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Life in a Shrinking World: Thermal Physiology and Activity of Diurnal Alpine Mammals in Relation to Climate Change

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LIFE IN A SHRINKING WORLD: THERMAL PHYSIOLOGY AND ACTIVITY OF DIURNAL ALPINE MAMMALS IN RELATION TO CLIMATE CHANGE

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✦ ABSTRACT

The effects of increased global temperatures are being measured in many biological systems. Given the complexity of these systems, their responses to a changing climate are difficult to predict. Physiologic processes are particularly susceptible to temperature, leading to a species specific optimal range of habitable temperatures. As global temperatures increase, species will be exposed to a changing range of potentially stressful temperatures, especially in species currently living at their thermal limits (*e.g.*, alpine mammals). Warming temperatures may force alpine species to move to higher elevations to maintain thermoneutrality. Ultimately, if temperatures increase as predicted, alpine mammals may be unable to move higher and may face localized extinctions.

We hypothesize that many alpine mammals are currently living at the upper range of their thermoneutral zone and, in response to warming temperatures alpine mammals will experience ambient conditions above their upper critical temperature which will limit their activity period. We will focus on small diurnal mammals (Uinta ground squirrels and pikas) as they are prolific and potentially susceptible to high temperatures. The proposed study will not only provide sorely needed information on the basic thermal requirements of alpine small mammals, but that information can be used to generate physiologically relevant models to predict future changes in the altitudinal ranges of these species.

✦ INTRODUCTION

The Earth has experienced substantial warming over the last century, with anthropogenic sources as the likely cause (Houghton et al. 2001). Within North America, mean atmospheric temperature has warmed by 0.7°C during the past century, leading to heterogeneous changes in precipitation across the continent. Houghton et al. (2001) predicted that individual physiographic regions of the USA will show unique alterations in response to warming trends. For example, the Sierra Nevada is predicted to have increased winter rainfall, less snowfall, more summer drying, and increased temperatures. In contrast, the Rocky Mountains will show an altitudinal increase in the winter-spring snowline, increased snowfall combined with earlier snowmelt, and increased summer temperatures and drying. Alterations in large-scale climate patterns are predicted to have important effects on species inhabiting these montane regions of the western United States. Many of these predictions are already being observed by scientists, including changes in phenology (Post and Stenseth 1999), species distributions (Payette 1987, Floyd 2004, Gian-Reto et al. 2005), body size (Smith et al. 1998, Fernández-Salvador et al. 2005), reproductive output (Lewis 1993), hibernation patterns (Inouye et al. 2000, Blumstein et al. 2004), and community structure (Brown et al. 1997).

Biological systems are complex, making it difficult to predict responses to climate change. As a result, McCarthy et al. (2001) state “there is a strong need for a long-term comprehensive system to monitor forest health and disturbance regimes over regional scales that can function as an early warning system for climate change effects on forests." In addition, McCarthy et al. (2001) warns that climate change can lead to loss of specific ecosystem types, such as high alpine areas. Complicating matters, it is not known whether species have the ability to adapt to rapidly changing environments through normal evolutionary processes (Berteaux et al. 2004, Humphries et al. 2004).

Monitoring the health of species requires an understanding of their basic requirements, many of which are based in their physiologic needs. At the basest level, living beings are constrained by their ability to tolerate various physical conditions (McNab 2002). Species have a range of ambient temperatures they can comfortably endure. Outside this range, individuals experience stress and eventually death. As global temperatures increase, species will be exposed to a warmer range of temperatures, some of which may place sensitive species in a thermally stressful environment.

Alpine species are rarely, if ever, exposed to high temperatures and will likely show the greatest response to warming. Their only options may be to move to higher, colder areas on the mountain or perish. Ultimately, if temperatures increase as predicted, alpine adapted mammals may be unable to move higher and may face localized extinctions.

Unfortunately, national parks across the United States are reporting that mammalian species are already moving to higher altitudes. For example, in Yosemite National Park, the American pika, once found at Olmstead Point (elevation 2,500m), no longer occurs at these lower elevations, and may be facing extinction pressure, as has been observed on other western mountains (Beever et al. 2003).

✦ METHODS

Capture of Animals

Animals were captured using standard traplines of Tomahawk (model 201) traps baited with rolled oats and black oil sunflower seeds mixed with peanut butter (ground squirrels) or locally collected vegetation (pikas). Traps were set in the early morning (just after sunrise) and checked every 2 hours. All traps were closed from 12:00–16:00 hrs to prevent thermal stress to captured animals. Captured animals were weighed, sexed, assessed for reproductive condition, and numbered eartags applied to each ear. Due to their fragility, pikas require modified trap methods, which are discussed below. All fieldwork was conducted under the auspices of an approved animal care and use protocol and met guidelines recommended by the American Society of Mammalogists (Gannon 2007).

Pikas are easily stressed, especially during warm or cold weather (>70°F or <45°F) and were trapped using open mesh traps to prevent overheating. Traps were set in the talus on a stable rock and covered on all sides, back, and top with additional rocks that protect the animal from sun, precipitation, and predators. Traps were opened early in the morning and checked every 2 - 4 hrs, depending on weather conditions.

Traps containing pikas were placed into a cloth bag for immediate transport to the on-site metabolic chamber. Pikas were transferred to an anesthesia jar, which consists of a see-through plastic jar with airholes perforating the bottom to prevent the build-up of carbon dioxide. A small perforated container containing cotton soaked with a liquid anesthesia (isoflurane) was placed in the larger anesthesia chamber with the pika. Following anesthetization pikas were removed from the chamber, weighted, sexed, given eartags, and placed into the metabolic chamber.

Metabolic Response Curves

Trials to measure metabolic parameters (thermal-neutral zone; upper/lower critical temperature) were performed in the field using a Sable Systems Inc. metabolic chamber (Hayes and O'Connor 1999, Campbell and Hochachka 2000, Terblanche et al. 2006). The Sable Systems Metabolic Chamber is highly mobile and was brought to the site of capture, powered by a portable generator. Individuals had metabolic rates measured *in situ* which reduced problems associated with capture, transport, and housing stress which may influence metabolic rates.

Metabolic rates were measured using a flow through respirometry system (Sable Systems, Inc., Las Vegas, NV). Individual animals were placed into individual respirometry chamber (950 ml volume) and attached to airflow lines. Individual respirometry chambers were placed into a controllable environmental chamber (Figure 1). To prevent dehydration and allow individuals access to food resources, an apple slice was provided to individuals inside the respirometry chamber. Apple slices do not affect metabolic measurements and during preliminary metabolic trials the addition of apple slices for water reduced problems with dehydration.

Individuals were subjected to a series of metabolic trials at increasing/decreasing temperatures. At each temperature that the environmental chamber was set, each individual animal was subjected to a metabolic trial. Each metabolic trial consisted of a 5 min baseline of ambient air, followed by a 15 min sample of the animal's respirometry chamber, followed again by a 5 min baseline. After all four individuals had run a metabolic trial the temperature in the environmental chamber was adjusted to the next experimental temperature and animals were allowed to acclimate to the new temperature for 45 min. Experimental environmental temperatures ranged from 10°C to 40°C and were adjusted in 3 or 5°C increments. Due to their lower heat tolerance, pikas were not subjected to high temperatures (>28°C). Following metabolic trials all animals were returned to the point of capture and released.

Airflow to the respirometry chambers was pumped at a rate of 500 ml/min and 300 ml/min for pikas and ground squirrels using individual Mass Flow Systems (Sable Systems, Las Vegas, NV) that standardize and monitor flow rates. After exiting the respirometry chambers air was directed through a computer controlled Baselining Unit and Multiplexor (Sable Systems, Las Vegas, NV) that allowed individual respirometry chambers or ambient air to enter the analyzer and be recorded by a laptop computer. Air being analyzed flowed into a Relative Humidity Meter (RH-300, Sable Systems, Las Vegas, NV) and then into the O_2, CO_2, and barometric pressure analyzer (Foxbox, Sable Systems, Las Vegas, NV). All data (airflow rate, ambient barometric pressure, chamber relative humidity, oxygen and carbon dioxide concentration, and environmental chamber temperature) was recorded to a computer file using the UI-2 Controller (Sable Systems, Las Vegas, NV).

Data files were analyzed using EXPEDATA (Sable Systems, Las Vegas, NV). For each recording, baseline concentrations of O_2 and CO_2 obtained from ambient airflow was used to calculate percent use of O_2 and percent addition of CO_2 by the animal. Rates of O_2 depletion and CO_2 addition (ml/hr) was calculated as the product of flow rate and percent depletion/addition. Rates of O_2 depletion and CO_2 addition were averaged across the entire 15 min sample from the respiration chamber resulting in a single metabolic response value (ml/hr) at the given environmental temperature. Therefore, each individual ground squirrel and pika had a series of metabolic rates at given environmental temperatures. These temperature-metabolic rate values were be plotted to give the metabolic response curve. The upper critical temperature of these metabolic response curves were calculated using a breakpoint analysis (Robbins 1986, Nickerson et al. 1989) that identified the point at which metabolic rates increase in response to warming temperatures.

Figure 1. The metabolic chamber is powered through a portable generator (right) and all metabolic equipment is contained within the vehicle.

Behavior Measurement

Individual squirrels and pikas were observed for behavior and activity using the focal technique of Altmann (1974). Individuals were captured using the trapping techniques above and given an eartag with a unique color bead attached to facilitate individual identification (Baack and Switzer 2000). Individuals were observed from the time of first sighting until the individual was out of sight. Once a focal animal was sighted the behavioral session began. Observers followed the focus animal and began recording the type of activity and the time that each activity started. This resulted in durations for all activities during the time individuals are observed.

When a focus animal was sighted, observers began the behavioral session by recording the start time, observer name, animal id, habitat, and weather conditions. Observers watched the focus animal using 7 x 35 binoculars and all behaviors were recorded. Start times of individual behaviors were monitored using a cumulative stopwatch, which recorded multiple time steps referencing the start time of multiple behaviors. Observers continued to record behaviors until the focus animal was lost from sight or 30 min has elapsed. Squirrel behavior was categorized into five major groups of behavior: exploration, food gathering, protection, social interactions, and maintenance (Sutton 1992). Pika behaviors were categorized into four major categories: surveillance, haying and feeding, vocalization, and territory defense

(Svendsen 1979, Smith and Weston 1995, Gliwicz et al. 2005).

Behaviors were monitored on consecutive days. Since both Pikas (*O. princeps*) and Uinta ground squirrels (*S. armatus*) are both diurnal, they were viewed starting shortly after sunrise until shortly after sunset. The behavioral event were recorded qualitatively and quantitatively as type of behavior and duration of behavior at the hour of day it occurs. Three microhabitats were monitored for temperature with iButton temperature loggers (Embedded Data Systems, LLC., Lawrenceburg KY): above ground exposed to solar radiation, above ground in shade and beneath ground in burrow/in rocks.

✦ RESULTS

Data collection occurred during the summer of 2009 and 2010 in Teton National Park, Wyoming and Rocky Mountain Biological Lab (RMBL), Colorado. In the summer of 2009, I took one graduate student to Teton NP and RMBL to collect metabolic data. We captured and ran metabolic trials on 12 pikas, 10 least chipmunks, and 3 yellow-pine chipmunks. During the preliminary study, data was successfully obtained, no animals were harmed, and all animals were released following metabolic trials. During the summer of 2010 I took a graduate student and an undergraduate student to both study sites. We collected more metabolic data on Uinta ground squirrels and pikas. In addition to metabolic data, we also collected behavioral data from Uinta ground squirrels and pikas.

Metabolic data has been collected and is currently being analyzed. We will be travelling to Sable Systems in Las Vegas, NV to obtain help in analyzing the metabolic traces. Due to the field conditions, the metabolic traces are not as clean as they would be in a lab and we need the expertise of Sable to help analyze the data correctly.

Pikas were observed for long blocks of time from 7am until 8pm. Total observation time varied throughout the day (Figure 2) and was used to standardize behaviors by the amount of time observers were watching.

Ambient temperatures in the talus slopes pikas inhabit increased throughout the day, as expected (Figure 3). Temperatures were constant and remained low within the rocks where pikas retire. Ambient temperatures rose with the day, peaked at 17:00 and then fell as the sun set. The addition of radiant heat from direct sunlight increased the effective temperature dramatically (Radiant Line).

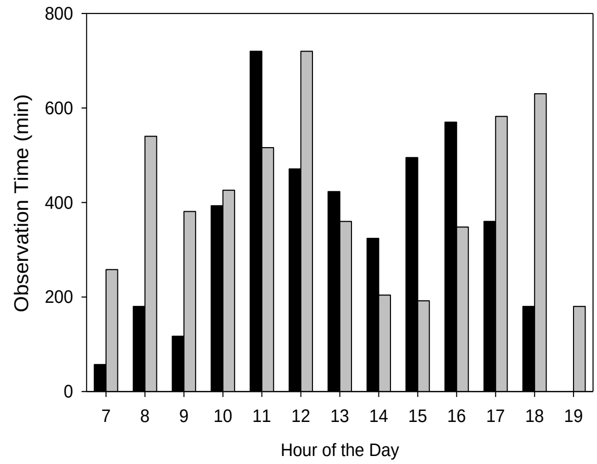

Figure 2 Number of minutes of observations per hour of day at Teton National Park (Grey) and Rocky Mountain Biological Lab (Black).

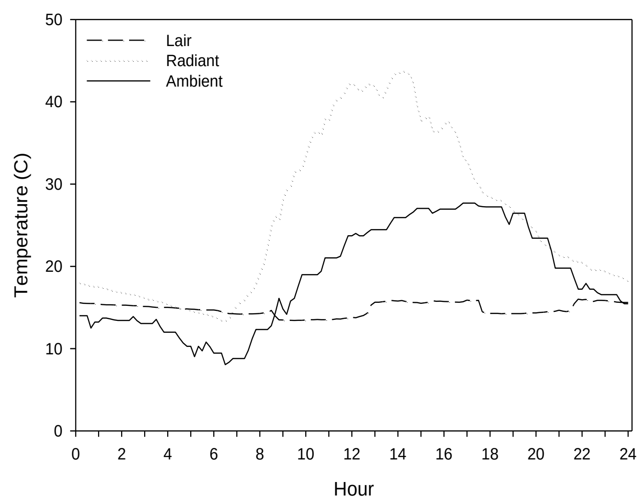

Figure 3. Temperatures under the rocks, where pikas hide, (lair), ambient temperature in the talus slope (ambient), and ambient temperature + radiant heat from the Sun (radiant).

Pikas did not have an even distribution of behavior throughout the day (Figure 4). Pikas in Teton NP were out doing behaviors during the morning (07:00 – 10:00) and evening (16:00 – 20:00), and were relatively inactive during the middle of the day (11:00 – 15:00). Pikas in Colorado also followed a similar pattern, increasing their active period from 07:00 – 10:00 and then had a period of decreased inactivity (10:00 – 15:00) during the middle of the day and then another active period in the afternoon (15:00 – 19:00).

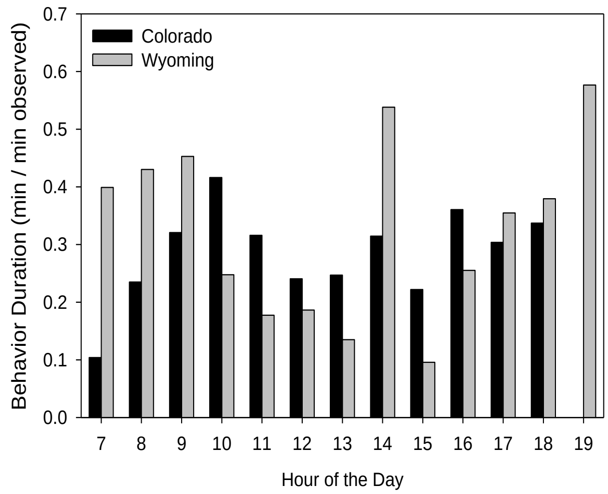

Figure 4. Total pika behavior by hour in Teton National Park (Grey) and Rocky Mountain Biological Preserve (Black).

The time pikas performed individual behaviors also varied throughout the day (Figure 5). In Colorado, calling, although a short behavior, was most frequent during late morning (10:00) and early afternoon (15:00 – 17:00). Running activities occurred throughout the day, but were common early in the morning. Observing their territory from a rock was also common throughout the day. Feeding activities were most common in the morning (09:00) and late afternoon (18:00).

In Teton NP, behaviors were also varied throughout the day (Figure 4). Calling was relatively constant throughout the day, but was more common in the middle of the day. Running was more common in the early morning. Observing on a rock was most prominent during early morning (07:00 – 09:00) and in early afternoon (14:00). Feeding tended to occur during the early morning and late afternoon. Haying activities occurred frequently from 09:00 to 12:00 and again at a relatively constant rate from 16:00 – 20:00.

✦ DISCUSSION

Metabolic Response Curves

We are currently analyzing the data files obtained during metabolic trials during the summer of 2009 and 2010. A problem with the relative humidity sensor was discovered after the 2009 summer session and was corrected for the 2010 field season. The humidity sensor was not calibrated properly and was overestimating water vapor in the chambers and throwing off the results. The humidity sensor was calibrated properly and a correction factor was calculated and applied to the 2009 summer data.

During the summer of 2010 we completed the measurement of metabolic rates for Uinta ground squirrels and pikas. The metabolic data for both species are currently being analyzed by Chris Effken, a graduate student, for use in his thesis.

Behavioral Observations

During the 2010 field season we observed 30 Uinta ground squirrels and approximately 25 pikas. Uinta ground squirrel observation data is still being analyzed and were used to publish an article on their behavior in relation to hour of the day and temperature. It is important to note that the data presented in this annual report are preliminary and are still being analyzed. Therefore, these data should not be used for any scientific purposes until the data have been fully analyzed.

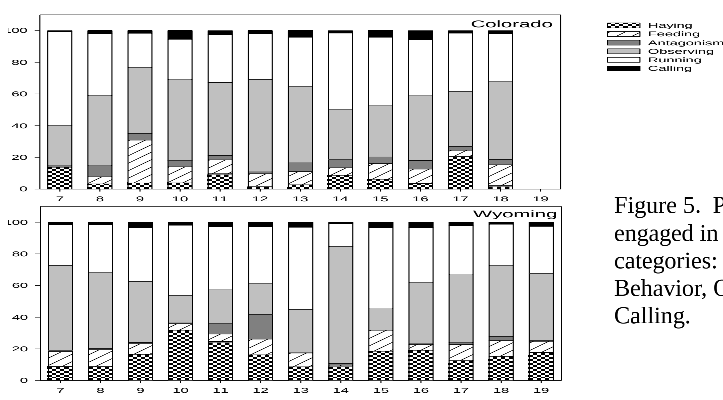

Figure 5. Percent of total behavior pikas engaged in one of the six major behavior categories: Haying, Feeding, Antagonistic Behavior, Observing on a Rock, Running, or Calling.

Ambient temperatures underneath the rocks in pika lairs, were constant throughout the day, remaining at low temperatures. Ambient temperatures in the talus slope increased as the sun rose, peaked at 17:00, and decreased with sunset. Interestingly, the addition of radiant heat increased the total temperature greatly. This would represent the added heat to a pika that is outside during the hot part of the day. The additional radiant heat may push pikas over their thermal limit, thus reducing the amount of time pikas may be active, even if ambient temperatures are within their thermoneutral zone.

Pikas in both Colorado and Wyoming tended to do most of their behaviors in the morning and afternoon hours and have decreased activity, remaining under the rocks, during the middle of the day. Haying activity was prominent in mornings and afternoons.

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