating local weather patterns at my field sites. In addition, I ran multiple regression analysis on climate variables vs. four categories (pregnant, lactating, post-lactating, nonreproductive) of reproductive data gathered on female bats. Within-species analyses were

run using paired *t* tests between years with average (29.6°C) or lower temperature and average (19.7 mm) or higher precipitation ($N = 7$; 1996, 1997, 1998, 1999, 2003, 2004, 2005) vs. those years with higher than average temperature and lower precipitation ($N = 6$; 2000, 2001, 2002, 2006, 2007, 2008). Data were tested for significance at the ≤ 0.05 level.

RESULTS

Multivariate analysis of abiotic variables

A correlation matrix among the climate variables (high temperature, precipitation, snow pack, and stream discharge) provided by principal components analysis (PCA) showed that mean precipitation was significantly and inversely correlated with mean high temperatures ($R = -0.88$), whereas mean stream discharge was most positively and significantly correlated with mean precipitation ($R = 0.63$) and secondarily with winter snow pack ($R = 0.35$). Bartlett's Test (28.35, $P < 0.0001$) generated by the correlation matrix indicated validation of running PCA on these data. Eigenvalues for each factor indicated that Factors 1 (66.69%) and 2 (27.73%) accumulated greater than 92% of sample variation. Factor 3 was discarded from further analysis because it was deemed to have insignificant bearing on the PCA using the scree-plot method (Cattell 1966), as well as the criterion that its eigenvalue was < 0.7 , thus providing less information than any single variable (Jolliffe 1986). Eigenvectors indicated that along Factor 1, high temperature, precipitation, and stream discharge were closely equal in weight, whereas for Factor 2, highest weighting was for snow pack (Appendix). Factor loadings, showing the correlations between the variables and the factors, corroborate eigenvector outcomes that mean high temperature, mean precipitation, and mean stream discharge for the months of June, July, and August account for the highest variation in the system and are the most important interlinked variables tested.

Bat captures and female reproductive patterns

A total 2329 bats of six species was captured from 1996 to 2008 across 27 sites. Of these captures, 844 (36.2%) were adult females. The little brown myotis (*Myotis lucifugus*), small-footed myotis (*M. ciliolabrum*), long-eared myotis (*M. evotis*), fringed myotis (*M. thysanodes*), and the big brown bat (*Eptesicus fuscus*) composed 98% of all captures. I pooled reproductive data on adult females of these six species into the categories of nonreproductive, pregnant, lactating, or postlactating. Year-to-year frequency data on females per reproductive category are given in Table 1. The mean frequency for nonreproductive females captured across years was 0.1758 (17.6%) with a standard deviation of 0.1224 (12.2%). Years that showed particularly high capture frequencies of nonreproductive females were 2002, 2007, and 2008, with 2007 having the highest frequency (0.513) recorded from 1996 through 2008.

TABLE 1. Frequencies of capture for pregnant, lactating, post-lactating, and nonreproductive females by year, with total captures for that year and number of females captured.

Year	Number of total captures	Number of females captured	Pregnant	Lactating	Post-lactating	Nonreproductive
1996	174	62	0.210	0.613	0.097	0.081
1997	305	99	0.273	0.616	0.061	0.050
1998	256	104	0.365	0.365	0.163	0.106
1999	174	68	0.221	0.529	0.206	0.044
2000	125	71	0.098	0.521	0.169	0.211
2001	123	32	0.385	0.346	0.115	0.154
2002	68	30	0.090	0.561	0.303	0.321
2003	92	33	0.263	0.526	0.105	0.105
2004	246	50	0.700	0.081	0.121	0.101
2005	184	67	0.119	0.522	0.179	0.179
2006	210	49	0.551	0.224	0	0.224
2007	175	39	0.256	0.076	0.154	0.513
2008	197	56	0.161	0.270	0.161	0.412

The frequency of nonreproductive females captured varied across years. However, those years that were hotter and drier (similar to anticipated anthropogenic climatic shifts) had a higher incidence of nonreproductive females. This is corroborated by the general patterns over the 13 years of increased capture of nonreproductive females represented by the trend line that aligned with increased hotter/drier conditions over this time period (Fig. 1). Linear regression analysis showed no significant relationship between yearly sample size and frequency of nonreproductive females captured ($R^2 = 0.185$, $P = 0.162$) across years.

Relationships between female reproduction and climate variables

The relationship between capture frequency of nonreproductive females and mean high temperature during the months of June, July, and August (Fig. 2a) was significantly positive ($R = 0.74$, $R^2 = 0.54$, $P = 0.001$). As mean high temperatures increased, the number of nonreproductive females captured was higher. Precipitation and frequency of nonreproductive females captured (Fig. 2b) were significantly and negatively correlated ($R = -0.85$, $R^2 = 0.72$, $P = 0.0001$), indicating that in years with less summer precipitation, more females were nonreproductive. Rates of stream dis-

charge (Fig. 2c) were also strongly and negatively correlated with number of nonreproductive females captured ($R = -0.79$, $R^2 = 0.62$, $P = 0.001$). Numbers of reproductive females fell precipitously when rates of stream discharge dropped below 7 cm.

In addition, when frequencies of pregnant and lactating females were regressed against rates of stream discharge over the study period (Fig. 3), the trend in lactation tracked and contributed strongest ($R^2 = 0.39$) to the overall trend of greater reproductive outputs as stream discharge increases. Frequencies of pregnancy appeared to contribute little ($R^2 = 0.09$) to the overall trends of reproductive output relative to stream discharge rates.

Species level analysis

Comparing intraspecific reproductive output in years with average or lower temperatures and average or higher precipitation ($N = 7$ years) gives some indication of the risk to each species when regional temperatures increase and precipitation decreases ($N = 6$ years). In all species, the frequency of reproductive females captured dropped in years that mimicked anticipated long-term climate warming and increased drought (Fig. 4). Drops in frequencies of reproductive females were accompanied by an overall decline in capture success across

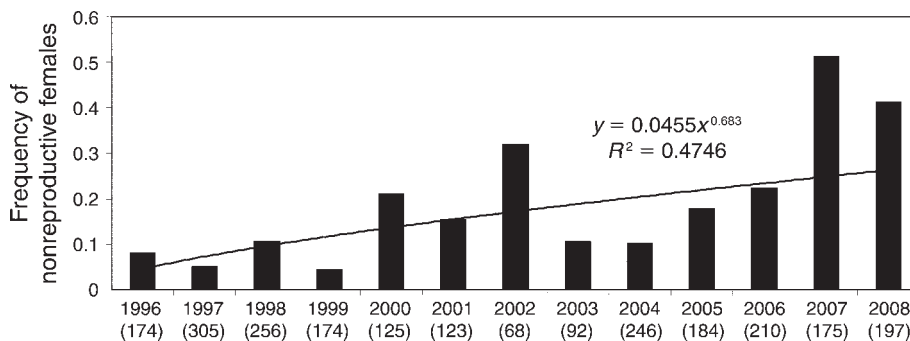


FIG. 1. Frequency of nonreproductive female bats captured by year. The number of total captures each year is shown in parentheses under the year.

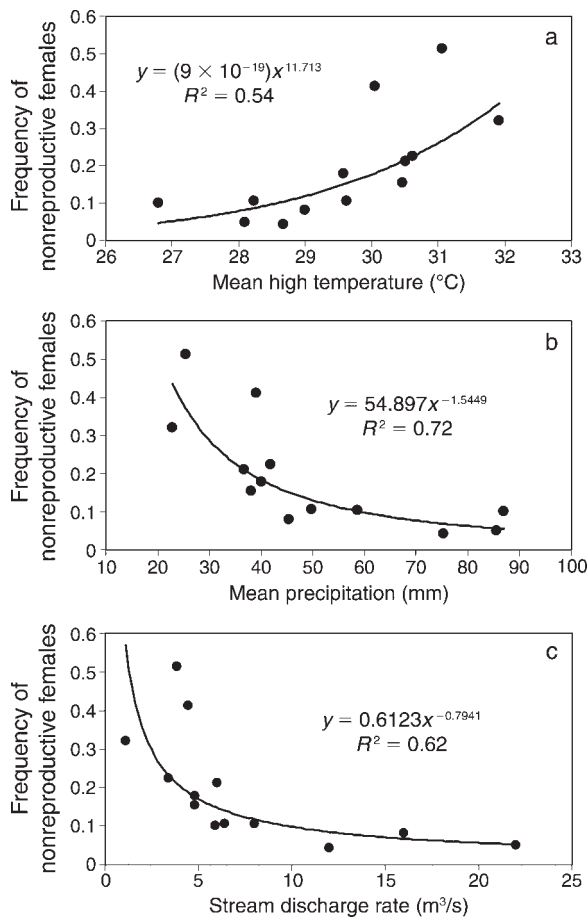


FIG. 2. Relationships between the frequency of nonreproductive females captured from 1996 through 2008 and (a) mean high temperature ($R = 0.74$, $P = 0.001$), (b) mean precipitation ($R = -0.85$, $P = 0.0001$), and (c) stream discharge rate ($R = -0.79$, $P = 0.001$).

species, with the exception of the long-eared myotis (*Myotis evotis*), for which captures increased in hotter/drier years. Significant reproductive declines occurred for the long-eared myotis (*M. evotis*; $df = 11$, $t = 3.01$, $P \leq 0.02$), little brown myotis (*M. lucifugus*; $df = 11$, $t = 3.18$, $P \leq 0.01$), and the fringed myotis (*M. thysanodes*; $df = 11$, $t = 2.5$, $P \leq 0.05$). However, declines in reproductive effort during drought years were not significant for all species. Although the capture frequency of reproductive females declined for both the big brown bat (*Eptesicus fuscus*) and the small-footed myotis (*M. ciliolabrum*) in drought years, the declines were not significant (Fig. 4). For the long-legged myotis (*M. volans*), drops in captures during drought years was so extreme that assumptions of the statistic tests could not be met.

DISCUSSION

Tracking the reproductive output of bat populations for 13 years has allowed for analysis of long-term trends in light of anticipated climate change in western North America. Herein, data clearly demonstrated that availability of water is crucial to the reproductive effort of insectivorous bats. Because temperature and precipitation are strongly and inversely related, understanding which factor most affects bat populations is important. These data indicate that availability of water is of high value to reproductive output of regional bat populations at my study sites. Several species of bats showed a threshold-type response to decreased stream flow rates, with reproductive output declining rapidly as stream discharge dropped from 7 cm to 2 cm. In addition, it was during the lactation period that females were most susceptible to loss in water accessibility (Fig. 3). These results corroborate a recent field experiment (Adams and Hayes 2008) showing that lactating female fringed myotis (*M. thysanodes*) visited to drink at an artificial

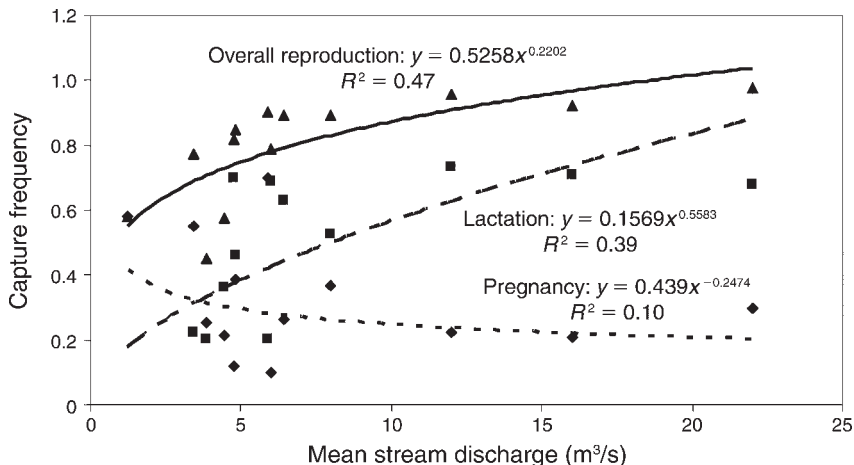


FIG. 3. Plot of average numbers of reproductive (pregnant and lactating) females captured (solid line), as well as average lactating females only (long-segmented line) and average pregnant females only (short-segmented line), against average stream discharge rates between 1.24 cm and 22 cm. Lactation provides the major contribution to the overall reproduction curve (solid line) in relation to stream discharge, whereas pregnancy shows a lower to nonexistent contribution.

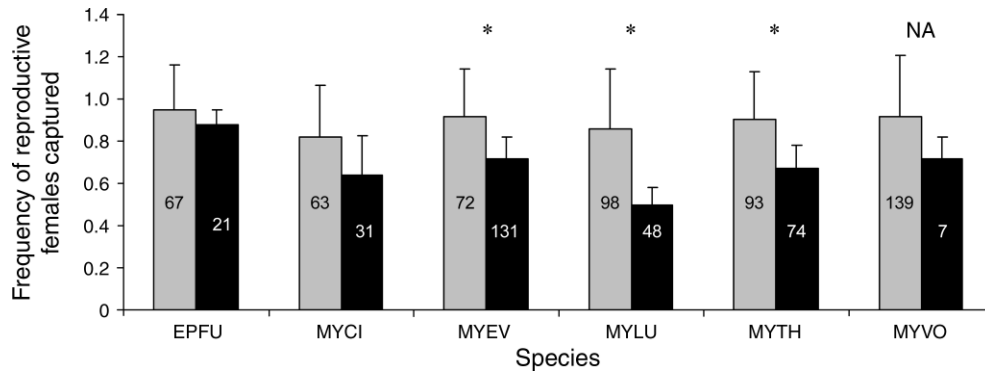


FIG. 4. Frequencies of reproductive females captured by species categorized into years when annual temperature was equal to or below the 13-year average and annual precipitation was equal to or above the 13-year average (gray bars) and years when conditions were above and below averages (black bars). Error bars indicate standard deviations from mean frequencies. Sample sizes for each category are illustrated within bars. Paired t tests were used for intraspecific comparisons between females grouped within wet vs. drought years (calculated at the $P \leq 0.05$ level of confidence). Significant differences are indicated with an asterisk. Species designations are: EPFU, *Eptesicus fuscus*; MYCI, *Myotis ciliolabrum*; MYEV, *M. evotis*; MYLU, *M. lucifugus*; MYTH, *M. thysanodes*; and MYVO, *M. volans*. NA indicates that the data did not meet assumptions of the statistical test, and thus no test was run.

water source 13 times more often than did nonreproductive females. Perhaps more importantly, nonreproductive adult females visited to drink only on days when temperatures were highest and humidity was lowest (Adams and Hayes 2008), whereas lactating females visited regardless of ambient conditions. In addition, the distribution of maternity colonies for many species living in arid landscapes is clustered around standing water sources (McLean and Speakman 1999, Adams and Thibault 2006), further underscoring the importance of accessibility to water.

Species-specific natural history traits likely play a key role in determining susceptibility to drought. The drought years of 2007 and 2008 yielded the highest frequencies of nonreproductive females, and two species were disproportionately affected. About 56% of female fringed myotis (*Myotis thysanodes* [a species of highest conservation concern by the Colorado Division of Wildlife, Denver]) and 64% of adult female little brown bats (*M. lucifugus*) were nonreproductive in the most severe drought years. Both of these species use maternity sites having south or southeast aspects that promote highest solar gains throughout the diurnal roosting period (Adams and Thibault 2006, Adams and Hayes 2008), maintaining internal temperatures between 27°C and 36°C (Adams, unpublished data). Such microenvironmental conditions within roost sites promote high evaporative water loss and consequently a greater need for water intake, especially during the lactation period. For the other two myotis species tracked in this study (*M. ciliolabrum* and *M. evotis*), we have found maternity roosts commonly located under large rocks on scree-slopes or under rocks on the ground that maintain cooler, more humid microclimates, thereby reducing evaporative water loss.

As for the overall reproductive phenology of female reproductive states at our study sites, some year-to-year

difference were noted particularly in years having seasons cooler and wetter than average. Under these conditions, delayed parturition and lactation by up to one to two weeks was evident, whereas in drought years, female parturition and lactation adhered to average trends, as did timing of captures of juvenile bats. Thus, the proportional differences in reproductive states of female bats across years were not likely a function of dramatic phenological shifts relative to our sampling period. Although the numbers of bats captured per season did vary, the proportion of nonreproductive females was not related to yearly sampling (Fig. 1), and hence, the disproportional captures of reproductive and nonreproductive females in cooler/wetter vs. hotter/drier years was not a product of sampling outcomes.

The high mobility of bats allows access to resources that, for many other species, are inaccessible. Indeed, due to the natural history trait of flight and associated vagility, bats may be overlooked as tractable indicator species for climate change (Jones et al. 2009). In addition, vagility of bats may imply that losses of water sources near roosting sites would not be catastrophic to reproductive effort. However, our data indicate that bats continue to inhabit traditional roost sites under detrimental environmental conditions, at least those documented in the present study. Rather than abandoning roosts, females tended to reduce reproductive output. Furthermore, flying farther to find water, such as human-made reservoirs, may have significant costs. A study by Tuttle (1976) on gray bats (*Myotis grisescens*) showed that the cost of traveling farther for water and food significantly increased the length of lactation of females, thereby slowing growth and developmental of newborn young. In temperate regions with well defined seasons, slowing of ontogeny may jeopardizes survival of both young and adult females by shortening the

window necessary for increasing body mass for hibernation or migration.

Forecasts from climate change models for the Southern Rocky Mountains (Kang and Ramirez 2006, Saunders et al. 2008) concerning essential water necessary for mammals and other wildlife during the summer reproductive season are gloomy. In light of significantly reduced snowpack and spring runoff, summer precipitation becomes even more important for sustaining water sources in natural systems. Summer precipitation not only adds to stream flow, but also provides ephemeral pools that can be used by wildlife, sometimes for days or weeks after heavy rains. This may be one of the reasons that precipitation was the most significantly related variable to successful reproduction by bats in this study. Unfortunately, regional precipitation is inversely correlated with temperature, and thus, is predicted to decline significantly during all seasons (Saunders et al. 2008).

Of equal concern is that the most current climate models for western North America have not adequately taken into account a significant variable. Kang and Ramirez (2006), using the South Platte River sub-basin in Colorado, showed that variation of the total volume of annual runoff and the peak flow are amplified by associated trends in evaporation, which can be of large magnitude and great impact on long-term stream flow responses to climate warming. Rates of predicted discharge for a stream throughout a given year are multi-factorial and must take into account predicted evaporation rates across seasons. Thus, current models that have not included anticipated effects of evaporation are likely not predicting accurately the extent to which climate change will negatively affect regional water availability (Kang and Ramirez 2006).

At the species level, several outcomes based upon ambient conditions relative to bats and their reproductive output were indicated (Fig. 4). All species in the study showed reduced proportional capture success of reproductive females in drought years. Curiously, with the exception of *M. evotis*, overall numbers of captures across species also declined in drought years. In part, this is somewhat a product of one less drought year ($N=6$) in the sample as opposed to non-drought years ($N=7$). But taking that into account, capture success was reduced at water sources during drought years when one might expect activity to increase due to an increased need for water. Insight into this paradox can be understood using a study by Adams and Hayes (2008), who showed that lactating females fringed myotis (*M. thysanodes*) visited to drink water 13 times more often than did nonreproductive adult females. Thus, if females are either not reproductive or have abandoned offspring due to lack of available water, they would be released from staying at the maternity colony and/or an excessive need for water intake, as shown by nonlactating females in the Adams and Hayes (2008) study. Fenton and Barclay (1980) showed that nonreproductive female

little brown bats (*M. lucifugus*) may move away from the hotter maternity roost to another cooler roost site nearby that offers better energy and water savings. If this were the case in the present study, then the magnitude of drought impact on bat reproduction may be underestimated by my data. Also, for some species, such as the long-legged myotis (*M. volans*), it is apparent that individuals are heat sensitive and move to higher elevations when summer temperatures at lower elevations apparently breach their tolerance limits (Mollhagen and Bogan 1997), thereby reducing capture success at lower elevation sites. The capture data support this hypothesis by showing a large drop-off in captures for this species in drought years. Therefore, although there was some risk that overall reduced capture rates in drought years as compared to wet years may have biased the capture data, there is no evidence for support, especially in light of the lack of a relationship between capture numbers and proportion of nonreproductive females (Fig. 1). Also, the reverse trend for reproductive effort in *M. evotis*, which increased in capture rate but declined in reproductive rate in drought years, support the conclusions of this study. Other factors, such as the increase in variance in reproduction in drought years by factors of 2 or 3 (Fig. 4), may very well indicate a level of reproductive instability due to environmental stress. Heat stress is known to negatively affect reproductive output of female domesticated farm mammals (Moberg 1975, Einarsson et al. 2008).

*Are bats ecological indicators
of climate-mediated changes?*

In a recent publication, Jones et al. (2009) provided a comprehensive discussion in support of the importance of bats as bioindicators of ecosystem health and change. The data presented herein shows a direct connection between ambient conditions and reproductive output of six vespertilionid bat species. In addition, the data underscore why bats should be considered an important indicator species for climate change, in particular for those regions where increased drought is predicted to occur. Monitoring maternity colony populations in relation to water availability may indeed provide an accurate gauge of impending climate impacts and predict that other small mammal populations, especially those less vagile than bats, may begin to fail reproductively long before succumbing to the direct effects of increased temperatures. Bats have been used as a model organism to predict climate-mediated changes in range limits for hibernating mammals (Humphries et al. 2002, 2004, Jones et al. 2009).

Patterns of bat reproduction at my field sites tracked water accessibility very closely, and all indications are that the lactation period is the most critical time for access to water in proximity to a maternity roosts. Long-term projections of further reductions in this resource base will lead to loss of individual fitness, eventually reductions in population numbers and foreseeable

negative impacts on the stability of local food webs for which insectivorous bats provide a unique and important role. Although other small mammals may respond somewhat less dramatically than bats (e.g., perhaps seek out cooler, more humid microclimates to help slow evaporative water loss during reproduction), the overall trend in xerification of ecosystems throughout the mountainous expanses of North America is bound to eventually affect reproductive effort for many species. Thus, bats provide us an early warning signal of changes to come in many regions of western North America.

Although humans cannot accomplish much to slow or reverse temperature increases in the short term, we may be able to mitigate some of the effects of climate change on regional biodiversity by providing artificial water sources in habitats that are losing, or have already lost, the availability of natural water sources.

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APPENDIX

A table showing that eigenvectors for Factors 1 and 2 contributed >92% of variation in the sample (*Ecological Archives* E091-175-A1).