Physiological constraints on the ecology of activity-limited ectotherms

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Dedication

To the life’s work, legacy, and memory of Frances Velay and Jennifer Elwood

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ABSTRACT

Physiological constraints on the ecology of activity-limited ectotherms

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Organismal exchanges of heat, water, and metabolizable energy with their environment are important influences on their behavior, physiology and, life history. Where extreme climates and resource-poor environments restrict an organism's overall activity budget, physiology—through performance, tolerance, acclimation, and trade-offs—becomes a primary influence on that organism's ecology. Vertebrate ectotherms exemplify these physiological constraints because their body temperatures are closely tied to thermal and hydric exchanges with their environment; they are typically highly tolerant of a broad range of conditions; and they exhibit boom-and-bust cycles related to release from constraints. This dissertation examines physiological constraints on wood frogs (*Rana sylvatica*) at the extreme southwestern edge of their range, desert tortoises (*Gopherus agassizii*) which spend >98% of their lives in burrows, and the eggs of leatherback turtles (*Dermochelys coriacea*) which incubate for months on a tropical beach during the dry season. The distribution of microhabitats available to each focal ectotherm delineated where and when these organisms could be surface-active, what constituted adequate refugia for intolerable surface periods, and why these activity-limited organisms behave differently from conspecifics elsewhere. Direct measurements of physiological performance (metabolic rates, locomotion) over the focal organism's tolerated range of body temperatures and hydrations assessed the consequences of thermal and hydric exchanges with suboptimal microhabitats. These exercises constitute a quantification of important influences on the physiological ecology of activity-limited vertebrate ectotherms. Comparative analysis of the allometry of physiological traits in a variety of mammals served to elucidate the functional and phylogenetic constraints on physiological adaptation. This quantitative and model-based approach is useful for quantifying risk (e.g., desiccation risk), estimating processes that are hard to measure (e.g., metabolic heating of sea turtle eggs buried 1 m deep in sand), and predicting responses to future changes (e.g., global warming). These qualities recommend this approach as a practical tool in conservation biology.

CHAPTER 1: General Introduction

Why study 'activity-limited ectotherms'?

So what ecology is there to study in organisms with extremely limited activity? In sedentary, fossorial animals, there is actually a pretty extreme (i.e., interesting) aspect to their ecology tied to the fact that they do not behaviorally alter the microhabitats with which they interact. When the going gets tough, activity-limited organisms do not get going. Instead, these organisms persist and thrive primarily via (1) exceptional microhabitat (refuge) selection, (2) their particular exchanges of heat, water, and energy with the microhabitat, and (3) the breadth of their physiological performance, acclimation, and tolerance. And in vertebrate ectotherms, whose body temperatures are derived primarily from environmental influences, the last two points are highly interconnected. Put simply, physiological mechanisms are of primary importance for activity-limited vertebrate ectotherms because they do not (and often cannot) move elsewhere when their microhabitat becomes intolerable. Activity-limited animals are typically found in extreme environments (e.g., deserts), seasonally extreme environments (e.g., winter), and at the edge of their geographical range, particularly in ectotherms.

How does one study the physiological ecology of activity-limited ectotherms?

Exchanges of heat and water with the environment have long been recognized as important influences on the ecology of ectotherms such as reptiles and amphibians (Thorson and Svihla 1943, Cowles and Bogert 1944). These abiotic aspects of the environment with which ectotherms interact and exchange either mass or energy are classified as part of the ectotherm’s “operative environment” (Mason and Langenheim 1957; Spomer 1973). They are key parts of the ectotherm’s ecological web of influences which can, indirectly and/or directly, affect its fitness (Andrewartha and Birch 1984).

I adopted the formalism of Dunham and others (1989) in using “operative environments” to examine the physiological ecology of activity-limited ectotherms. Dunham and others (1989) extend the definition of “operative environment” to the population-level by specifying series of mechanistic relationships between operative environments and an organism’s life history phenotypes via transduction through that organism’s physiology. Operative environments are those aspects of an organism’s habitat with which it interacts and exchanges resources, and that thereby influence the organism’s expected fecundity and survivorship (Dunham et al. 1989; Dunham 1993; Dunham and Overall 1994). Operative environments are transduced through individual physiologies to population level processes via influences on the organism’s activity and resource accrual (e.g., Congdon et al. 1982; Grant 1990; Grant and Dunham 1990; Huey 1991). Transduction occurs through allocations of time and resources to competing functions which can be important over relatively short time frames (e.g., being active exposes the organism to predators; Sears 2005) or become important over longer time frames (e.g., allocating acquired energy for maintenance/storage versus growth/reproduction in different demographic environments, Tinkle et al. 1993). These allocations are specified based upon a combination of biophysical constraints, energy resource limitations, the constraints and trade-offs imposed by the organism’s physiology, and, for individuals, their inherited set of rules for allocation under the preceding constraints (i.e., their life histories, Dunham et al. 1989; Huey 1991; Stearns

1992). Taken together, these allocations determine age- or size-specific birth rates and probability of survivorship in individuals and their contribution to population dynamics.

The preceding forms a paradigm for studying organismal interactions with their environment which is the basis for the chapters herein that are focused aspects of physiological ecology. I rely on the quantification of mechanistic relationships in these organismal interactions with their environment in order to understand them and to expand the domain of generality to the prediction of future effects (e.g., global warming on leatherback turtle, *Dermochelys coriacea*, sex ratios), comparisons across the range of an organism (e.g., the desert tortoise, *Gopherus agassizii*, throughout the Mojave Desert), and effects that are difficult to measure directly, but which are important to conservation (e.g., wood frog, *Rana sylvatica*, risk of desiccation).

Chapters 2 and 3

Wood frogs have an extensive range across North America, from north of the Arctic Circle to the northern edge of Alabama and Georgia. They are pond-breeding amphibians, and, as their name suggests, they typically inhabit forested habitat as juveniles and adults. Throughout their range, wood frogs are also the first amphibians to migrate back to the breeding pond in late-winter/early-spring. I assembled a comprehensive table of wood frog activity characteristics from the literature, including the seasonal timing of breeding and the daily timing of their surface activity (Table 1). Values from introduced wood frog populations were excluded, including those from Newfoundland (reviewed by Campbell et al. 2004), near St. Louis, Missouri (Guttman et al. 1991), and in west-central Illinois (Thurow 1994). Overall, wood frogs increase daily surface activity the farther north they are located without changing markedly in body size or preferred upland habitat (forest), where available. Wood frogs also do not exhibit significant phylogeographic patterns in genetic structure beyond the effects imposed by absolute dispersal barriers (large bodies of water; Lee-Yaw et al. 2009). Thus, plasticity in behavior is not likely to be genetically determined.

At the southwestern edge of their range in Missouri, daily surface activity is reduced to essentially nil (Rittenhouse and Semlitsch 2007a). This is unusual in wood frogs that typically exhibit at least some diurnal and/or nocturnal activity in other parts of their range (Table 1). I investigated the environmental constraints on Missouri wood frog activity throughout the spring and early-summer and the implications their microhabitat selection (primarily of refugia) has in terms of physiological exchanges and performance consequences. This study also captured variation in microhabitat characteristics related to timber harvest, a major threat to North American amphibians (Semlitsh et al. 2009), and Missouri topographical features (drainages) which were highly preferred microhabitats for post-breeding wood frogs (Rittenhouse and Semlitsch 2007a, 2009). Because the wood frog is a state species of conservation in Missouri, the assessment of critical habitat requirements and the relative effects of different anthropogenic impacts from several timber harvest techniques will better inform conservation practices in their managed forest habitat.

Chapter 4

Across their Sinaloan, Sonoran and Mojave Desert range, desert tortoises persist in areas with drastically differing resource environments (tolerable surface microhabitats, vegetative forage) both spatially and temporally (Table 7). The study herein departs from the traditional method of understanding desert tortoise physiological ecology via comparisons between drier and wetter regions (e.g., Wallis et al. 1999) or periods in time (e.g., Henen et al. 1998; Duda et al. 1999) by focusing instead on microgeographic variation in constraints on activity across a rainfall gradient. The desert tortoise exhibits genetic structure across its range related to absolute barriers to dispersal (large bodies of water) as well as landscape features (e.g., urban development; Murphy et al. 2007). Within Ivanpah Valley, however, significant differences in surface activity, body size, and reproduction are likely to be driven by environmental factors because assessments of home ranges (Franks 2002) and preliminary assessments of genetic structure (Izzo 2003) indicate that there is no significant barrier to genetic dispersal across the valley. The desert tortoise is federally listed as threatened. Development of portions of Ivanpah Valley for solar energy generating systems may render necessary the use of translocation of individuals to alternate habitat (BLM 2009). Current determination of suitable alternate habitat relies on assessments of ‘typical’ desert tortoise habitat (Nussear 2004) and mitigation of other anthropogenic effects (e.g., fencing of habitat near roads; Heaton et al. 2008). The assessment of how desert tortoise microhabitat use and reproductive ecology is tied to environmental factors in surprising ways (i.e., resource-poor habitat increases reproductive success in average-rainfall years), provides ecological insight into the selection of appropriate alternative habitat for translocated individuals.

Chapter 5

Leatherback turtles are critically endangered in the Eastern Pacific. Current conservation efforts focus on their nesting beaches, and Playa Grande, Parque Nacional Marino Las Baulas, Costa Rica is one of the major remaining rookeries for Eastern Pacific leatherback turtles (Santidrián Tomillo et al. 2007). Because conservation efforts for sea turtles, including leatherback turtles, typically include removal of egg clutches at greater risk for mortality (e.g., from tidal inundation) to beach hatcheries (Pfaller et al. 2009), I assessed the effects of this hatchery removal on clutch metabolic heating (an indicator of survivorship) and resulting sex ratios for these hatchlings with temperature-dependent sex determination (Bull 1980). Egg incubation temperatures were monitored both in hatcheries and in natural nesting sites over almost a decade, and the effect of hatchery removal on overall sex ratios was minimal compared with inter-annual effects due to climatic changes (e.g., increased rainfall). The major climatic influences at this location are from the El-Niño Southern Oscillation and Atlantic Tropical Cyclone activity (Waylen and Harrison 2005), both of which will be influenced by global warming (IPCC 2007; Saunders and Lea 2008). This long-term study is the first to reveal the relative influences of climate and hatchery translocation on leatherback turtle reproductive success, and will serve as an important consideration for land managers charged with protecting and recovering sea turtle nesting beaches worldwide in the face of global warming.

Chapters 6 and 7: Significance of Research

Allometries are the ubiquitous scaling relationships observed between a variety of organismal traits and the organism's body size (Peters 1983; Calder 1984; Schmidt-Nielsen 1984). These relationships are incredibly useful in a variety of disciplines including engineering, medicine, and conservation biology (reviewed by O'Connor et al. 2007). Chapter 6 comprehensively demonstrates the pitfalls of oversimplifying allometric relationships between species-specific physiological traits (e.g., metabolic rates, body temperatures) and choosing appropriate analytical models for allometric data. This is useful analytically as well as in understanding functional and phylogenetic constraints on basal metabolic rates in different clades. This broad-scale analytical approach to studying energetics represents an important addition to the conceptual framework for studying physiological ecology laid out by Costa and Sinervo (2004). Finally, the operative environmental modeling approach to physiological ecology yields mechanistic insight into systems that are often complex and yet need to be understood quickly and adequately to meet the exigencies of conservation. This approach is applied in two very different systems, a small desert lizard (*Sceloporus merriami*, Big Bend, TX) and the wood frog (Daniel Boone Conservation Area, MO), in Chapter 7 in order to illustrate its utility in a range of conservation applications.

Table 1. Macrogeographic variation in wood frog (*Rana sylvatica*) habitat, reproduction, and activity reported in the literature. 'Temperate forests' refers to wood frogs found in deciduous, coniferous, and mixed forests

Location	Upland Habitat	Breeding Period	SVL* (mm)	Active Period	Citation
Yukon Territory	temperate forests, meadow, muskeg, tundra	late-April – June	≤ 60		Hodge 1976; Yukon Amphibians 2005
Northwest Territories/Nunavut	temperate forests, muskeg, tundra (remain near ponds)	May 14**	≤ 50		Hodge 1976; Mathisen 2008
British Columbia	tundra, taiga, temperate forests, field, muskeg	late-February/March†	35 – 50	diurnal	Corkran & Thoms 2006; Campbell 2004; Green & Campbell 1984
Alberta	Aspen parkland, boreal mixedwood forest	late April – June	30 – 60	diurnal	Stevens & Paszkowski 2004; Russell & Bauer 2000
Manitoba	forest-tundra transition, boreal coniferous forest, mixed woodlands, aspen parkland, grasslands	mid-April – late-April	43 – 47	at least occasionally at mid-day near water (July)	Preston 1982
Saskatchewan	boreal forest, aspen parkland, grasslands, tundra	mid-April – early-May	30 – 60 (max 80)		Cook 1978
Ontario	temperate forests, open field	late-March – mid-May	41 – 65	at least occasionally at night†	Licht 1991; MacCulloch 2002; De Solla et al. 2006
Quebec	temperate forests, wet fields, peat bogs	late-May – early-June			Denman & Lapper 1964; Desroches & Rodrigue 2004; Oullet et al. 2009

Labrador	peat bogs (remain near ponds)	early – mid-June			Hildebrand 1949; Murray 1990
New Brunswick	peat bogs, forest	early – mid-May		nocturnal	Mazerolle 2001; Oseen & Wassersug 2002
Prince Edward Island		May 13**	≤ 60		Macphail Woods Survey 1992
Nova Scotia	temperate forests	late Mar – early Apr (inland), May (Cape Breton Island)	≤ 59		Gilhen 1984
Alaska	boreal forest, subalpine alder scrub, humid taiga, tundra, meadow	June – mid-July (North); late-April – June (Interior Alaska); late-April – mid-May (South)		mid-day	Kessel 1965; Herreid & Kinney 1966; Hodge 1976; Anderson 2004; Hokit & Brown 2006;
Idaho	(Rocky Mtns.)		58.5**		Dumas 1957
Wyoming	(Rocky Mtns.)	mid-May	42 – 50		Dunlap 1977; Corn & Livo 1989; Cerovski et al. 2004
Colorado	mixed forest bordering multiple mesic area types	Apr 29 – June		daytime (Spring), day/night (Summer)	Corn & Livo 1989; Vertucci & Corn 1996; Hammerson 1999
South Dakota	temperate forests	late-Mar – early Apr	50 – 70		Fischer et al. 1999
Minnesota	temperate forests, floodplain forest, spruce/tamarack bog	late-March – early-May	50 – 70	diurnal; occasionally day & night†	Bellis 1962, 1965; Karns 1992; Oldfield & Moriarty 1994
Wisconsin	temperate forests, prairie	late-March – early-May	30 – 50 (max 75)	daytime (coniferous; deciduous†)	Vogt 1981; Tekiela 2004b

Michigan	temperate forests, hardwood swamp, prairie	March – early-April	≤ 75	daytime (near water); diurnal (mid-May)	Heatwole 1961; Berven 1995; Wright & Wright 1995; Tekiela 2004a
Illinois	temperate forests, floodplains	Feb 26 – March	43 – 57		Smith 1961; Redmer 2002
Maine	mature mixed forest, lagg, forested bog, wooded heath, shrub heath, moss-*Chamaedaphne*, streamside meadow, shrub thicket	late-March (South), late-April (North)	40 – 58	day & night	Stockwell & Hunter, 1989; deMaynadier & Hunter 1999; Hunter et al. 1999; Vasconcelos & Calhoun 2004; Baldwin et al. 2006; Blomquist & Hunter 2007
Massachusetts	temperate forests	Feb 28 – early-April			Banta 1914; Regosin et al. 2003
Rhode Island	temperate forests	late-Feb – early April	35 – 65		Paton et al. 2000; Paton & Crouch 2002; Univ. of Rhode Island, *unpub. data*
Connecticut	maritime forest, temperate forest	Feb 9 – early-Apr	39 – 63		DeGraaf et al. 1983; Klemens 1993; Skelly 2004
New York	mature deciduous forest	Mar 7 – Apr 14 (South); Mar 26 – Apr 20 (Central); Apr 9 – May 25 (North)†			Gibbs et al. 2007; Banta 1914
Pennsylvania	deciduous forest	Mar 4 – early May		diurnal/nocturnal (Spring), nocturnal/rainy day (Summer)	Hulse et al. 2001
Maryland	temperate forests	mid-Feb – mid-March	34 – 56		Berven 1982, 1995

West Virginia	moist deciduous woodlands	mid-Feb	76.2	daytime	Green & Pauley 1987
North Carolina	deciduous forest	Jan – Feb	35 – 83		Dodd 2004; Martof et al. 1980
South Carolina	deciduous forest	Feb	35 – 83		Martof et al. 1980
Virginia	deciduous forest	Feb – mid-March	35 – 83		Martof et al. 1980; Berven 1982, 1995
Kentucky	moist woodlands	early-Mar	38 – 70		Barbour 1971
Tennessee	deciduous forest	Jan – Feb	55 – 75		Meeks & Nagel 1973; Dodd 2004
Missouri	mesic deciduous forest	early-Feb – late-March†	35 – 70	nocturnal†	Johnson 1977; Johnson 2000; Hocking et al. 2008; Rittenhouse and Semlitsch 2007
Arkansas	forest	early Feb – early Mar	35 – 70 (max 83)		Trauth et al. 2004
Alabama	semideciduous forests, mesic woodlands	mid-Jan – late Feb†	50 – 60 (max 85)		Mount 1975; Davis & Folkerts 1986
Georgia	deciduous hardwood forest, mixed forest	Jan – mid-Feb	50 – 67		Jensen et al. 2008

* Range of mature adult snout-vent lengths; ** Isolated sighting; † Associated with rainfall

CHAPTER 2: Biophysical and physiological ecology of wood frogs in forested habitat impacted by land-use alteration

ABSTRACT

Amphibians are declining worldwide at a faster rate than any other vertebrate group and habitat loss due to land-use is a major contributing factor. Pond-breeding amphibians, such as wood frogs (*Rana sylvatica*), require aquatic habitat as larvae and terrestrial habitat as juveniles and adults. We examined wood frog operative environments in forested habitat surrounding breeding ponds altered by different timber harvest methods (selective, clearcut) in the Daniel Boone Conservation Area (DBCA), Missouri, USA. Clearcuts generated brushpiles and vegetative regrowth which limited wind and, coupled with greater incident solar radiation, maintained hot, humid air near the ground. We estimate that wood frogs occupying clearcuts have elevated body temperatures and evaporative water loss (EWL) rates relative to those in less-severely harvested forest. Selective harvest was similar to the control in retaining canopy cover that decreased incident solar radiation and ground-surface temperatures. However, wind promoted vapor deficits at the ground-surface and leaf litter refugia were the only terrestrial microhabitats affording adequate protection from desiccation in periods between rainstorms. Drainages, a common landscape feature throughout DBCA, were effective wind shelters, but their steep slopes and thin soil limited canopy cover and leaf litter accumulation. We estimate that body temperatures and EWL rates in drainages run intermediate between those in clearcuts and the control. An important benevolent characteristic of drainages was their extended retention of soil water potentials above levels that would dehydrate frogs. In

terrestrial habitat, desiccation risk for pond-breeding amphibians, such as wood frogs, is location and time-dependent, and intricately tied to thermal and hydric conditions near the ground. Our results indicate that use of selective timber harvest over clearcutting is advisable, and protection of microhabitats that specifically decrease desiccation risk in periods between rainstorms—in Missouri, thick leaf litter—should be a priority in land-management decisions for the terrestrial habitat of pond-breeding amphibians.

INTRODUCTION

Amphibians are declining worldwide at a faster rate than any other vertebrate group and habitat loss due to land-use is a major contributing factor (Wake 1998; Stuart et al. 2004). Particularly in forest ecosystems, amphibians play an important role in terms of their relative abundance and biomass, nutrient and energy flow, and sensitivity to a suite of habitat conditions (Welsh and Olivier 1998, Wyman 2003). Pond-breeding amphibians, such as wood frogs (*Rana sylvatica*), have biphasic lifecycles requiring aquatic habitat as larvae and terrestrial habitat as juveniles and adults. Due to their limited vagility and movements, these amphibians are likely to be found in high densities near breeding ponds (Semlitsch and Bodie 2003; Rittenhouse and Semlitsch 2007b), and timber harvest of forested areas in the vicinity of aquatic areas may be particularly detrimental to these amphibians (Wilbur 1980; Semlitsch 1998).

Investigators at the Universities of Missouri, Maine, and Georgia created a landscape-level test of the effects of different timber harvest methods on pond-breeding amphibian demography and movements (LEAP, Land-use Effects on Amphibian Populations). They hypothesized that amphibian breeding ponds surrounded by highly disturbed habitat are isolated and prone to local extinction because of ecological impedance to dispersal and recolonization (Semlitsch et al. 2009). They further hypothesized that different timber harvest methods, such as clearcuts versus selective harvests, will impede amphibians to different degrees (i.e., clearcuts create the greatest impedance) which would be detectable demographically, behaviorally, and in microcosm (Semlitsch et al. 2009). Indeed, several of these hypotheses were supported for a variety of amphibians by biotelemetry and mark-recapture data from 5 years of monitoring preand post- timber harvest (Patrick et al. 2006; Rittenhouse and Semlitsch 2009; Semlitsch et al. 2008, 2009; Todd et al. 2009). However, responses to timber harvest, including behavioral, reproductive, and survival schedules, were also seasonally, geographically, life-stage and species-specific (e.g., Hocking and Semlitsch 2007; Blomquist and Hunter 2009; Rittenhouse and Semlitsch 2009). For instance, adult wood frogs in Missouri avoided clearcuts while Missouri gray treefrogs preferred them as sites for reproduction (Hocking and Semlitsch 2007; Rittenhouse and Semlitsch 2009).

Wood frogs exiting LEAP breeding ponds were caught in 2004, 2005, and 2006, fitted with radio transmitters and released into the quadrant most closely corresponding with the location of the pitfall trap they were caught in (Rittenhouse and others 2007, 2009). Tracked wood frogs were visually relocated every other day during daylight hours for 50 consecutive days (end of transmitter battery life). Rittenhouse and others (2007, 2009) used this biotelemetry approach to track post-breeding wood frogs on their spring migrations away from breeding ponds, and her findings were surprising given previously understood activity patterns in wood frogs (Table 1). Missouri wood frogs only move on rainy nights, and otherwise, they remain underneath leaf litter often without even turning around (Rittenhouse and Semlitsch 2007, 2009; Rittenhouse et al. 2009). Furthermore, pre-timber harvest wood frogs made significantly more, smaller movements within LEAP arrays relative to post-harvest movements (Rittenhouse and Semlitsch 2007, 2009). Post-harvest wood frogs made longer, directed movements often toward the nearest drainage, and many made it outside of LEAP arrays in their first rainy night movement (Rittenhouse and Semlitsch 2009).

The missing link in the preceding results is a quantification of the biophysical and physiological mechanisms underlying amphibian responses to timber harvest. Thermoregulation is widely recognized as an important aspect of an ectotherms' ecology because of the influence of body temperature on performance (Thorson and Svihla 1943; Hutchison and Dupre 1992). Body temperatures of small ectotherms are primarily affected by substrate (e.g., ground surface) temperatures via conductance (Tracy 1982), but the wet skin of amphibians further forces them to balance simultaneous exchanges of water and heat with their environment (Spotila 1972; Lillywhite 1975; Tracy 1975, 1976; O'Connor 1989; Spotila et al. 1992). Water is therefore thought to be a primary constraint on amphibian habitat utilization because of their high rates of cutaneous evaporative water loss (Thorson and Svihla 1943; Spotila 1972; Preest and Pough 1989, 2003).

Because thermo- and hydro-regulation are such important influences on amphibian ecology, we used micro-meteorological measurements and physical models of frogs to describe the distribution of available microhabitats, thermal and water exchanges in those microhabitats throughout the LEAP-array, and how microhabitats vary among timber harvest quadrants. Physical operative environment models integrate multiple abiotic factors to measure thermal and hydric conditions in the microhabitats available to the frogs (Tracy et al. 2007). We concentrated on one representative pond and the four timber harvest quadrants in the array surrounding that pond.

MATERIALS AND METHODS

Study Site

We monitored the habitat, and estimated thermal and hydric exchanges, for wood frogs migrating away from breeding ponds from March – July 2007 in the Missouri

Department of Conservation’s Daniel Boone Conservation Area (DBCA, ~1400 ha; Fig. 1), Warren County, Missouri. DBCA is a Missouri state forest in the upper Ozark Plateau consisting of mature, second-growth oak (*Quercus* spp.) and hickory (*Carya* spp.). Amphibian breeding sites are fishless, wildlife watering holes (i.e., ponds) constructed along ridgelines ca.1960 – 1980’s, and colonized naturally by a variety of amphibian species (Hocking et al. 2008).

Experimental timber harvest was conducted in the summer and fall of 2004 on forest immediately surrounding five Missouri amphibian breeding ponds as part of the NSF-collaborative project, Land Use Effects on Amphibian Populations (LEAP). Landscape-level replication of this experiment was implemented in Maine and South Carolina (Semlitsch et al. 2009). Timber harvest arrays consisted of a clearcut with high levels of coarse woody debris (CWD) retained (“Clearcut CWD Retained”), a clearcut with CWD removed (“Clearcut CWD Removed”), a selective harvest with 50 – 60% canopy removal (“Partial”), and an unmanipulated control (“Control”; Semlitsch et al. 2009). Each array (e.g., Fig. 2) was centered on an amphibian breeding pond, and arrays were divided into four equal quadrants (~2.11 ha each) with Clearcuts randomly assigned to opposing quadrants and likewise for the Partial and Control. All marketable timber greater than 25 cm in diameter at breast height was removed from the two Clearcut treatments. In the Clearcut CWD Retained, the remaining trees were felled and left on the ground. In the Clearcut CWD Removed, remaining trees were girdled. The Partial was harvested by girdling or felling trees. Due to logistical constraints, data reported in this study are just from LEAP-Missouri Pond 2.

Local relief in Pond 2 was ~30 m from the ridgetop containing the breeding pond to the downslope, outside edges of the array (Fig. 2). Rocky drainages occur in several parts of the Pond 2 array where streams that form following rainstorms carve ravines into limestone hillsides. Throughout all array quadrants, the forested land immediately surrounding these drainages was not experimentally harvested due to erosion concerns. Beyond the Pond 2 array, the downslope hillsides are part of the overall drainage network of DBCA. In drainages, a thin layer of soil 6 – 10 cm deep covers limestone bedrock on steep hillsides that undulate between exposed rocky outcroppings and carved rocky ravines. Drainages within the LEAP-Missouri arrays and the hillsides along the large valley streambed (e.g., between Ponds 2 and 5, Fig. 1), were highly preferred post-breeding habitat for wood frogs (Fig. 2; Rittenhouse and others 2007, 2009).

Micrometeorology

We erected meteorological stations in each quadrant surrounding Pond 2 in 2007 (March – July). At each meteorological station, measurements included incident solar radiation at the ground surface (Li-Cor LI200X-L, Lincoln, Nebraska), wind speeds at 50 cm height (R.M. Young Wind Sentry, Traverse City, Michigan), an air temperature profile with shielded thermocouples (Christian and Tracy 1985) at -2, 0, 5, 10, 25, and 50 cm height relative to the ground. Recordings were taken every 15 minutes by a datalogger (CR-10X, Campbell Scientific, Logan, Utah) connected to a multiplexer (AM-32, Campbell Scientific, Logan, Utah).

In the fall of 2006, the Clearcut CWD Retained was subjected to a prescribed burn, and meteorological measurements therein were in an area devoid of vegetation and brushpiles (still some charred remains). Within the Clearcut CWD Removed, we erected two meteorological stations, (1) in a ridgeline area with very dense vegetative re-growth and brushpiles (Clearcut CWD Removed – Ridgeline) and (2) a downslope site in a wide clearing (Clearcut CWD Removed – Downslope). In addition to the four Pond 2 quadrants, we also monitored a meteorological station in a Drainage site 320 m straight-line distance, and around 60 m lower in elevation, from Pond 2. Additional monitored sensors included, (1) rainfall (TE-525, Campbell Scientific, Logan, Utah) in a Clearcut CWD Retained clearing; (2) soil moisture probes permanently placed in the Clearcut CWD Removed – Ridgeline and the Drainage (ECH$_2$O EC-5, Decagon Devices, Pullman, Washington); and (3) a mast of low wind speed heated needle anemometers (Model ANE1, East 30 Sensors, Pullman, Washington) placed daily in different treatments with needles at 2, 5, 10, and 20 cm height off the ground.

Soil

We took 4 soil samples down to just over 10 cm depth. There were 2 samples from the Clearcut CWD Removed – Ridgeline and 2 from the Drainage. We measured soil water potential in homogenized samples from the top 5 cm of the soil (0 to 5 cm depth), and soil from the depth of the soil moisture probe end (5 to 10 cm soil depth). We used the WP-4T Dewpoint Potentiameter (Decagon Devices, Pullman, Washington). Large organic material and rocks were removed from the soil. We dried the soil to constant mass at 60°C for 72 hours and then rehydrated it gravimetrically in serial quantities to obtain a soil moisture potential curve over a range of concentrations.

Physical Models

We created arrays of wood frog mannequins at locations within quadrants associated with wood frog migratory movements (Rittenhouse and others 2007, 2009). To create the mannequins, frog molds were originally created using cold immobilized, small adult leopard frogs casted in dental investment material (Jeltrate, Dentsply International, Inc., Milford, Delaware). We filled these molds repeatedly with plaster to form mannequins. Holes were drilled into the mannequin core and thermocouple wire (Omega Engineering, Stamford, CT) was inserted and glued into the core with epoxy. Plaster frog models had been used successfully in a past study to measure operative temperatures of temperate anurans (O'Connor 1989). We modified their use slightly by sewing form-fitting denim jackets with extended tails that were placed tightly over the surface of the plaster mannequin. The tails ran to a water reservoir dug into the ground near the model. The denim material wicked water from the reservoir to the model surface. Models and denim jackets were soaked in water the night before placement in the field. Both the wick (tail) and the top of the water reservoir were wrapped in self adhering plastic wrap with a gardeners twist tie wrapped around the lip of the reservoir. A small strip of wax paper was also placed beneath the model to prevent any exchanges with the ground.

At wood frog migration locations within a quadrant, and in the near vicinity, arrays of 15 plaster frogs were assembled in five groups of three with 2 frogs under "Litter" for every 1 frog on the "Surface." In Clearcut treatments, Litter consisted of a single layer of leaves, bark, debris, and/or grass tussocks. Otherwise, Litter consisted of multiple layers of leaves in varying stages of decomposition. Mannequin thermocouples were connected to the dataloggers and recorded body temperatures every 15 minutes. A handheld hygrometer was placed adjacent to the model during daily weighing and refilling of water reservoirs. This yielded measurements of air vapor densities in each quadrant.

Despite careful attempts to level the water reservoirs and plaster mannequins with each other, the hilly study location created a gravitational draw on the wicking of the water which caused the plaster models to overestimate water loss rates in hilly areas (reviewed by Tracy et al. 2007). We subsequently measured evaporative water loss rates by sculpting frog mannequins out of cellulose sponge which mimicked a wood frog in a crouched resting pose (see Hasegawa et al. 2005). We used a random number generator (MATLAB 2008a) to create randomized coordinates throughout the Pond 2 array at which we placed the sponge frogs. Sponge frogs were placed with two under the Litter for every one at the Surface in each location with a small strip of wax paper underneath each one. Sponge frogs were fully hydrated before 0700 hours each morning, weighed using a Pesola, and subsequently re-weighed every 4 hours until sunset. Sponge frogs were employed specifically in the days following a major rainfall event (> 10 mm) and two such rainstorms and their hydric consequences for frogs over the subsequent 7 days without rain were tracked using this approach.

Computer Models

We used classical biophysical equations and the parameters values measured by the meteorological stations in each timber harvest quadrant to estimate EWL rates for 15 g wood frogs at the Surface. These rates could then be extrapolated to estimate how much time the amphibian would have in a particular Surface microhabitat before it reached critical (80%) dehydration. We compared these results with the modeled Litter EWL rates described in Chapter 7.

Analyses

Two-way analysis of variance (ANOVA) tested the effects of forestry treatment and position under the litter versus on the surface on air vapor densities and daytime body temperatures of plaster model frogs. Generalized estimating equations tested whether EWL rates of sponge frogs were significantly affected by forestry treatment, position under Litter versus on the Surface (fixed effects), and number of days post-rainstorm (covariate). The correlation matrix structure was specified as exchangeable to account for the effects of multiple observations of individual sponge frog locations on the variation in the response variable (Zuur et al. 2009). Least Significant Difference-adjusted pairwise comparisons were performed to assess differences between factor levels.

Two-tailed Pearson correlations assessed (1) relationships between Pond 2 meteorological variables and the same variables measured at nearby weather stations, and (2) relationships between daily soil moisture changes post-rainstorm (taken from an exponential fit to the original soil moisture measurements, MATLAB 2009a), ground surface temperatures, and air water vapor densities. The nearby FencePost-Warrenton weather station was most closely correlated with Pond 2 meteorological measurements, and daily air water vapor density measurements from FencePost-Warrenton were substituted for missing measurements at Pond 2. Finally, quadratic regressions (MATLAB 2008a) were used to fit soil water retention relationships between soil moisture (independent variable) and soil water potential (dependent). We carried out statistical analyses using SPSS 15.0 except as noted. The significance level for all analyses was $P < 0.05$, and all data are presented as mean ± 1 SEM unless otherwise specified.

RESULTS

Microhabitats

The Clearcuts at midday received the highest solar radiation intensity and had the hottest ground surface temperatures (Table 2). Relative differences between Clearcuts and the other, less severely harvested quadrants increased with progression through the season from early-spring into summer primarily due to canopy leaf out around mid-May (data not shown). Clearcuts were fairly heterogeneous, and wind shadows formed by brushpiles (up to 3 m high) and dense vegetative regrowth (Clearcut CWD Removed – Ridgeline) reduced ground surface evaporation and produced higher surface water vapor densities relative to clear, Clearcut areas (i.e., burned Clearcut CWD Retained, Clearcut CWD Removed – Downhill; Fig. 3).·

Partial was similar to Control in retaining canopy cover that substantially decreased incident solar radiation and ground surface temperatures relative to the Clearcuts (Table 2). Increased wind speeds, however, promoted vapor deficits at the ground surface, and leaf litter refugia were the terrestrial microhabitats with the highest air vapor densities (Fig. 3). There were significantly elevated air vapor densities in microhabitats underneath Litter relative to the Surface (+3.4 g · m^{-3}, CI: 2.6 to 4.2; $F_{1, 761}$ = 67.8, $P < 0.001$). There was also a significant effect of forestry treatment air vapor density ($F_{4,761} = 10.3$, $P < 0.001$) with Drainage vapor densities significantly depressed relative to each of the other forestry treatments ($P < 0.001$). Leaf litter, where available (e.g., Control, Partial), and location in the Drainage overall decreased evaporation potentials.

Microhabitat meteorological variables in each of the timber harvest quadrants were significantly positively correlated with the same measured variables in the nearby FencePost – Warrenton. These variables included rainfall amount (Fig. 4; $r = 0.722 – 0.851$, $P < 0.01$), air temperatures at 50 cm (Fig. 5A; $r \geq 0.954$, $P < 0.001$), and air water vapor densities (Fig. 5B; $r = 0.782 – 0.958$, $P < 0.01$).

Soil

Field measurements of soil moisture yielded a range from around 18% to a low of around 3% gravimetric soil moisture in both the Drainage and Clearcut CWD Removed, with peaks in soil moisture corresponding to rainfall amounts (Fig. 6). Decreases in soil moisture in days post-rainstorm were significantly positively correlated with ground surface temperatures (Fig. 7A; $r = 0.357$, $P = 0.001$) and air water vapor densities (Fig. 7B; $r = 0.225$, $P = 0.039$) in the respective timber harvest treatments. The Clearcut CWD Removed and Drainage soils achieved similar saturation points at about 20% (Fig. 8). However, the Drainage soil overall had a higher propensity to liberate water (i.e., less negative soil water potential) at a given soil moisture than the Clearcut CWD Removed (Fig. 8), particularly at the depth of the soil moisture probe (10 – 15 cm depth; Table 3).

Physical models

Body temperatures of plaster models were significantly affected by the different timber harvest methods ($F_{3, 376} = 4.63$, $P = 0.003$), but there was no significant effect of position on the Surface versus under Litter. Body temperatures were significantly elevated in the Clearcut CWD Removed and in the Drainage relative to the Control ($P < 0.05$), but Partial body temperatures were not significantly different from those in the Control or the Drainage (Fig. 9).

EWL rates for sponge frogs not well protected by leaf litter ran to several body water volumes per day (Fig. 10A). Sponge frog EWL rates were interactively affected by timber harvest method and position on the Surface relative to the Litter (Wald $\chi^2_1 = 13.8$, $P = 0.003$). While Surface EWL rates did not significantly differ between the Control, Partial, and Clearcut CWD Removed, all were significantly less than EWL rates at the Surface of the Clearcut CWD Retained ($P \leq 0.034$). Litter EWL rates progressively increased between different timber harvest quadrants with Partial < Control < Clearcut CWD Removed < Clearcut CWD Retained (Fig. 10B; $P \leq 0.018$). EWL rates also significantly positively covaried with increasing number of days post-rainstorm (+0.173 g/hr, CI: 0.128 to 0.217; Wald $\chi^2_1 = 58.0$, $P < 0.001$).

Computer Models

Estimated Litter EWL rates (Fig. 11A) were two orders of magnitude less than those at the Surface (Fig. 11B). Litter permitted survivorship of several weeks to several months, depending on the thickness and overlap of leaves, without reaching critical dehydration (Fig. 11C). Even under the wettest conditions in which air vapor densities neared saturation (i.e., around the time of a rainstorm), the maximum time to critical dehydration anywhere on the Surface was about 60 hours (Fig. 11D).

DISCUSSION

The primary constraint on wood frog activity throughout DBCA is water. Wood frogs cannot be surface active because of the lack of tolerable surface microclimates throughout DBCA. Both physical models and computer models of EWL rates at the Surface indicated that only a few hours of activity there would be possible, even around the time of rainstorms. Litter in all timber harvest quadrants markedly decreased EWL, even when that litter was very thin. As early spring progressed into summer, desiccating conditions in the timber harvest quadrants became increasingly severe, and the Drainage was the only monitored site that maintained accessible soil moisture over several days post-rainstorm and lesser air vapor density deficits both at the Surface and underneath the Litter. These findings support the migratory observations by Rittenhouse and others (2007, 2009) which indicated that wood frogs exit timber harvest arrays via Drainages and are not found near breeding ponds in May, and likely beyond. Computer modeling in Chapter 7 provides further mechanism-based risk estimation which support observations of desiccation mortalities in wood frogs leaving Pond 2 in 2005 during a drought.

Micrometeorology

Timber harvest treatments to the forest abutting LEAP Missouri amphibian breeding ponds created heterogeneous habitat both between and among quadrants. Across timber harvest quadrants differential removal of forest canopy had a straightforward effect on solar radiation levels reaching the ground surface with Clearcuts permitting the most solar penetration and selective harvests were also subjected to increased solar radiation levels. Clearcuts with CWD retained contained large patches characterized by windshadows created by giant brushpiles and subsequent vegetative regrowth. These windshadows held hot air near ground surface, and coupled with increased solar radiation and the higher saturation point of hotter air, led to increased air water vapor densities near the ground. Contributions to moist air likely included increased evapotranspiration of vegetation and latent heat of vaporization of surface soil moisture. Clearcuts with CWD removal either mechanically or via prescribed burns eliminated the higher air vapor densities near the ground because of increased wind levels. Soil degradation also prevented dense vegetative regrowth in some areas within Clearcuts which also allowed wind to strip away moist air. Aside from increases in solar radiation reaching the ground surface, selective harvest (Partial) did not differ significantly from the Control either in terms of wind speeds or air water vapor densities near the ground. This is an indication that selective timber harvests may be sustainable forest management applications in areas near amphibian breeding ponds, an observation further supported by demographic and behavioral observations (Semlitsch et al. 2009).

The meteorological stations in this study provided a relatively cost- and labor-efficient means of better understanding the biophysical and physiological ecology of LEAP focal amphibians, such as wood frogs. However, due to instrument constraints, many of the patterns in the meteorological variables measured are good for illustrating relative differences between timber harvests, but much less accurate in terms of the actual values for those measured variables. Our pyranometers were calibrated against an Eppley Precision spectral pyranometer under natural daylight conditions, but they are subject to error > 5% under vegetative canopy. The observed incident solar radiation levels in this study illustrate relative differences between quadrants only. Cup anemometers were calibrated against a hotwire anemometer in a laminar flow wind tunnel, but the cup anemometer stall speed (0.2 m/s) was too high to permit accurate general comparisons between quadrants such as the Drainage and the Clearcut CWD Removed – Ridgeline with low wind speeds. Furthermore, wherever possible, cup anemometers in the field were located far away from obstructions (e.g. trees, brushpiles), but this was really only feasible in the Clearcut CWD Removed – Clearing and the Clearcut CWD Retained. The low wind speed, heated needle anemometers were also differentially sensitive to high and low wind speeds (i.e., increasing measurement error with increasing wind speeds) and are most appropriately utilized to understand the wind speeds very close to the ground (i.e., frog height).

Soil

The ridgeline soils surrounding LEAP Pond 2, including the site of the Clearcut CWD Removed – Ridgeline meteorology station, were composed of Hatton silt loam near the surface that graded into silty clay at least 15 cm below the surface (US Department of Agriculture, Web Soil Survey 2.2). Much of the hillside soil going out away from Pond 2 and down toward drainage areas, including the site of the Drainage meteorology station, was composed of Lindley loam which graded into clay loam at least 15 cm below the surface (US Department of Agriculture, Web Soil Survey 2.2). There was considerable variation in the soil water potential measurements at a given soil moisture content across replicated samples from the Drainage and Clearcut CWD Removed. This variation could be important over the range of soil moistures with any propensity for uptake by frogs, but it is unclear without greater replication whether this variation is (1) an artifact of the measuring procedure and device, (2) due to differences in soil composition within sites, or (3) actually exploitable by frogs in the field. Future use of soil water potential sensors coupled with permanently installed soil moisture probes should elucidate the nature and relevance of some of the variation in soil water potential.

Once Drainage soil moisture dropped below 10% (between 10 and 15% in the Clearcut CWD Removed) well-hydrated frogs would be unable to take up water from the soil, and they would lose body water to the soil if in contact with it. Frogs dehydrated to near critical levels of 80% hydration can exhibit body water potentials that permit soil water uptake from soils as dry as 7% in the Drainage and 10% in the Clearcut CWD Removed (Fig. 8; Tracy 1976). This is important because, at least in May through June 2007, soil moisture regularly rose to and retained levels that would be available to even well hydrated frogs for several days following rainstorms in which as little as 2 – 3 mm fell. However, small rainstorms in July, particularly if they occurred during daytime hours did not equivalently recharge soil moisture levels, and desiccating conditions were more extreme in July days post-rainstorm.

Physical Models

Plaster frogs in Clearcuts had significantly elevated body temperatures compared with plaster frogs in the Control, and there was very little daily variation in body temperatures in any timber harvest quadrant due to EWL. EWL in most amphibians occurs freely and primarily across the cutaneous surface (pulmonary evaporative water loss is insignificant; reviewed by Young et al. 2005). Most amphibians rely on behavioral recourse (posture changes, microhabitat utilization) to prevent desiccation, although some are able to form cocoons or waxy surface layers (Shoemaker et al. 1992).

Since this study was carried out, Tracy and others (2007) have revolutionized the use of plaster models as operative environment models of field amphibians by introducing the use of a capillary tube as a wicking device to better control for gravitational pull. There is still a lot of work to be done to create remote-sensing plaster models of EWL, but Tracy and others (2007) have dramatically improved upon the labor-intensive original methodology for plaster frog models (O’Connor 1989). Other types of operative environment models for wet-skinned amphibians include agar models (Spotila and Berman 1976) which lose their shape at low hydration levels; wicked copper pipes with water reservoirs connected to strain gauges that require huge battery inputs (Bartelt and Peterson); preserved amphibians (Seebacher and Alford 2002) which is not feasible when working with threatened species; and sponge frogs (Hasegawa et al. 2005) which do not lose their shape, but they are very labor intensive. Operative environmental models offer a lot to studies of physiological ecology by integrating the complex, time-varying thermal and hydric environments experienced by amphibians to produce accurate measurements of body temperatures and EWL rates.

Table 2. Midday (1200 to 1400 hours) environmental conditions in the different timber harvest methods in each quadrant of the experimental array surrounding LEAP Pond 2.

Location	Solar Radiation (W/m^2)	Wind Speed (m/s)			Soil Temp. (°C)	Air Temp. (°C)		
		+2 cm*	+20 cm*	+50 cm*	-2 cm*	0 cm*	+5 cm*	+50 cm*
Control	134.1 (±4.6)	0.025 (±0.006)	0.13 (±0.03)	0.40 (±0.01)	19.0 (±0.1)	23.6 (±0.2)	24.8 (±0.2)	24.1 (±0.2)
Partial	213.5 (±6.4)	0.024 (±0.002)	0.17 (±0.08)	0.51 (±0.01)	22.0 (±0.3)	28.4 (±0.3)	27.2 (±0.3)	25.8 (±0.2)
Drainage	320.7 (±9.3)	0.035 (±0.027)	0.12 (±0.05)	0.26 (±0.004)	20.3 (±0.1)	27.1 (±0.2)	25.6 (±0.2)	24.6 (±0.2)
Clearcut CWD Removed - Ridgeline	541.2 (±13.7)	0.13 (±0.05)	0.091 (±0.04)	0.28 (±0.01)	21.8 (±0.1)	32.9 (±0.3)	30.9 (±0.3)	28.3 (±0.3)
Clearcut CWD Removed - Downhill	362.4 (±7.7)	--	--	0.54 (±0.01)	24.0 (±0.2)	35.5 (±0.4)	30.0 (±0.3)	26.7 (±0.2)
Clearcut CWD Retained	459.7 (±7.9)	0.060 (±0.031)	0.14 (±0.01)	0.38 (±0.01)	25.8 (±0.2)	29.3 (±0.2)	30.0 (±0.3)	27.9 (±0.3)

Data are means (± 1SEM); -- indicates not measured; * Height/depth

Table 3. Coefficients of the quadratic fits relating soil water potential (y; -MPa) to soil volumetric water content (x; $m^3 \cdot m^{-3}$) at depths near the soil surface (0 to 5 cm) and at the position of the soil moisture probe (5 to 10 cm).

Location	Depth (cm)	β_0	β_1	β_2	r^2
Drainage	0 – 5	4.13 (±0.33)	-0.91 (±0.10)	0.02 (±0.004)	0.92
Drainage	5 – 10	3.84 (±0.22)	-1.16 (±0.06)	0.04 (±0.003)	0.96
Clearcut CWD Removed	0 – 5	4.73 (±0.36)	-0.89 (±0.10)	0.02 (±0.005)	0.95
Clearcut CWD Removed	5 – 10	4.66 (±0.24)	-0.82 (±0.07)	0.02 (±0.004)	0.98

Data are means (± 1SEM)

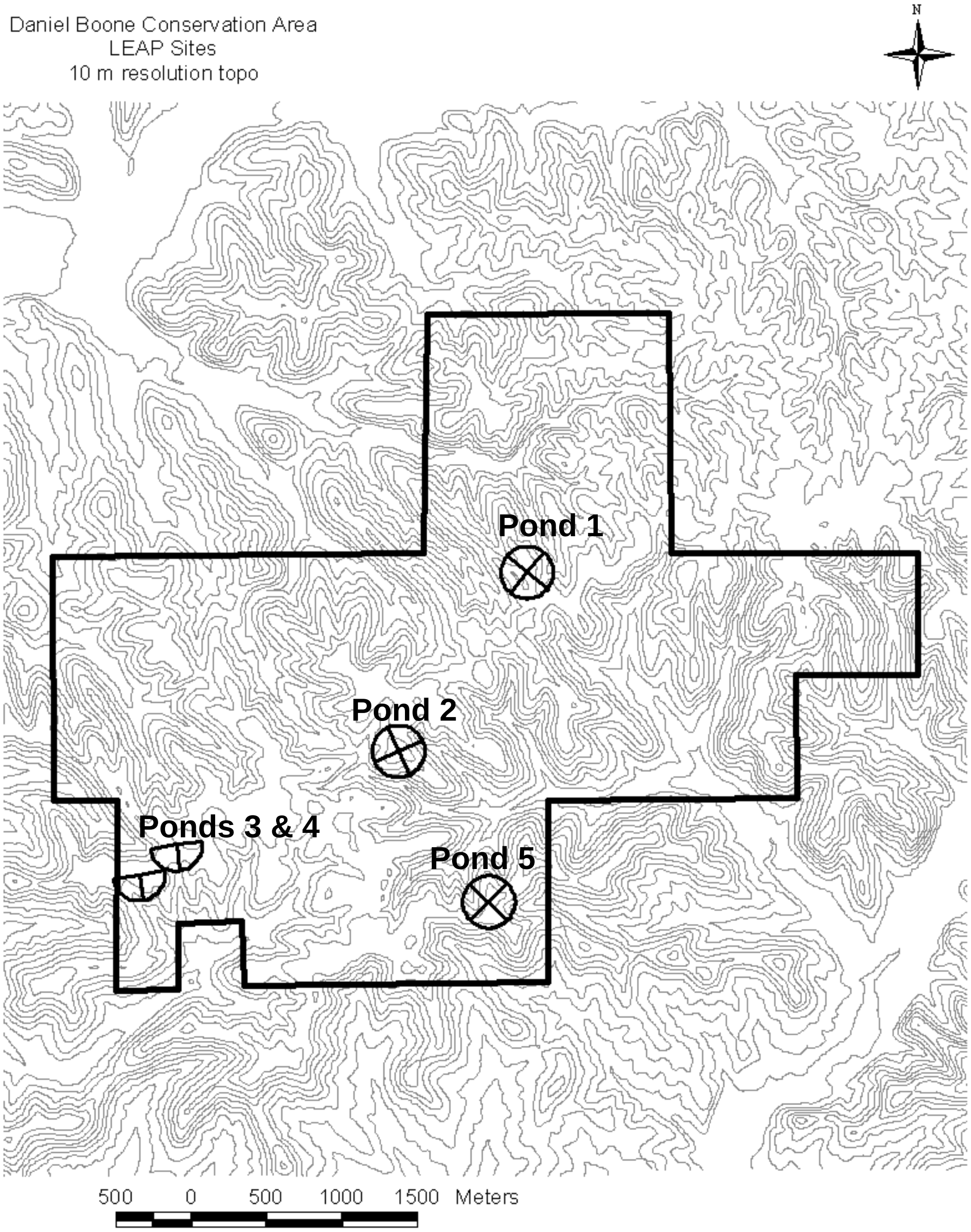


Figure 1. Topographical map of the Daniel Boone Conservation Area with the locations of each of the Missouri LEAP Pond arrays. Amphibian breeding ponds were on ridgetops and the experimental timber harvest quadrants within the arrays generally ran downhill away from the ponds (map courtesy of T.A.G. Rittenhouse).

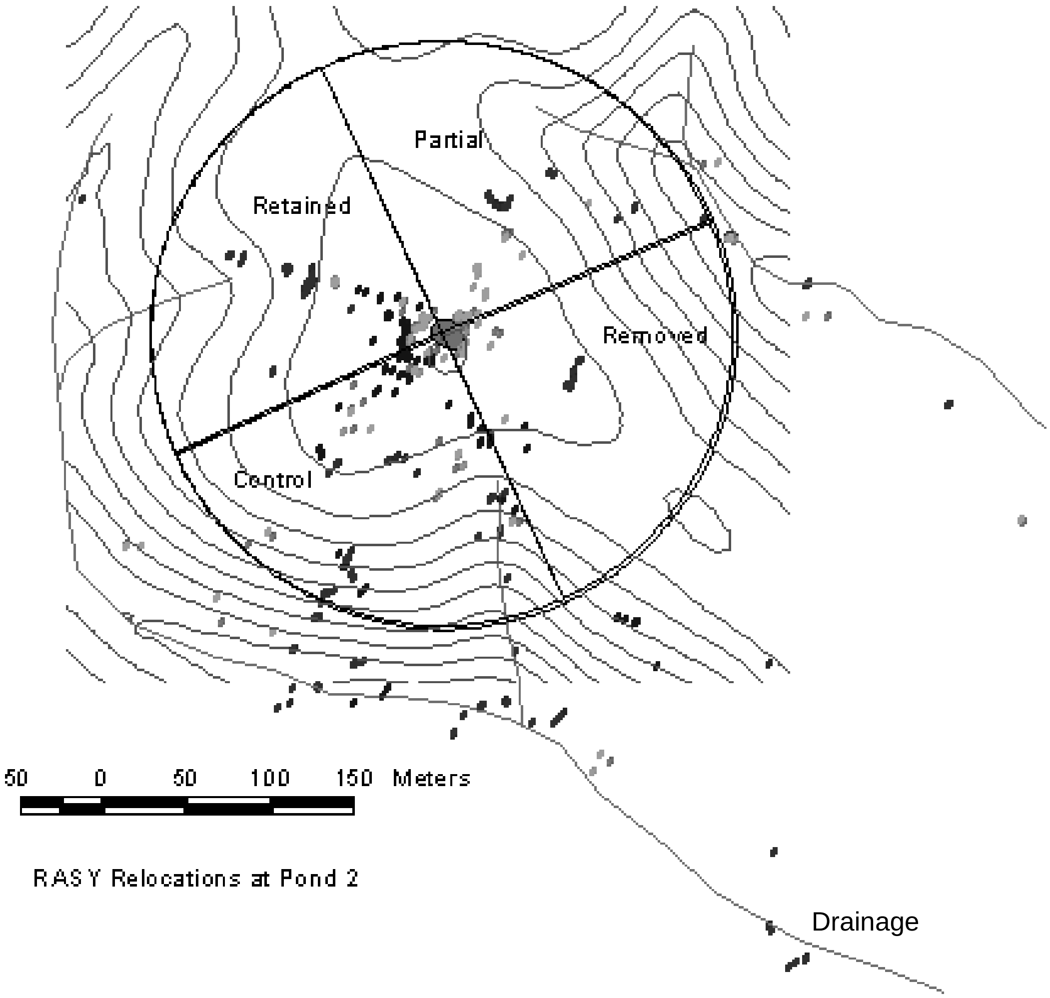


Figure 2. Topographical map of Missouri LEAP Pond 2 and post-breeding, migrating wood frog locations in 2004 (black circles, pre-timber harvest), and in 2005 and 2006 (gray circles, post-timber harvest; Rittenhouse and others 2007a, 2009). “Drainage” indicates the location of the Drainage meteorological station and plaster frog model array (map courtesy of T.A.G. Rittenhouse).

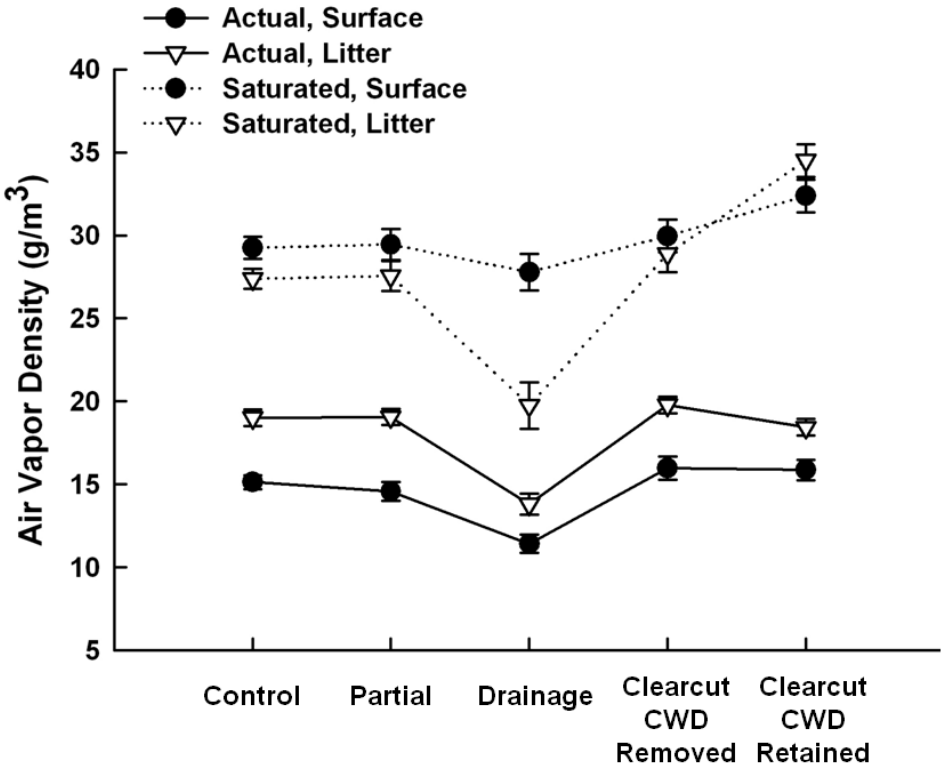


Figure 3. Actual vapor densities, and the corresponding saturation vapor densities, measured at the surface and underneath leaf litter in each of the timber harvest quadrants. Differences between saturation and actual indicate deficits in air moisture availability.

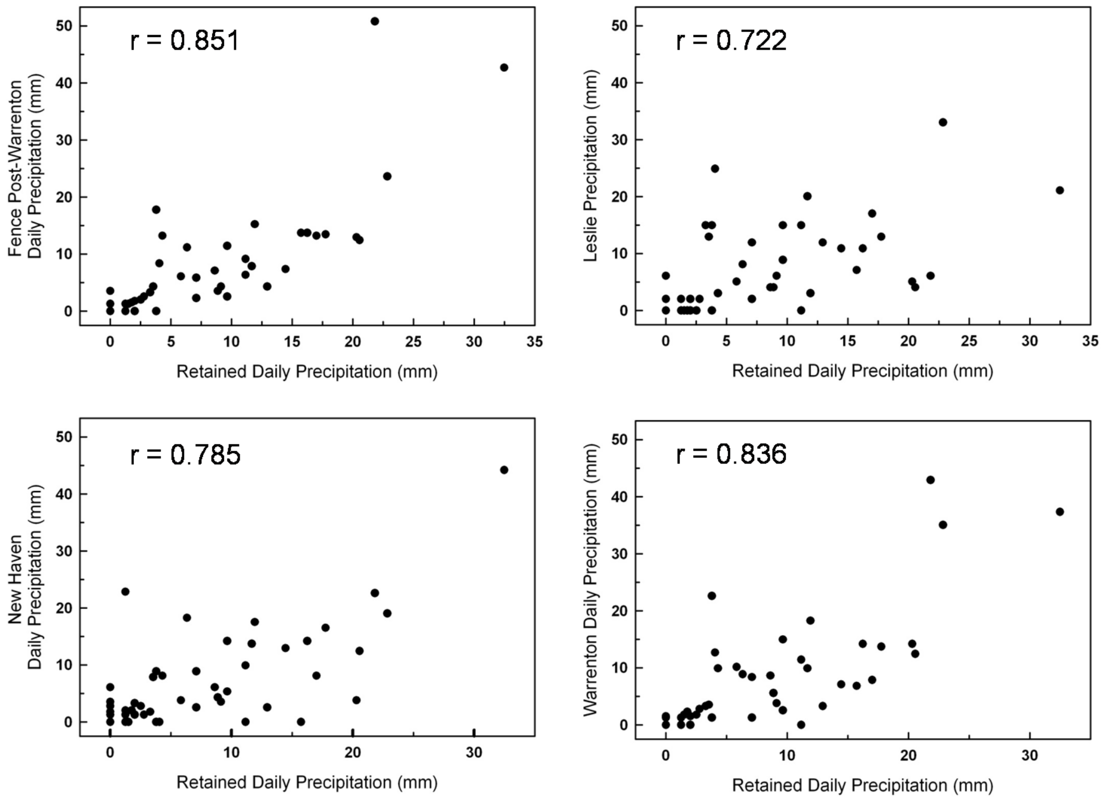
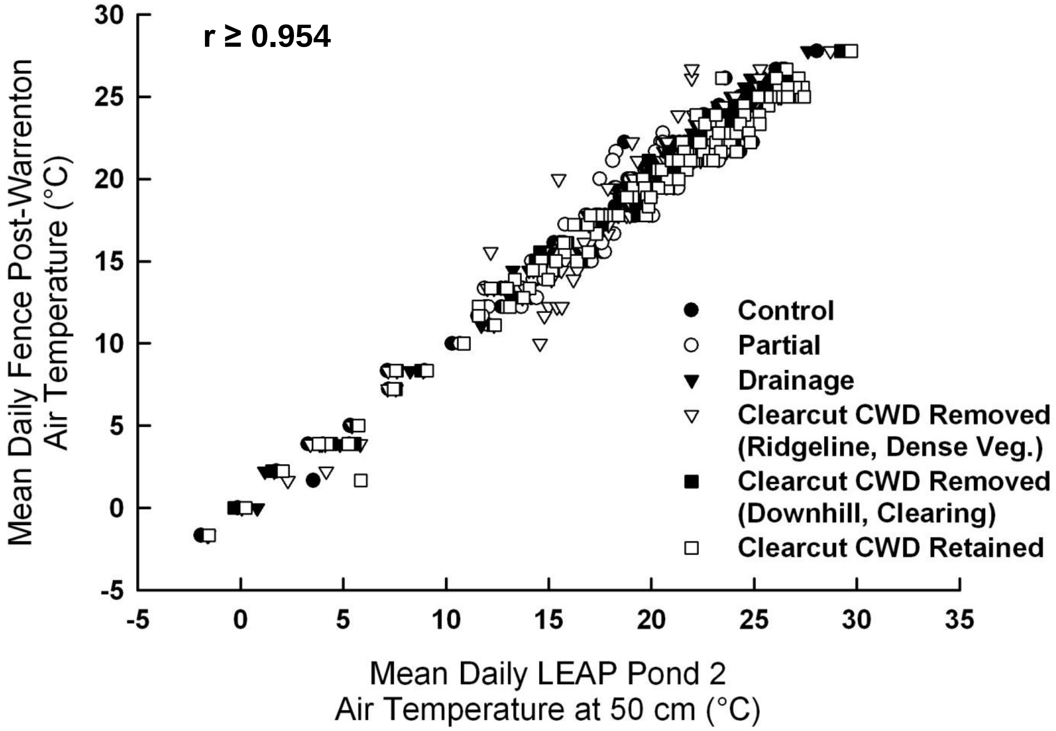


Figure 4. Correlations between rainfall in LEAP Pond 2 and rainfall in each of the four nearby monitored weather stations.

5A)


r ≥ 0.954
Mean Daily Fence Post-Warrenton Air Temperature (°C)
Mean Daily LEAP Pond 2 Air Temperature at 50 cm (°C)
30
25
20
15
10
5
0
-5
-5
0
5
10
15
20
25
30
35
● Control
○ Partial
▼ Drainage
▽ Clearcut CWD Removed (Ridgeline, Dense Veg.)
■ Clearcut CWD Removed (Downhill, Clearing)
□ Clearcut CWD Retained

5B)

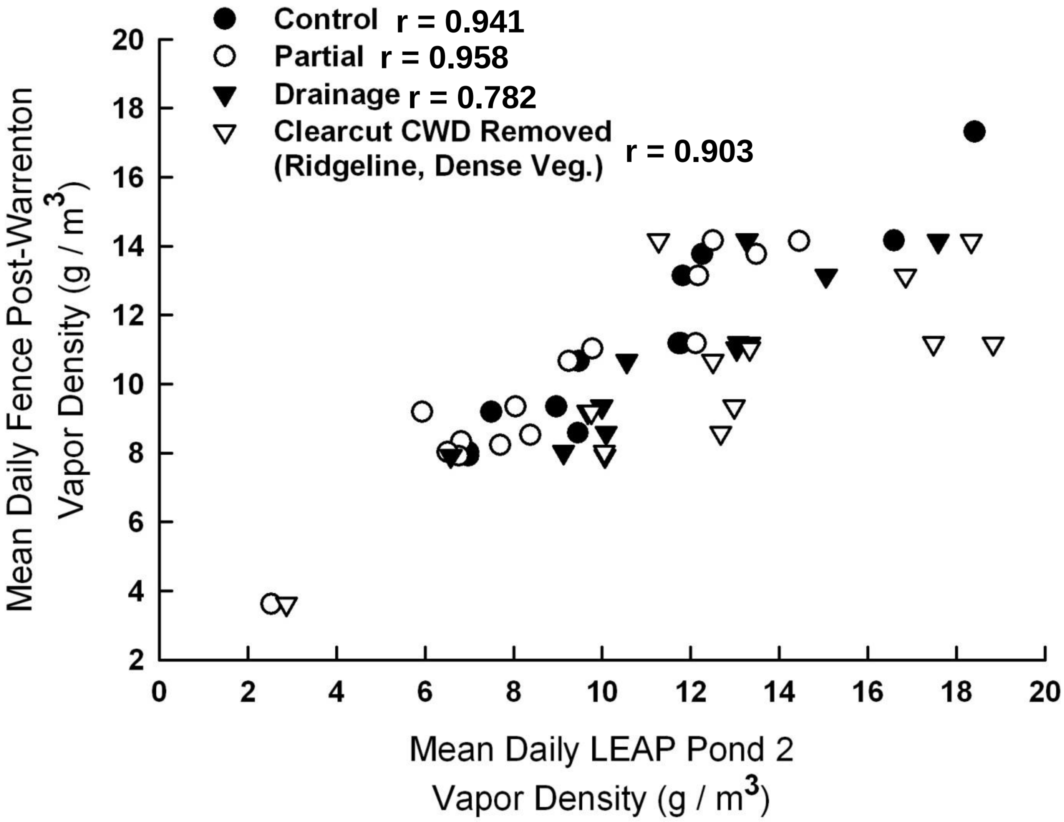


Figure 5. Correlations between LEAP Pond 2 and FencePost – Warrenton meteorological variables **5A)** air temperature and **5B)** air water vapor density.

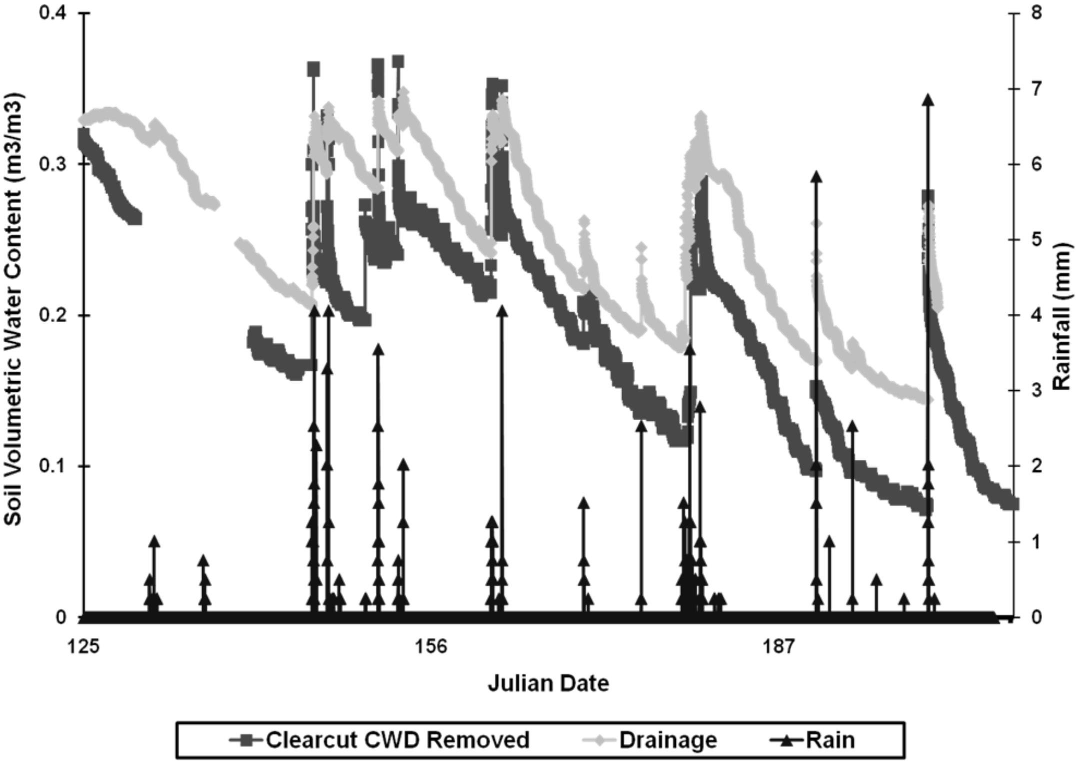
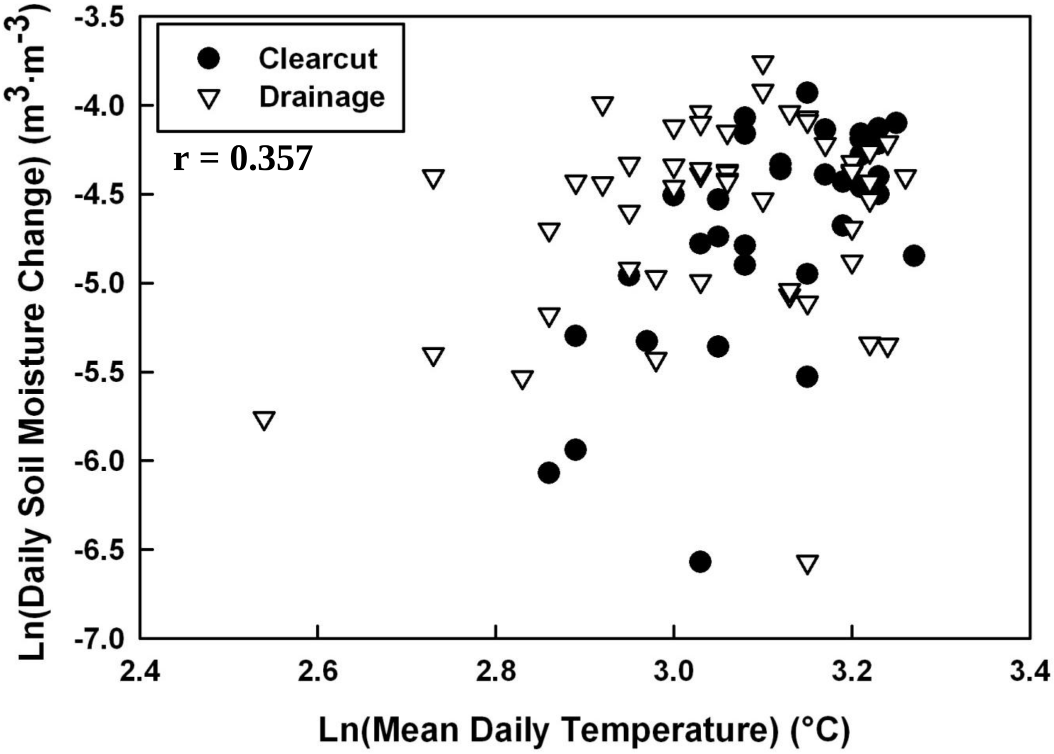


Figure 6. Rainfall incidence at Pond 2 and its effects on soil moisture in the Clearcut CWD Removed (Ridgeline, Dense Vegetation) and in the Drainage.

7A)



Clearcut
Drainage
r = 0.357
Ln(Daily Soil Moisture Change) ($m^3 \cdot m^{-3}$)
-3.5
-4.0
-4.5
-5.0
-5.5
-6.0
-6.5
-7.0
2.4
2.6
2.8
3.0
3.2
3.4
Ln(Mean Daily Temperature) (°C)

7B)

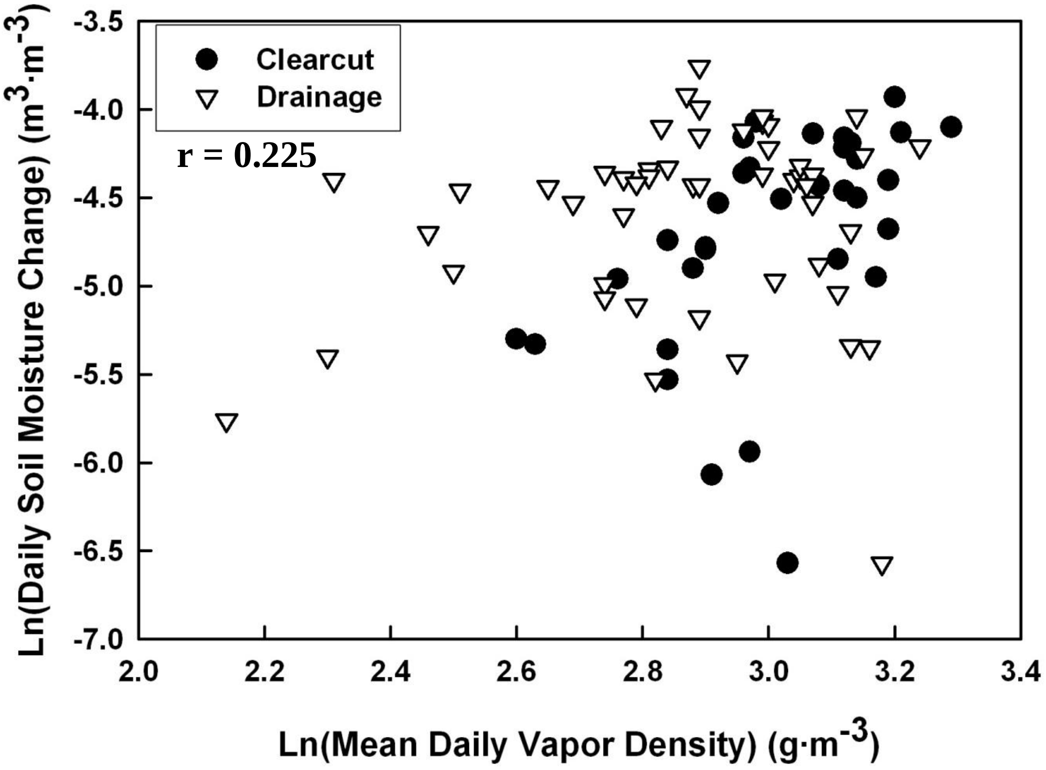


Figure 7. Correlations between daily change in soil moisture and meteorological variables **7A)** air temperature and **7B)** air water vapor density in the Drainage and the Clearcut CWD Removed (Ridgeline).

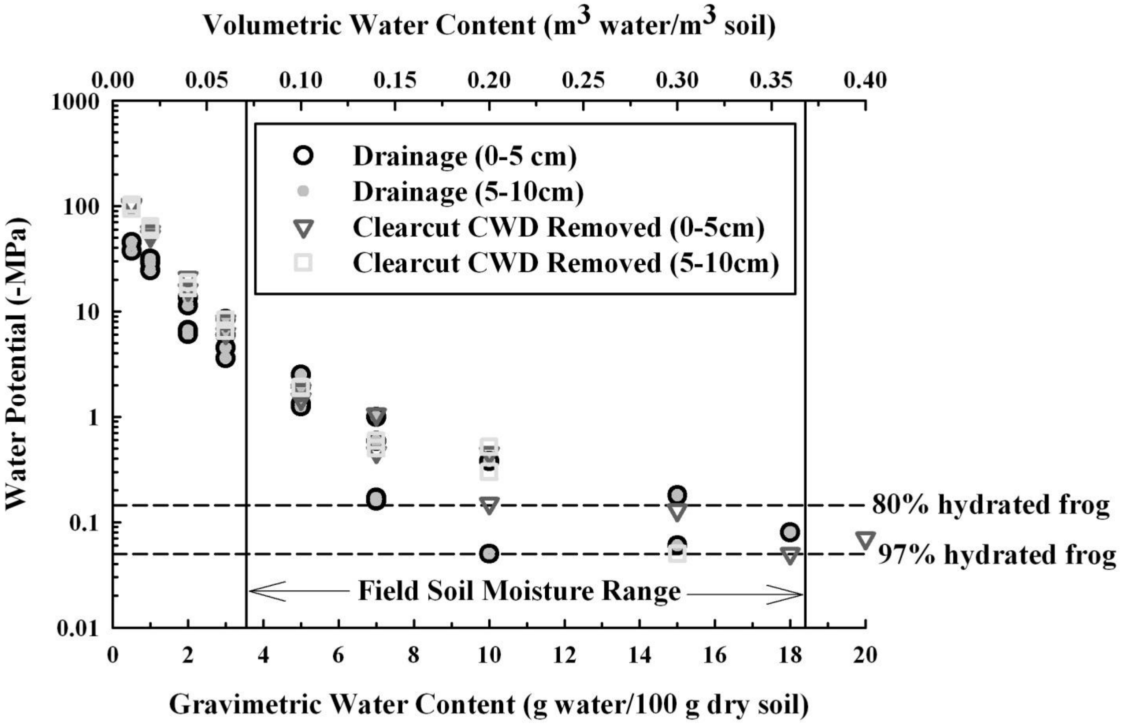


Figure 8. Water retention curves for soil from the Drainage and the Clearcut CWD Removed (Ridgeline) over a series of gravimetric (and volumetric) water contents. Data are for soil samples taken from the surface to a depth of 5 cm and from 5 to 10 cm corresponding to the depth of the soil moisture probe. Frog body water potentials are also plotted for ranid frogs at 97% and 80% hydration (based on Tracy 1976).

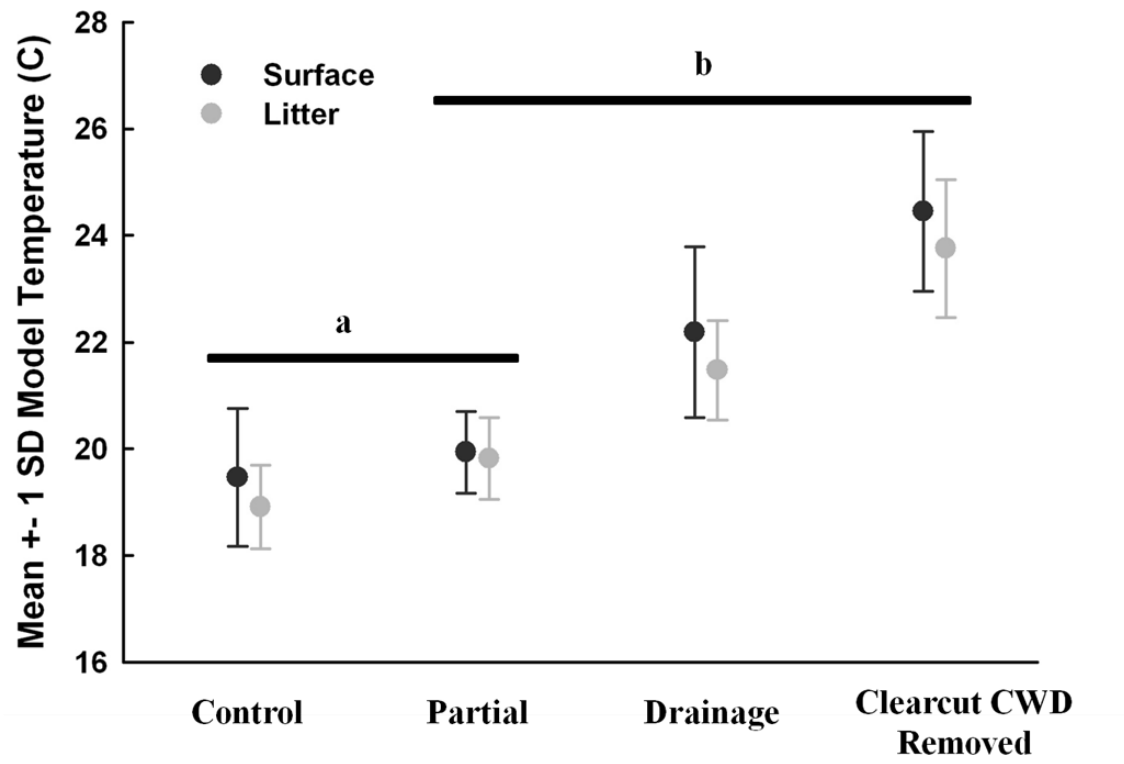


Figure 9. Body temperatures of plaster model frogs at the Surface and under Litter in wood frog post-breeding migratory locations in each of the timber harvest quadrants.

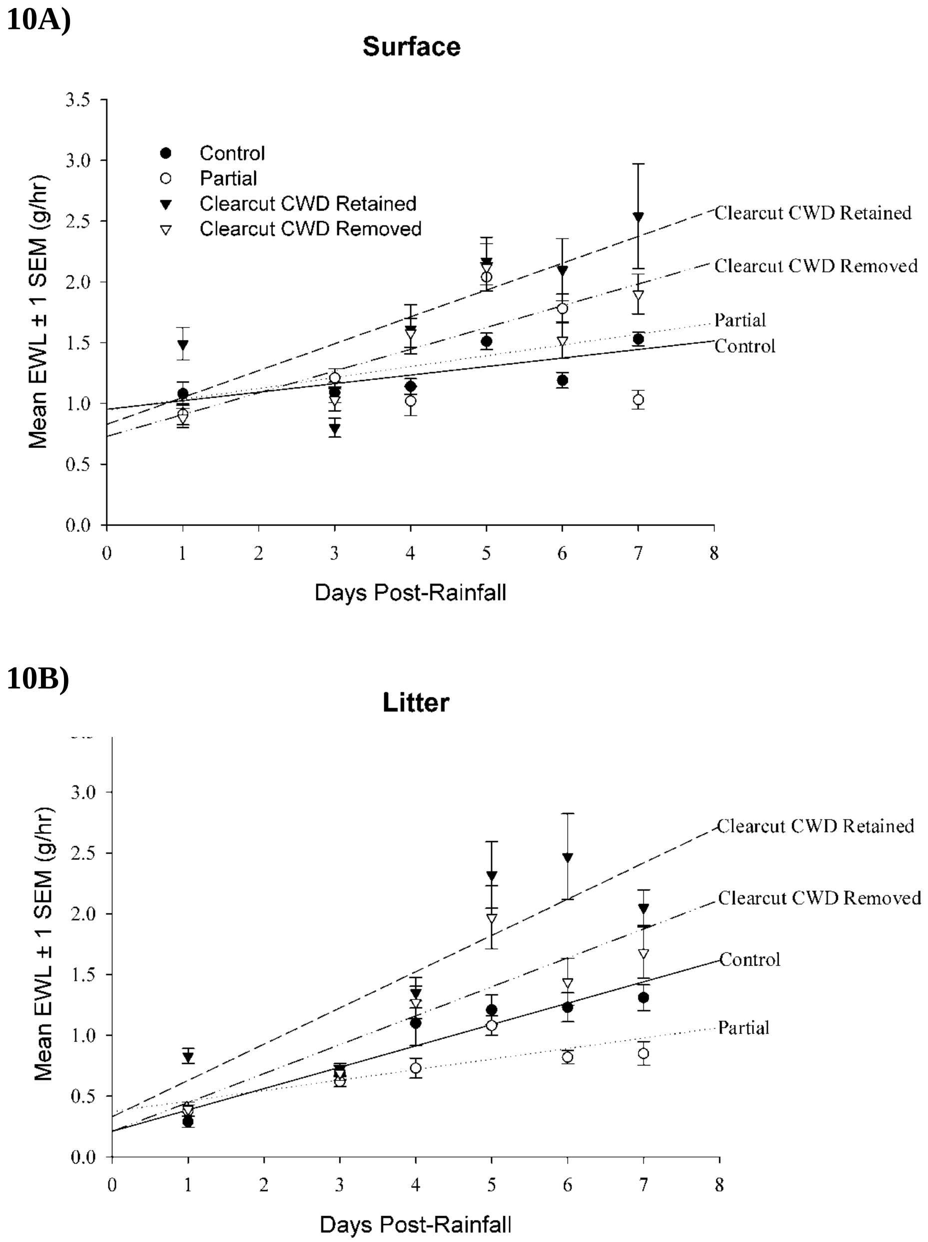
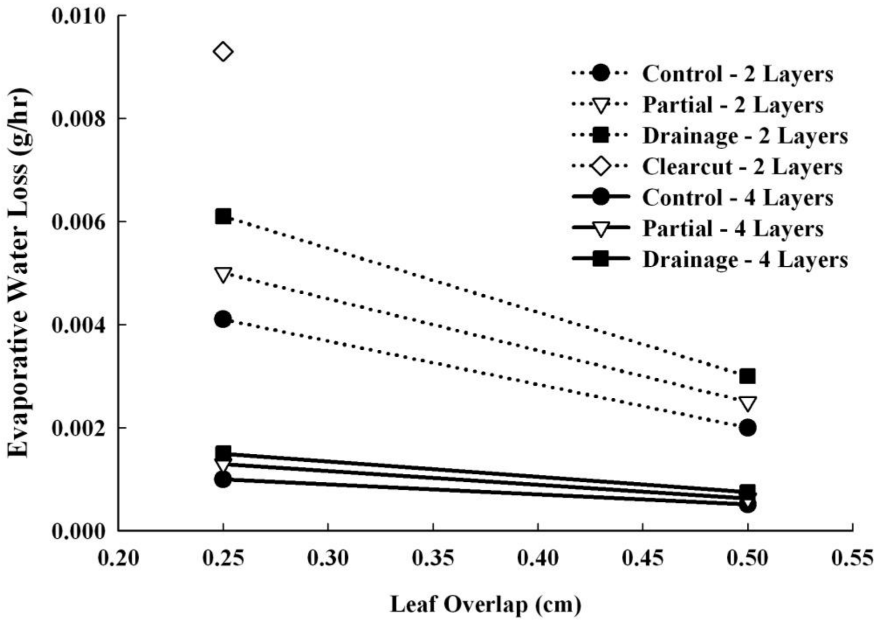
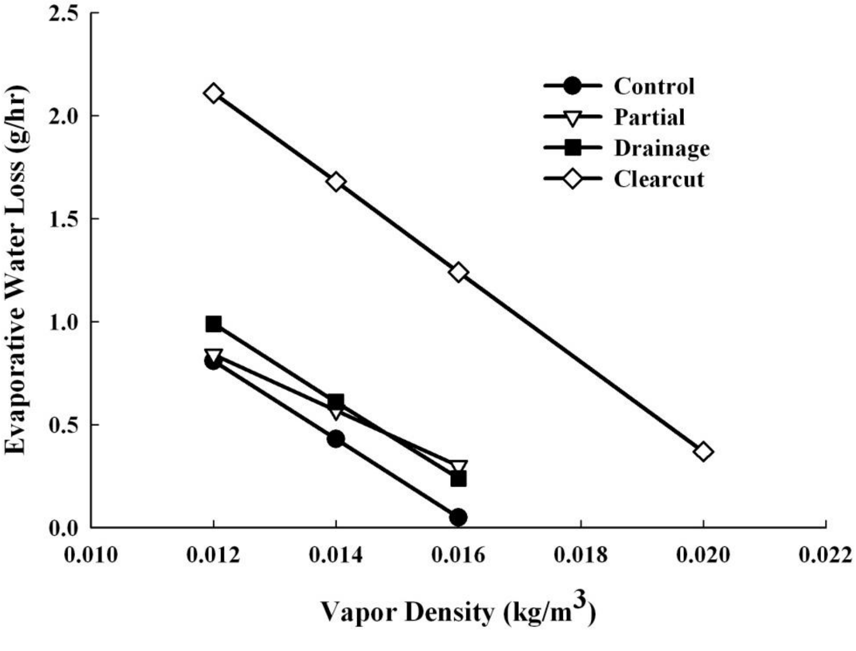


Figure 10. Wet sponge models of wood frogs estimate daily mean evaporative water loss rates **10A)** at the Surface and **10B)** under Litter in each timber harvest quadrant for one week following each of two large (> 10 mm) rainstorms.

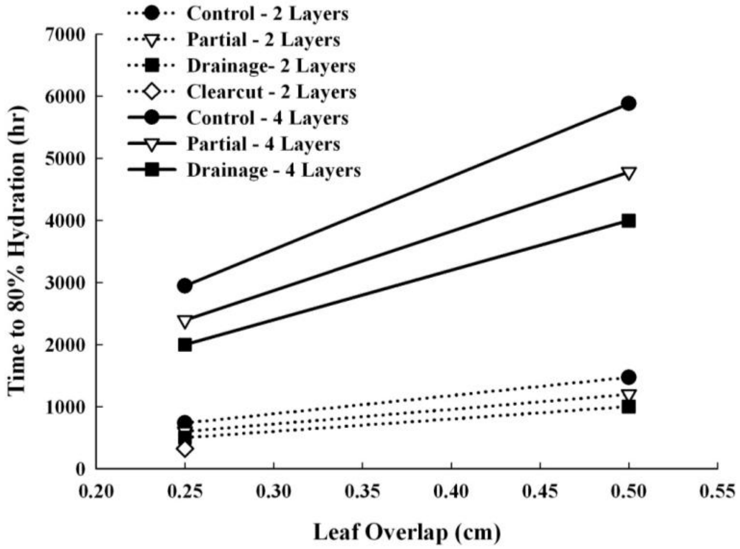
11A)


0.010
0.008
0.006
0.004
0.002
0.000
Evaporative Water Loss (g/hr)
0.20
0.25
0.30
0.35
0.40
0.45
0.50
0.55
Leaf Overlap (cm)
Control - 2 Layers
Partial - 2 Layers
Drainage - 2 Layers
Clearcut - 2 Layers
Control - 4 Layers
Partial - 4 Layers
Drainage - 4 Layers

11B)


2.5
2.0
1.5
1.0
0.5
0.0
Evaporative Water Loss (g/hr)
0.010
0.012
0.014
0.016
0.018
0.020
0.022
Vapor Density (kg/m3)
Control
Partial
Drainage
Clearcut

11C)



11D)

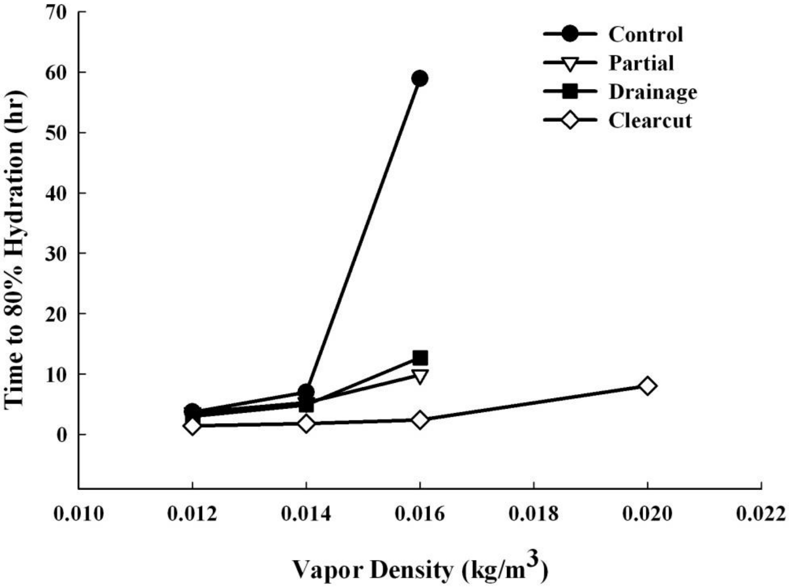


Figure 11. Computer models of evaporative water loss (EWL) rates parameterized from the meteorological measurements in each forestry treatment (see Table 1). **11A)** Litter estimates of EWL, **11B)** Surface estimates of EWL, **11C)** time to critical dehydration (80% hydration) under the Litter and **11D)** at the Surface.

CHAPTER 3: Physiological consequences of habitat alteration due to land-use in a threatened anuran amphibian

ABSTRACT

Amphibians are declining worldwide at a faster rate than any other vertebrate group, and one of their primary threats is habitat modification by human land-use. Due to their wet-skin and ectothermy, amphibians are particularly sensitive to habitat alterations that affect their thermal and hydric state. We measured locomotory and metabolic performance of wood frogs (*Rana sylvatica*) over a range of ecologically relevant body temperatures and hydrations. Wood frogs tolerated a range of body temperatures from 5 to 30°C for both performance measures, and metabolic rates, in particular, progressively increased over the range tested. Extremely high body temperatures and low body hydrations were the likely outcomes of occupying cleared forest habitat for any extended period of time. These extreme combinations tended to reduce hopping performance as well as resting metabolic rates, relative to maximal performance, in wood frogs. Overall, hydration state did not significantly affect resting metabolic rates, but reduction to critical dehydration (80%) did reduce hopping performance at both the high and low range of body temperatures. With an increased cost of living and reduced hopping ability as consequences of clearcut occupation, this type of habitat modification is demonstrably detrimental to already threatened native wood frogs.

INTRODUCTION

Amphibians, like other small ectotherms, are remarkably tolerant of a broad range of body temperatures (Hutchison and Dupre 1992). With their wet-skin (unique in terrestrial vertebrates) and over-wintering adaptations (e.g., supercooling, freezing), amphibians are resilient to dramatic decreases in body water content and osmolarity (Shoemaker et al. 1992; Churchill and Storey 1993; Costanzo et al. 1993; Jorgenson 1997).

In amphibians, changes in body hydration and body temperature tend to have synergistic effects on physiological performance (Preest and Pough 1989, 2003; Walvoord 2003), and frogs will often maintain body temperatures and hydration in ranges that maximize performance (Huey and Stevenson 1979; Rogowitz et al. 1999; Walvoord 2003). Physiological performance measurements estimate tolerance for temperatures and hydration states, as well as energy costs as environmental conditions vary. Locomotion is well-recognized as an ecologically relevant measure of temperature effects on physiology in amphibians (Preest and Pough 1989, 2003; Rogowitz et al. 1999; Walvoord 2003) particularly due to its connection with the potential to escape predation. Resting metabolic rates of amphibians at different temperatures and hydrations measures the effects of abiotic factors on the cost of living. We will use the wood frog (*Rana sylvatica*) physiological performance to describe its tolerance for change in body temperature and hydration, define the limits that constrain the frogs' activity, and estimate the potential energy costs of different microhabitat choices. We seek to estimate both tolerance limits and dependence of energy exchange on environmental conditions in pristine versus wood frog terrestrial habitat modified by human land-use (see Chapter 2).

MATERIALS AND METHODS

Wood frogs

We obtained subadult wood frogs raised from larvae extracted from the Missouri Department of Conservation's Daniel Boone Conservation Area wildlife ponds. These frogs were raised in experimental pens at the University of Missouri (see full description in Harper and Semlitsch 2007). They were long-term acclimated to outdoor semi-natural enclosures in grounds near the Columbia, Missouri campus. These individuals were then brought back to Drexel University where they were housed in 18°C and high humidity in large aquaria with saturated sphagnum moss and access to a small pool of water. Wood frogs were fed crickets dusted with vitamin and mineral powder (ReptiCal) three times a week and kept on a 12:12 hour light-dark cycle. Experiments were all performed on frogs kept in captivity at Drexel for 12 months.

Resting metabolic rates

We performed physiological measurements on 7 individuals with snout-vent lengths of 32 – 43 mm and 11.6 – 17.7 g in standard mass. We measured resting metabolic rates on individuals using a MicroOxyMax respirometer (Columbus Instruments, Columbus, Ohio) with temperatures controlled by incubators ranging from 5 to 30°C. Feeding was stopped at least 3 days prior to measurements. For a detailed description of the respirometer setup, see Hall (2008). Briefly, we used small, sealed canning jars (138 – 154 mL) as metabolic chambers, chambers remained in the (darkened) incubator throughout the measurement period, and measurements were performed between 0800 and 2100. One set of measurements was on fully hydrated individuals, and they were given 2 – 3 hours to acclimate to each temperature before measurement. Frogs often lost < 1% of their standard mass during metabolic rate measurements, although it was occasionally as high as 5%.

Another set of metabolic rate measurements were performed on frogs dehydrated to 80% of their standard mass. To dehydrate frogs, we placed them in small fish bait holders and put them in a wind tunnel with low wind speed to dehydrate them over a period of around 3 hours. During the dehydration, frogs were weighed every 30 minutes using a precision balance until they were within 5% of their target mass, and then frogs were weighed every 10 minutes. Dehydrated frogs were then placed again in metabolic chambers, and after a 2 – 3 hour period to acclimate to the measurement temperature, dehydrated resting metabolic rates were measured. Weight measurements taken after metabolic rate measurements indicated mass losses of less than 1% of their initial dehydrated mass. Body temperatures at both hydrations were estimated after acclimation by measuring skin temperatures following Young and Tracy (2005). Dehydrated frogs were immediately rehydrated in buckets with water following the conclusion of measurements.

Hopping performance

In a separate set of experiments, individual frogs were hopped at the different combinations of hydration and body temperature spanned in the metabolism measurements. Each frog was brought to a particular temperature and hydration combination in the same way as described above. Individual frogs were each placed at one end of a rectangular chute with high mesh walls and butcher paper taped to the floor. A poker chip-sized piece of cardboard was placed at the location of the frog’s pygostyle at each of 5 jumps in the chute. Frogs were prodded into 5 hops in quick succession.

Following replacement of the frog into a bucket of water, the distance in between cardboard pieces placed on the butcher paper was measured and recorded.

Statistical analyses

We used generalized estimating equations to test whether resting metabolic rates and hop distances were significantly affected by hydration (fixed factor) and body temperature (covariate). The correlation matrix structure in both models was specified as exchangeable to account for the effects of multiple observations on individual frogs on the variation in the response variable (see Zuur et al. 2009). We carried out all statistical analyses using SPSS 15.0. The significance level for all analyses was $P < 0.05$, and all data are presented as mean ± 1 SEM.

RESULTS

Resting metabolic rates

Resting metabolic rates positively covaried in both fully hydrated and 80% hydrated wood frogs with increases in body temperature from 5 to 30°C (Fig. 12, +2.2 μL/min, CI: 1.8 to 2.6; Wald $\chi^2_1 = 118.4$, $P < 0.001$). Despite a decrease in metabolic rate at the highest body temperature in 80% hydrated frogs, there was no significant effect of hydration state on wood frog resting metabolism (Wald $\chi^2_1 = 1.0$, $P > 0.05$).

Hopping performance

Hopping performance was significantly affected by hydration (Fig. 13, Wald $\chi^2_1 = 28.4$, $P < 0.001$) with greater hop distances at full hydration as compared to at 80% hydration (+76.0 ± 14.3 mm, $P < 0.001$). Hopping performance also positively covaried with body temperature from 5 to 30°C (+13.5 mm, CI: 10.9 to 16.2; Wald $\chi^2_1 = 67.5$, $P < 0.001$).

DISCUSSION

Resting metabolic rates

Resting metabolic rates in adult amphibians and other vertebrates are tied to a suite of interrelated physiological functions that are broadly influenced by body size, geographical (e.g., latitudinal) location, and phylogeny (reviewed by Hutchison et al. 1968; Shoemaker et al. 1992; McNab 2002). Because amphibians are wet-skinned ectotherms, variation in resting metabolism is also linked to body temperature, degree of terrestriality, cutaneous surface area, buccal (and tidal) volume, metabolic substrate, and total body hydration (Hutchison et al. 1968; Muir et al. 2007).

Dehydrated wood frogs experience increased levels of sodium and chloride ions just due to decreases in total body water (Shoemaker 1964), but they also mobilize glucose (to a limited extent) and urea as a response (Muir et al. 2007). Mobilization of organic solutes is a common strategy for increasing osmotic pressure without damaging macromolecules and as a source of cryoprotectant for overwintering. It is also urea, and not glucose, that is empirically tied to metabolic depression in cold-acclimated wood frogs (Muir et al. 2007) potentially because it inhibits several key enzymes involved in ATP production (reviewed by Muir et al. 2007). This physiological mechanism did not appear to apply to our laboratory wood frogs that were long-term acclimated to 18°C. In this study, hydration did not play a significant role in resting metabolism. Resting metabolism did increase by around 25% over the range of body temperatures measured in Chapter 2 in the Control relative to the Clearcut. This projected increase in energetic cost of living in the Clearcut would have to be supplemented with increased food intake, but it is not known how insect densities vary with timber harvest.

Locomotory Performance

In several terrestrial amphibians, both body temperature and hydration are known to significantly, and synergistically affect locomotory performance (Preest and Pough 1989, 2003; Rogowitz et al. 1999). However, care has to be taken in which performance measures are considered because this can influence the results (e.g., Marvin 2003). More reductive studies of the locomotory (exercise) physiology of anuran amphibians have tended to focus on the performance of individuals at maximal levels of activity (reviewed by Taigen and Beuchat 1984). During maximal exercise, dehydration decreases blood plasma volume, increases blood viscosity, and leads to vasoconstriction, all of which combines to limit blood flow, cardiac output and aerobic metabolism (Hillman 1987). Whether these same physiological constraints apply in sub-maximal measures of locomotory performance is not completely clear.

Wood frogs do demonstrate a remarkably labile locomotory performance over such a broad range of body temperature and hydration states, and the breadth of performance for the frogs in this study are similar to past measurements for wood frogs in Michigan (O’Connor 1989). O’Connor (1989) tested hopping performance in frogs that were pushed to even higher body temperatures (~32°C) and lower body hydrations (75%), and he observed even greater drop-offs in performance at the highest body temperature and lowest hydration. Wood frogs from both Missouri and Michigan exhibit maximal hopping performance at intermediate body temperatures and full hydration (and down to as low as 90% hydration). Again, by this physiological performance measure, occupancy of Clearcuts with attendant increases in body temperature and decreases in hydration would have substantially decreased wood frog hopping ability.

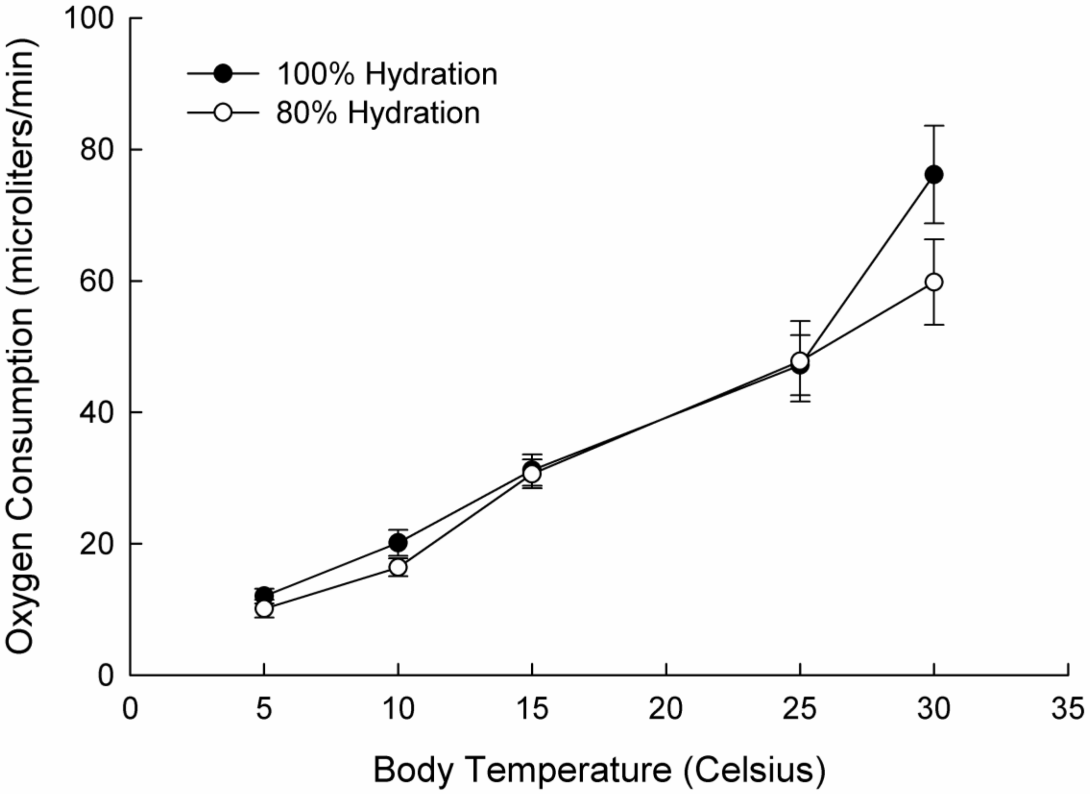


Figure 12. Resting oxygen consumption in wood frogs with body temperatures from 5 to 30°C and body hydrations of 80% and 100%.

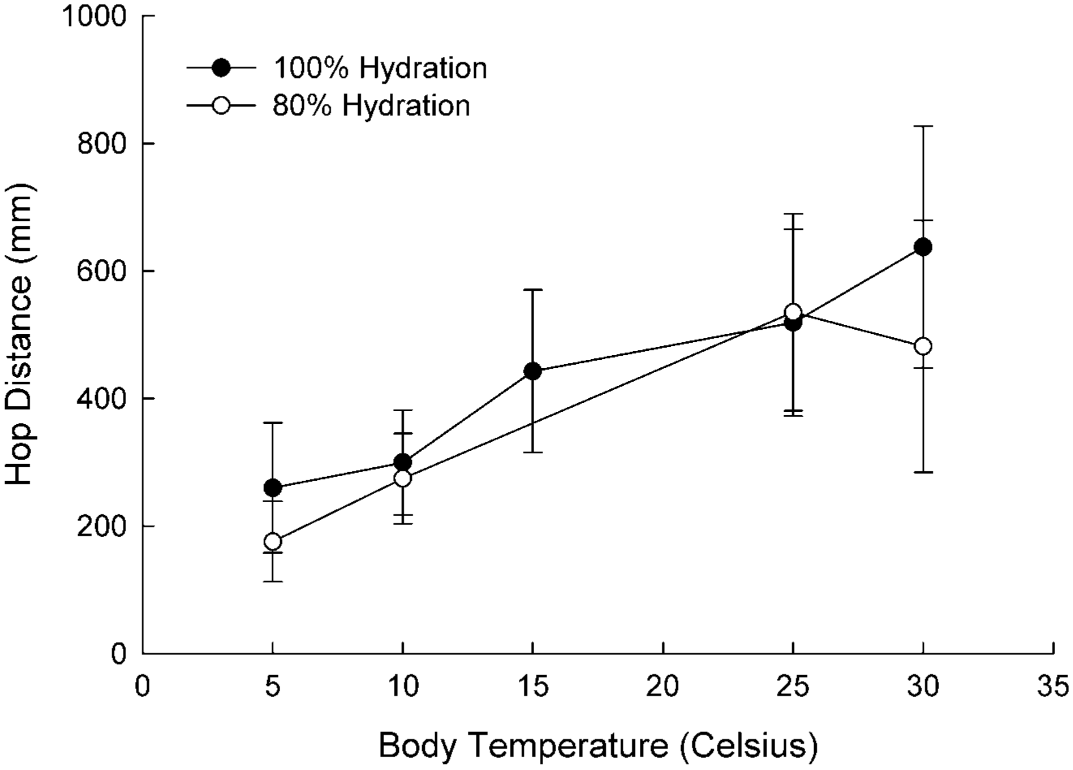


Figure 13. Hop distances in wood frogs with body temperatures from 5 to 30°C and body hydrations of 80% and 100%.

CHAPTER 4: Microgeographic variation in reproductive success and its effects on conservation strategies for threatened desert tortoises

ABSTRACT

Desert resource environments are tied to limited, highly localized rainfall regimes which generate microgeographic variation in the life histories of inhabitants. U.S. federally threatened desert tortoises (*Gopherus agassizii*) inhabit the Mojave Desert where myriad land-use impacts (urban development, solar energy generation) are eliminating parts of their range and increasingly necessitating conservation action that includes translocation. We examined microgeographic variation in desert tortoise reproduction at opposite ends of a 250-m elevation-related rainfall cline within Ivanpah Valley, California, Eastern Mojave Desert. Biophysical operative environments in both upper-elevation, “Cima,” and lower-elevation, “Pumphouse,” plots corresponded with daily and seasonal patterns of incident solar radiation. Cima received 22% more rainfall and contained greater perennial vegetative cover which conferred 5°C-cooler daytime shaded temperatures. In 2003, an average rainfall year, Cima tortoises had longer potential activity periods by up to several hours and greater ephemeral forage. Enhanced resource availability in Cima was associated with larger-bodied females producing larger eggs, while still producing the same number of eggs as Pumphouse females. However, reproductive success was lower in Cima because 90% of eggs were predated versus 11% in Pumphouse, indicating that predatory interactions produced counter-gradient variation in reproductive success across the rainfall cline. Due to strong ecosystem responses to enhanced resource availability, conservation strategies designed to protect and recover threatened desert inhabitants, such

as desert tortoises, should incorporate information on the effects of regional resource variation within the organism’s range. Relatively resource-poor areas merit inclusion in considerations of quality, alternative habitat for desert organisms displaced by land-use.

INTRODUCTION

Deserts are characterized by scant and often unpredictable rainfall with resource environments (e.g., food, microclimates) that are closely tied to water (Ehleringer and Mooney 1983, Sowell 2001). Regional variation in desert ecosystems arises from strong responses to relatively modest changes in rainfall associated with different combinations of latitude, elevation, and location relative to nearby topographical land features (e.g., bajadas, washes; Beatley 1974 a, b; Sowell 2001).

The aridity of deserts is frequently coupled with hot, highly variable environmental temperatures (Sowell 2001). In desert ectotherms, the thermal environment and thermoregulation are particularly strong influences on their ecology because environmental temperatures directly affect their body temperature. This, in turn, affects their habitat utilization, physiological processes, and energy acquisition (reviewed by Zimmerman et al. 1994). Studies of resulting life history variation in vertebrate desert ectotherms have tended to focus on the influences of elevation, rainfall and environmental temperatures on small, relatively short-lived lizards (e.g., Dunham 1978; Grant and Dunham 1988, 1990; Adolph and Porter 1993; Sears 2005). In general, higher altitude sites and/or wetter years are associated with increased rainfall, cooler temperatures, greater activity periods, increased food availability and intake, higher growth rates, larger mature females, and greater size-specific fecundity (Dunham 1978; Grant and Dunham 1988, 1990). However, greater activity periods can expose small lizards to greater predation risk (Adolph and Porter 1993; Sears 2005) and cooler temperatures constrain digestion and limit energy accrual from ingested food (Grant and Dunham 1988, 1990).

We examined how the thermal ecology and reproduction of desert tortoises (*Gopherus agassizii*), large, long-lived ectothermic herbivores, are tied to their resource environments. The desert tortoise is federally listed as threatened in the United States across its Mojave Desert range (USFWS 1990), and its habitat is divided into areas containing distinct population segments: the Western Mojave, the Northeastern Mojave, and the Eastern Mojave (Murphy et al. 2007). Each Mojave site is characterized by different amounts of seasonal and annual rainfall (Lovich et al. 1998; Sowell 2001), and the effects of these (macrogeographic) differences in rainfall on desert tortoise life history are well established. Despite similar winter rainfall, summer rainfall increases from negligible in the Western Mojave to intermediate levels in the Eastern and Northeastern Mojave (Averill-Murray and Klug 2000). Rainfall increases the density and aboveground productivity of shrubs (Beatley 1974a; Ehleringer and Mooney 1983; Thomas et al. 2004) that provide wind shadows and shade for desert tortoises on the surface (Shreve 1931; O'Connor et al. 2000). Rainfall also increases the biomass of herbaceous forage (Beatley 1974b), temporarily cools surface operative temperatures (Gates 1980), and increases water intake by tortoises, allowing them to flush accumulated waste and digest senescent plant material (Peterson 1996; Henen 1997). Macrogeographic and temporal (e.g., drought vs. pluvial years) variation in rainfall thereby induce substantial changes in activity (Nagy and Medica 1986; Duda et al. 1999), food intake and energetics (Nagy and Medica 1986; Peterson 1996; Henen 1997; Henen et al. 1998), growth rates (Curtin

2006), and reproductive output (Turner et al. 1984, 1986; Wallis et al. 1999; Averill-Murray et al. 2002a).

Elevation differences within the habitat of a Mojave population also lead to differential rainfall (Beatley 1974a, b), but microgeographic variation in their life history is essentially unknown. Long-term annual rainfall differences exist at opposite elevation extremes of desert tortoise habitat within Ivanpah Valley in the Eastern Mojave Desert, California (Lovich et al. 1998, 1999; Avery 2001; Curtin 2006). We established study plots in which the higher altitude plot (1,116 m, “Cima”) receives an average 22% greater annual rainfall than the lower (879 m, “Pumphouse”; Fig. 13). We hypothesized that lower rainfall in Pumphouse creates a relatively resource-poor environment in which lower food availability and increased biophysical constraints on activity (e.g., fewer shade plants, lower shade quality) limit energy accrual and reproductive output. While increased rainfall has clear benefits for desert tortoises, it is unknown whether predation incidence increases in response to greater rainfall and greater small mammal prey availability (e.g., *Vulpes macrotis*; Dennis and Otten 2000), or whether predation incidence increases in response to lower rainfall due to prey switching (Peterson 1994). We assessed predation on tortoise eggs to determine if predation enhanced or counteracted the effects of the biophysical and resource environments on reproductive success.

This research has conservation implications because desert areas are increasingly affected by myriad land use impacts (e.g., urban development, Tracy et al. 2004, Field et al. 2007; military facilities expansion, Heaton et al. 2008; solar energy generation, BLM 2009), and current conservation strategies for threatened species, such as desert tortoises, include the translocation of individuals to alternate habitat (reviewed by Tracy et al. 2004; Field et al. 2007). Indeed, in Ivanpah Valley just north of Interstate 15 (Fig. 14), solar energy developers are proposing to translocate desert tortoises from land that will receive heliostat arrays (BLM 2009). Better understanding of the contributions of desert resource environments to population growth rates will enhance assessments of potential alternative habitat for displaced organisms by adding ecological considerations beyond those related to anthropogenic effects (Heaton et al. 2008).

MATERIALS AND METHODS

The two Ivanpah Valley (Lat. 35° 29' 60", Long. 115° 20' 3") study plots are separated by 7 km straight line distance from Pumphouse (northeast) to Cima (southwest). The 60 km^2 total study site contains creosote bush mixed scrub vegetation that transition into mid-elevation, mixed desert scrub (Thomas et al. 2004). Desert tortoises inhabit sites between the two plots and some of the surrounding area in Ivanpah Valley not incorporated in this study. Focal females in this study had been monitored for over five years without observation of movement between plots (Avery 1998; Franks 2002), but some adult male tortoises had home ranges that spanned both plots (Franks 2002). Hatchling and juvenile movements are unknown.

Rainfall and vegetation

We recorded rainfall from 11 plastic rain gauges (8 in Pumphouse and 3 in Cima, Avery 1998). Precipitation from October to March and June to September was considered winter and summer rainfall, respectively (Beatley 1974b; Wallis et al. 1999). Winter rainfall is the necessary precursor for spring vegetative forage for desert tortoises

(Beatley 1969, 1974b) and summer rainfall is important for nutrient balance (Nagy and Medica 1986; Henen et al. 1998).

A vegetation study conducted by the United States Geological Survey included measures of rooted herbaceous biomass and shrub species richness in April/May from 2001 to 2003 (Beever and Pyke 2005; Beever et al. 2006). We analyzed vegetation data from Beever and others (2005, 2006) from six sites within 500 m of the meteorological station (see next section) in each plot. Twenty transects of line-intercept measurements from June 1997 provided additional measures of individual perennial plant canopy cover within each plot (following Ludwig et al. 1975). *Ambrosia dumosa*, *Hilaria rigida*, and *Larrea tridentata* occurred in Cima and Pumphouse in great enough densities to permit comparisons between plots. With the exception of *H. rigida*, each of these species exhibits slow population turnover (> 15 years; Cody 2000) and little response to interannual variation in rainfall (Beatley 1974a). Because the major canopy species are long-lived and differences in annual rainfall have been consistent since 1997 (Table 4), these 1997 canopy measurements add to our understanding of relative shade availability in Cima versus Pumphouse.

Thermal habitat and thermoregulation

From May through July 2003, we set up one automated meteorological and tortoise operative temperature model arrays in Cima and Pumphouse. A datalogger (Campbell Scientific CR-10X, Logan, UT) and multiplexer (AM32, Logan, UT) recorded environmental data every 15 min. from a cup anemometer (R.M. Young Wind Sentry, Traverse City, MI) at a height of 50 cm, a pyranometer (Li-Cor LI200X, Lincoln, NE) on the ground surface, and an air temperature profile with shielded thermocouples (Christian and Tracy 1985) at -2, 0, 2, 5, 10, 25, and 50 cm height. The -2 cm thermocouple corresponded to the depth of a typical pallet, or ground depression, used by tortoises as a refugium. We recorded temperature measurements from thermocouples placed within a burrow in each plot, positioned 1 m from the entrance (approximate tortoise retreat distance). A live tortoise displaced the thermocouple in the Cima burrow several times during the study period. Hereafter, we present burrow temperature measurements solely from the Pumphouse burrow (< 1°C difference between burrow temperatures during unoccupied periods in the Cima burrow). All thermocouples (Omega Engineering, Stamford, CT) were accurate to ± 0.1°C.

We placed 40 thick-walled solid aluminum tortoise models (200 mm, midline carapace length, MCL), painted teal blue (Krylon enamel 1904) to match the integrated spectral absorptivity of desert tortoises, in 25 x 25 m arrays at each plot (following Zimmerman et al. 1994). Models were positioned on vertices 5 m apart within the array so that 3-4 were in full-sun (i.e. not shaded during the daytime), 3 in full-shade (placed at the base of a creosote bush), and 13-14 in partial-shade at different cardinal directions relative to a shrub.

Using tortoise biotelemetry (see mark-recapture methods below), at each capture we recorded the date, time, behavior of the tortoise (e.g., inactive in burrow, foraging), body temperature (by pressing a thermocouple into the inguinal area) and shaded air temperature (~ 10 cm above the ground). Due to logistical constraints, we only captured tortoises during morning hours and we did not measure body temperatures at every capture.

Reproduction

From April to July 2003, we maintained a mark-recapture study using focal adult female tortoises equipped with 50 g radio transmitters (Advanced Telemetry Systems; following Boarman et al. 1998) and incidental captures of other females in the plots. Tortoises were initially measured with calipers (MCL; ±0.5 mm). We then repeatedly recaptured 19 focal females, 8 in Pumphouse and 11 in Cima. A combination of x-radiography (every two weeks) and frequent weighing (every second day) was used to monitor reproduction. A drop in mass of ~100g indicated timing of egg clutch deposition (Turner et al. 1984). X-radiography, with safe radiation exposure levels (portable x-ray machine; Minxray-HF100, Northbrook, Illinois; settings of 60 kVP for 0.02 sec, Hinton et al. 1997), measured egg clutch characteristics (egg quantity and size). To obtain mean egg volume for each clutch, egg size (maximum length and breadth) was determined using digital calipers (±0.02mm) on x-ray images. Egg volume was then calculated based on the assumption that the eggs were ellipsoids (Preston 1974, Rose et al. 1996). We corrected for image magnification of the true egg size following Graham and Petokas (1989). We also x-rayed untransmittered adult females. We returned all tortoises to the point of capture within 30 min.

We located nest sites based on tortoise capture locations around the time of egg deposition and by using slight excavation and palpation of the soil in burrow interiors. We prevented researcher scent transfer to the area by using gloves and a ground cloth (following Bjurlin and Bissonette 2004). During the incubation period, we regularly observed nest locations from a distance in order to determine timing of predation events, if they occurred. After at least 100 days of incubation, we excavated nests to determine hatching and emergence success.

Analyses

Date are presented as mean ± 1 SEM. Repeated measures analysis of variance (rmANOVA) tested rainfall variation between plots in Summer 2002, Winter 2002-2003, and Summer 2003. ANOVAs compared plot herbaceous plant biomasses and canopy areas (m^2).

Thick-walled aluminum operative temperature models exhibit thermal inertia and their longer thermal time constants result in integrated, as opposed to instantaneous, operative temperatures (O'Connor 2000). An iterative deconvolution routine estimated instantaneous operative temperatures by reducing the difference between measured model temperatures and calculated operative temperatures based on the wind speed at each time step (O'Connor 2000). Spearman's ρ tested for a significant two-tailed correlation between time of capture and the difference between body temperature and shaded air temperature. A Mann-Whitney U tested for significant differences in body temperatures between plots.

Two-tailed Student t-tests compared MCLs and total annual egg production between plots. Generalized estimating equations tested whether egg volumes or clutch sizes were significantly affected by plot and clutch number (fixed factors) with MCL as a covariate. We specified the correlation matrix structure in both models as exchangeable (see Zuur et al. 2009). A Poisson distribution with a log link was specified for clutch size analysis. Mann-Whitney U tested for differences in frequency of second clutch production and predation between plots. We carried out all statistical analyses using

SPSS 15.0. Estimated marginal means for significant fixed effects were compared using the least significant difference. The significance level for all analyses was $P < 0.05$.

RESULTS

Rainfall and vegetation

There was a significant effect of plot on precipitation from 2002 to 2003 ($F_{1, 9} = 30.3$, $P < 0.001$) with significantly more rain in Cima (Table 4; $P < 0.001$). There was also a significant effect of plot on herbaceous biomass in 2003 ($F_{1,28} = 7.7$, $P = 0.01$), with significantly greater Cima biomass ($P = 0.01$). Perennial species richness was 2 to 3 times greater in Cima from 2001 to 2003, and in 1997. Cima total perennial cover was significantly greater ($t_{18} = 3.5$, $P = 0.003$). The most frequently encountered perennial species in both plots were *H. rigida* (Cima 44.9%, Pumphouse 9.5%), *A. dumosa* (Cima 16.5%, Pumphouse 41.8%), and *L. tridentata* (Cima 13.0%, Pumphouse 22.6%). *H. rigida* is a bunch grass and *A. dumosa* is a sub-shrub. Therefore, canopy cover in both plots was dominated by *L. tridentata*, and was significantly greater in Cima ($P<0.001$). Cima also contained several larger canopy plants not found in Pumphouse, including *Yucca schidigera* (1.7%), *Lycium andersonii* (1.7%), and *Ephedra nevadensis* (1.2%).

Thermal habitat and thermoregulation

Incident solar radiation levels were generally greater in Cima (Fig. 15A), and levels increased from May to July in both plots (Table 5). Wind speeds were similar between plots during the day, but they were lower in Pumphouse at night (Fig. 15B). Morning ground surface temperatures increased more rapidly in Pumphouse, but they were higher at midday and into the afternoon in Cima (Fig. 15C). In both plots, ground surface temperatures increased almost 40ºC during daytime hours. Daytime air temperatures were up to 15ºC cooler than the ground. Pallet temperatures (-2 cm) remained below 40ºC until almost midday, were similar to burrow temperatures in the evening up until midnight, and remained warmer than ground surface temperatures throughout nighttime hours.

In both plots, operative temperatures in full-shade were generally depressed throughout daytime hours by 10 to 15ºC compared to those in full-sun (Fig. 16), with the greatest difference observed in Cima at midday and into the afternoon hours. Daytime (0700 to 2100 hours) partially-shaded operative temperatures were only moderately different from full-sun operative temperatures (within ~5ºC, Fig. 17). Summer monsoonal rains occasionally cooled all operative temperatures (e.g. Julian Day = 157, Fig. 17). Based on differences in full-shade operative temperatures, and a mean critical thermal maximum of 45ºC (Naegle 1976), we estimated that the morning active period for Pumphouse tortoises was 1 – 1.5 hours greater than in Cima (Table 5), and the afternoon Cima active period was 3 – 3.75 hours greater than the Pumphouse (Table 5). Partial-shade in both plots resulted in estimated morning and afternoon active periods differing by up to 0.5 hours. Seasonal progression increased mandatory periods of inactivity (full-shade operative temperatures above 45ºC) throughout Ivanpah Valley from the early-spring, when activity was possible throughout daytime hours, to mid-summer, when desert tortoises were inactive at least 4 to 6 hours during the day (Table 5).

The extended window for morning activity in Pumphouse corresponded with our increased observations of morning (0700 to 1200 hours) tortoise activity outside of burrows in Pumphouse as compared to in Cima (Fig. 18). Regardless of plot, tortoise activity outside their burrows decreased as the season progressed from spring into summer (Fig. 18). There was no significant correlation between time of capture and the difference between body temperature and shaded air temperature in either plot (Fig. 19a, $P > 0.05$), and this pattern did not change with seasonal progression (Fig. 19b). There were also no significant differences overall between plots in tortoise body temperatures (Mann-Whitney $U = 228.0$, $P > 0.05$).

Reproduction

During 2003, 18 of 19 transmittered adult female tortoises deposited at least one clutch of eggs, with first clutches deposited between 26-May and 9-June and second clutches between 12-June and 3-July. We detected egg clutches in 8 untransmittered female tortoises. Because these untransmittered tortoises were not captured regularly, we could not determine with confidence whether detected clutches were first or second clutches (Unknown Clutch, Table 6). Three transmittered tortoises also had incomplete x-ray records due to the tortoise eluding capture (Unknown Clutch, Table 6). There was no significant difference between plots in the proportion of transmittered tortoises depositing a second clutch, with 6 out of 10 in Cima depositing two clutches and 2 out of 5 in Pumphouse (Mann-Whitney $U = 20.0$, $P > 0.05$). There was also no significant difference between plots in the total annual number of eggs deposited per tortoise with 4.6 ± 1.2 ($N = 5$) in Pumphouse and 5.5 ± 0.62 ($N = 10$) in Cima ($t_{13} = 0.74$, $P = 0.47$).

The MCL of all captured gravid female tortoises in Cima was 235.0 ± 4.9 mm ($N = 13$), and this was significantly greater than in Pumphouse (222.2 ± 3.8 mm; $N = 13$, $t_{24} = 2.1$, $P = 0.048$). Using just the observations for known clutch numbers, we found that desert tortoise MCL was not a significant covariate with clutch size (Wald $\chi^2_1 = 1.6$, $P > 0.05$) and there was no significant effect of plot (Table 6; Wald $\chi^2_1 = 0.2$, $P > 0.05$) or clutch number (Wald $\chi^2_1 = 1.0$, $P > 0.05$) on clutch size. There was, however, a significant interactive effect of plot and clutch number on egg volume (Wald $\chi^2_1 = 10.3$, $P = 0.001$), with the largest egg volumes in Cima first clutches (Table 6). MCL was positively correlated with egg volume (+0.2 mL, CI: 0.02 – 0.3; Wald $\chi^2_1 = 5.0$, $P = 0.025$).

We monitored 20 nests (11 nests in Cima and 9 in Pumphouse) from 17 different females. All nests were within burrows dug into coppice mounds either directly underneath or near *L. tridentata* or *A. dumosa*. Predation levels were significantly higher in Cima where 9 out of 10 nests (1 unknown) were predated as compared to 1 out of 9 nests (11%) in Pumphouse (Mann-Whitney $U = 9.5$, $P = 0.001$). In the former, predation events were evenly distributed over 10 weeks of monitored incubation with ~1 observation of nest predation per week. The most common nest predators in Ivanpah Valley were *V. macrotis*. At least one nest in this study was probably predated by either *Canis latrans* or *Taxidea taxus* because the burrow opening was greatly enlarged and there was substantial excavation of the burrow near the nest site. The hatching success in Cima was 40% for the only non-predated nest, and 67.5 ± 13.3% in Pumphouse, where 7 out of 8 nests produced at least one hatchling and 1 nest was predated.

DISCUSSION

Elevation differences in desert tortoise habitat within Ivanpah Valley corresponded to environmental differences in rainfall, perennial and ephemeral vegetation, as well as opportunities for surface activity. Pumphouse was more resource-poor in every respect which corresponded to smaller-sized mature female desert tortoises, and smaller eggs (i.e., volume). However, the differences in thermal and food resources at the two plots did not create a divergence in the number of eggs produced or the number of clutches laid. Instead, predation had the greatest effect on reproductive success in these tortoises.

Rainfall-based resource environments

Ivanpah Valley regional differences in rainfall were positively correlated with higher elevation, and this relationship is similar to that in the Northeastern Mojave (Beatley 1974b). Long-term rainfall differences across the study plots had one noted exception occurring in a drought year 1998 – 1999 (Avery 2001), but this is unlikely to have produced a resource pulse for organisms in the Pumphouse plot. There is consistent macrogeographic variation in precipitation across the range of the desert tortoise, with the Sonoran and tropical Sinaloan Deserts receiving greater annual rainfall than the Mojave (Table 7). Incremental decreases in summer rainfall occur going from a high in the Sonoran to almost negligible in the Western Mojave (Averill-Murray and Klug 2000). The Sonoran and Mojave Deserts further experience strong temporal variation in rainfall because the El Niño-Southern Oscillation induces large inter-annual changes in winter rainfall, with increased winter rainfall in El Niño years (e.g., Henen et al. 1998). Comparable to other desert ecosystems, large inter-annual variation in rainfall is the norm throughout the desert tortoise’s Mojave and Sonoran range (Ehleringer and Mooney 1983).

Ephemeral vegetation is positively correlated with winter rainfall (Beatley 1969, 1974b; Henen et al. 1998), and it tracks inter-annual, macro- and micro-geographic changes in rainfall (Table 7). Herbaceous plant biomass (1) is greatest at higher elevations in pluvial years (Beatley 1974b); (2) increases in response to higher winter rainfall, but this is dependent on the timing of the rainfall (Beatley 1974b; Turner et al. 1986); and (3) it is extremely patchy with standard deviations often greater than the means in quadrat measurements (Nussear 2004). The creosote bush mixed scrub perennial vegetation characterizing much of the desert tortoise habitat in the Mojave Desert, including Cima and Pumphouse, ranges from two species co-dominance (*L. tridentata* and *A. dumosa*) in low-elevation xeric stands to high-elevation shrubland with up to 20 co-occuring perennials in higher elevation mesic stands (Thomas et al. 2004). Perennial canopy cover and the density of perennial shrubs are generally greater in higher-elevation desert tortoise habitat (Beatley 1974a; Ehleringer and Mooney 1983), and active desert tortoises tend to select larger than average shrub species for shade, preferring *Ephedra* spp. and *Y. schidigera* where available (Nussear 2004). Shade quality of perennial vegetation was key to the microgeographic variation in surface activity and, presumably, food resource acquisition of Ivanpah Valley desert tortoises.

Thermal ecology

Shade availability from perennial shrubs and succulents in Cima extended periods of daily potential surface activity for desert tortoises during afternoon hours. Otherwise, strict thermal constraints (e.g., lethal surface operative temperatures at midday) on desert tortoise microhabitat utilization necessitated the use of burrows (*this study*; Nagy and Medica 1986; Zimmerman et al. 1994). Overall, daily and seasonal patterns of operative temperatures and activity periods tracked temporal changes in incident solar radiation, which is also observed elsewhere in the Eastern Mojave and Sonoran Deserts (Zimmerman et al. 1994; Averill-Murray 2002b). Monsoonal rainfall occasionally relaxes these constraints on desert tortoise surface activity in the summer (Nagy and Medica

1986; Peterson 1996; Henen et al. 1998). Adult desert tortoise activity transitions from full-day spring activity to summer bimodal, back to full-day fall activity (September – late-October; Zimmerman et al. 1994), and finally into hibernation when operative temperatures are too low for activity (November – early-March; Nagy and Medica 1986).

Biotelemetry measurements supported operative temperature modeling-based estimates of surface activity in each plot during morning hours. Pumphouse tortoises had greater potential and actual morning surface activity, and this was likely due to the aspect and slope of the Pumphouse plot. Although afternoon activity was not assessed directly in this study, estimates of extended surface activity in Cima are supported by observations of Eastern Mojave desert tortoises active in the late-afternoon and evening (Zimmerman et al. 1994; Avery 1998). Relative differences between plots in microhabitat utilization do not appear to be counteracted by differing thermoregulatory strategies. Desert tortoises generally do not defend precise body temperatures during surface activity (*this study*; Zimmerman et al. 1994; Nussear 2004), nor do they appear to drastically alter their behavioral or thermoregulatory tactics in response to relative opportunities for surface activity in a particular habitat. Instead, large-bodied desert tortoises rely on thermal inertia to dampen heating rates, and this may be energetically favorable due to the patchy distribution of resources in their habitat and the energetic expense of moving their large mass (Zimmerman et al. 1994; Nussear 2004).

Reproductive success

Pumphouse MCLs are among the smallest in mature female desert tortoises across their range (Table 7). Only females at Goffs, 60 km to the southeast of Ivanpah Valley, are smaller (mean: 220 mm; Turner et al. 1986; Wallis et al. 1999). Mature female desert tortoise body size tends to be positively correlated with reproductive output parameters such as clutch frequency, clutch size, and total annual egg production (reviewed by Averill-Murray and Klug 2000). Reproductive output also increases in response to El Niño-related increases in rainfall (Wallis et al. 1999). Because female pelvic width is positively correlated with body size, variation in egg size, particularly egg width, may also be correlated with body size if upper-limit constraints on egg size are imposed by pelvic width (Congdon and Gibbons 1987). In Ivanpah Valley, mature female pelvic apertures were positively correlated with MCL (Cima: 51.6 ± 0.8 mm versus Pumphouse: 47.4 ± 1.1 mm), and we found a positive correlation between female size and egg size. This positive correlation also occurs in the Western Mojave and Sonoran desert tortoises (Wallis et al. 1999; Averill-Murray and Klug 2000). However, Ivanpah Valley plot-related egg size differences only occurred in first clutches, and it is possible that the size differences were actually due to differential allocations of yolk and/or albumen regardless of adult female size. Greater accumulation of energetic and/or hydric resources in Cima females may have permitted larger allocations to reproductive output, and larger first-clutch eggs in Cima could confer an advantage in terms of neonate size, water and/or energy reserves (Wallace et al. 2006). Future study of how variation in egg size relates to hatchling survivorship, particularly in drought versus pluvial years, will be an important contribution to understanding exactly how finely tuned desert tortoise reproduction is to regional resource differences.

In average rainfall years, desert tortoise egg clutch predation appears to be positively correlated with rainfall. To our knowledge, only one other study has rigorously measured desert tortoise hatching success in relation to predation (Bjurlin and Bissonette

2004). In the Western Mojave, predation levels were 47% in 1998 (*N* = 17) and 12% in 1999 (*N* = 25; Bjurlin and Bissonette 2004), but it remains unclear whether this result is tied primarily to environmental effects or researcher influence due to scent transfer in the first year of study (Bjurlin and Bissonette 2004). Several anecdotal reports further suggest that there is temporal and inter-population variation in desert tortoise egg predation (reviewed by Bjurlin and Bissonette 2004). The population density of the primary desert tortoise egg predator, *V. macrotis*, positively covaries with rainfall (Dennis and Otten 2000), and this may be related to the influence of rain on small mammal prey species (Beatley 1969; Arjo et al. 2007) as well as the availability of water for the kit foxes themselves.

Conclusions

Strong regional ecosystem responses to enhanced resource availability are commonly observed in studies focusing on life history variation in a variety of desert organisms including small ectothermic vertebrates (Dunham 1978; Grant and Dunham 1990), plants (Beatley 1974a; Cody 2000), and small mammals (Beatley 1969, Dennis and Otten 2000). Typically, growth, survivorship, and reproductive output are positively correlated with enhanced resource availability (Beatley 1969, 1974a; Dunham 1978; Grant and Dunham 1988, 1990), but juvenile and adult predation risk can counteract these positive effects (Sears 2005). Similar effects on life history are observed within and across the range of the desert tortoise with greater opportunities for activity and increased reproductive output (larger eggs) in resource-rich versus resource-poor habitat. However, resource-poor habitat offers higher hatching success (lower egg predation), at least in average-rainfall years. Desert tortoises exhibit substantial plasticity in female size at reproductive maturity and in reproductive output (annual egg production, egg size) at macro- and micro-geographic scales. Our results suggest that plasticity in desert tortoise reproduction is primarily tied to environmental heterogeneity, but to what extent this is due to adult phenotypic plasticity versus developmental plasticity is unknown. It is therefore advisable that conservation strategies designed to protect and recover desert organisms, such as desert tortoises, (1) utilize ecological information at appropriate scales in addition to minimizing anthropogenic effects, (2) monitor reproductive success, which includes egg predation, and (3) carefully consider potential tradeoffs for population growth rates in both resource-rich and resource-poor habitat.

Table 4. Habitat characteristics of the two *Gopherus agassizii* study plots in Ivanpah Valley.

	Cima	**Pumphouse**
Elevation (m)	1,116	879
Precipitation (mm)		
Annual mean 1997 – 2003 (Range)	139.9 ± 22.3 (57.2 – 237.7)	105.7 ± 15.7 (38.5 – 175.4)
Summer 2002	21.2 ± 1.3**	12.6 ± 0.6
Winter 2002 – 03	102.7 ± 1.8**	80.8 ± 4.5
Summer 2003	51.4 ± 5.7**	23.5 ± 3.1
Herbaceous plant biomass 2003 (g m^{-2})†	45.6 ± 9.7	13.5 ± 6.4
Shrub species richness 2001 – 2003†	7.8 ± 0.5	2.6 ± 0.2
Perennial plant species richness 1997	8.1 ± 0.6	4.3 ± 0.4
Total perennial plant cover 1997 (%)	25.5 ± 1.8**	16.3 ± 1.9
Canopy cover 1997 (m^2)		
Larrea tridentata	37.9 ± 1.2**	24.1 ± 1.3
Ambrosia dumosa	1.5 ± 1.1	2.8 ± 0.9
Hilaria rigida	0.9 ± 0.9	2.4 ± 2.2

Data are means ± 1 SEM; Ranges in parentheses
**Significantly greater $P < 0.05$
†(Beever and Pyke 2005, Beever et al. 2006)

Table 5. Monthly maximum incident solar radiation levels, maximum ground surface temperatures, and estimated inactivity periods for *Gopherus agassizii* in Ivanpah Valley based on when operative temperatures exceeded the critical thermal maximum (45°C, Naegle 1976).

		Cima	**Pumphouse**
Max. Incident Solar Radiation (W m^{-2})			
	May	981.0 ± 16.3	911.5 ± 40.2
	June	990.6 ± 6.2	857.8 ± 49.2
	July	994.0 ± 27.7	973.5 ± 15.7
Max. Ground Surface Temperature (°C)			
	May	55.7 ± 1.5	53.9 ± 1.2
	June	58.8 ± 0.8	57.5 ± 0.7
	July	60.9 ± 1.5	60.8 ± 0.7
Inactivity Period (hours)			
	Full-Sun		
	May	6.5 (1030 – 1700)	6 (1045 – 1645)
	June	7.75 (945 – 1730)	8.25 (930 – 1745)
	July	8.75 (930 – 1815)	9.25 (915 – 1830)
	Full-Shade		
	May	--	--
	June	1.25 (1045 – 1200)	3 (1200 – 1500)
	July	4 (945 – 1345)	6.75 (1045 – 1730)

Means ± 1 SEM

Range of recorded hours when operative temperatures exceeded 45°C in parentheses

-- N/A, operative temperatures never exceeded 45°C

Table 6. Reproductive characteristics of *Gopherus agassizii* in Ivanpah Valley, 2003. Clutch sizes and egg volumes were determined from x-rays, and the percent predated was determined from nest excavation.

	Cima	**Pumphouse**
First Clutch		
N	10	5
Clutch Size (# eggs)†	3.5 ± 0.2	3.7 ± 0.4
Egg Volume (mL)†	71.7 ± 1.8	62.5 ± 3.0
Predated (%)	100	0
Second Clutch		
N	6	2
Clutch Size (# eggs)†	3.1 ± 0.3	3.2 ± 0.6
Egg Volume (mL)†	61.3 ± 1.8	64.8 ± 2.7
Predated (%)	100	0
Unknown Clutch*		
N	3	8
Clutch Size (# eggs)	3.3 ± 0.3	3.5 ± 0.3
Egg Volume (mL)	67.8 ± 2.2	56.6 ± 2.0
Predated (%)	0	25
Overall Clutch Size†	3.3 ± 0.2	3.4 ± 0.2
Overall Egg Volume†	67.7 ± 1.7**	60.3 ± 2.2
Overall Predation Level	90.0 ± 9.5**	11.0 ± 1.1

Data are means ± 1 SEM; *N* = sample size (# clutches)
*Could not determine clutch number (see Results)
†Estimated marginal means ± 1 SEM
**Significantly greater $P < 0.05$

Table 7. Reproductive characteristics of mature female *Gopherus agassizii* and key comparable environmental characteristics, across their geographic range. Sample size for mature desert tortoises includes multiyear observations of individuals.

	Elevation (m)	Winter Rainfall (mm)	Herbaceous Biomass (g m^{-2})	# Clutches	Mean Clutch Size	MCL (mm)	*N* (tortoises)	Citation
Northeastern Mojave (1992–95)	1000 – 1500	32 – 179*	4.4 – 44.8	0 – 2	3.3 – 5.4	209 – 276	32	Mueller et al. 1998
Eastern Mojave (1980–85**, 1992–93)	680 – 976	20.6 – 212	0.1 – 42	0 – 2	4.1 – 5.1	189 – 247	81	Turner et al. 1986; Wallis et al. 1999
Cima (1997–2003†)	1,116	5.8 – 237.7	0.25 – 45.6	0 – 2	3.3 – 5.4	207 – 268	27	Avery 2001; Beever and others 2005, 2006; *this study*
Pumphouse (1997–2003†)	879	7.3 – 175.4	0.05 – 13.5	0 – 2	3.4 – 4.0	199 – 245	18	
Western Mojave (1992–93)	750	22 – 245	0.05 – 35	0 – 2	3.9 – 4.4	198 – 270	47	Wallis et al. 1999
Northern Sonoran (1993, 1997–99)	549 – 853	72 – 367	--	0 – 1	3.8 – 5.7	220 – 289	56	Averill-Murray and others 2000, 2002a
Southern Sonoran (1997)	600 – 702	--	--	0 – 1	3.3	226 – 249	4	Averill-Murray and others 2000, 2002a

Data are ranges for all years observed; -- Not available; * Annual rainfall reduced by 1/3 (see Mueller et al. 1998); ** Desert tortoises monitored from 1983 – 1985; † Herbaceous biomass and desert tortoises from 1999 and 2003

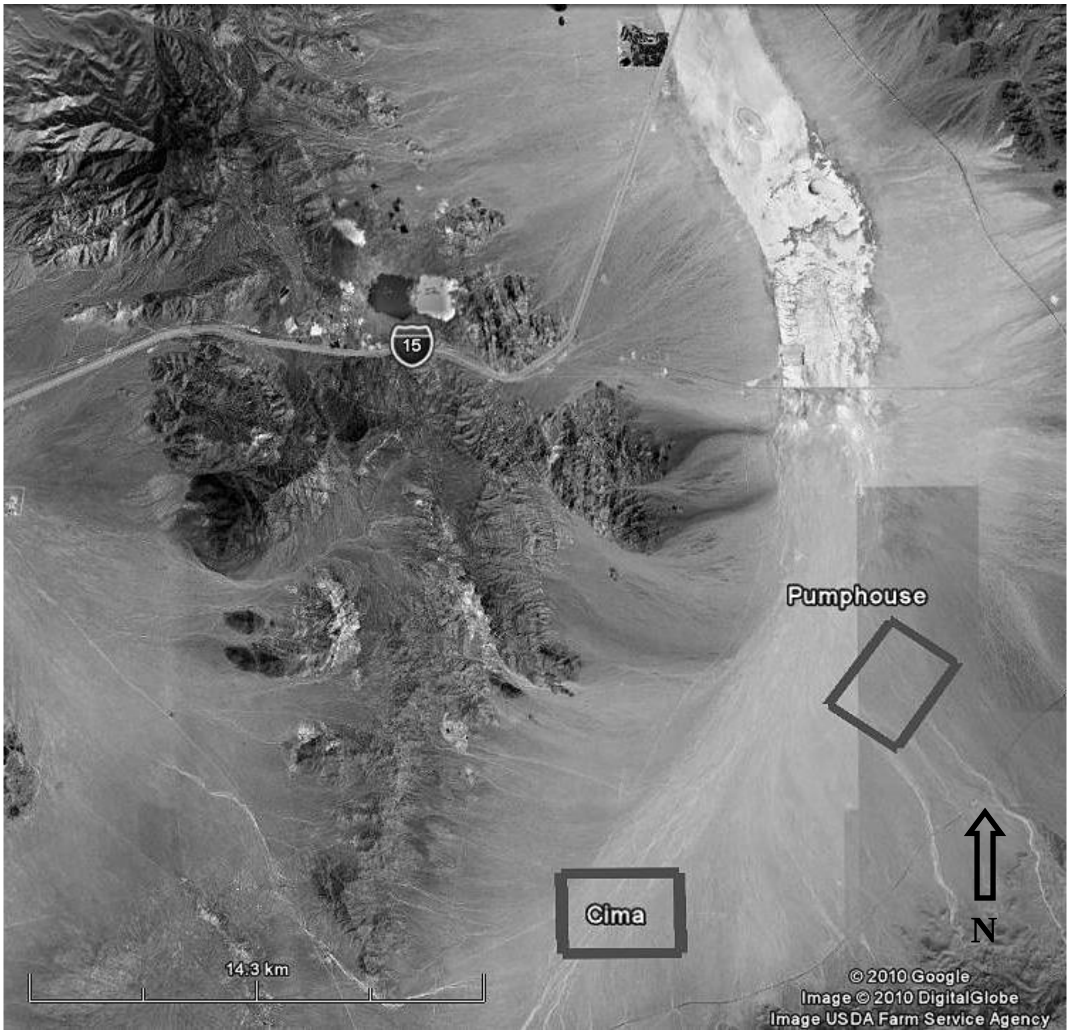
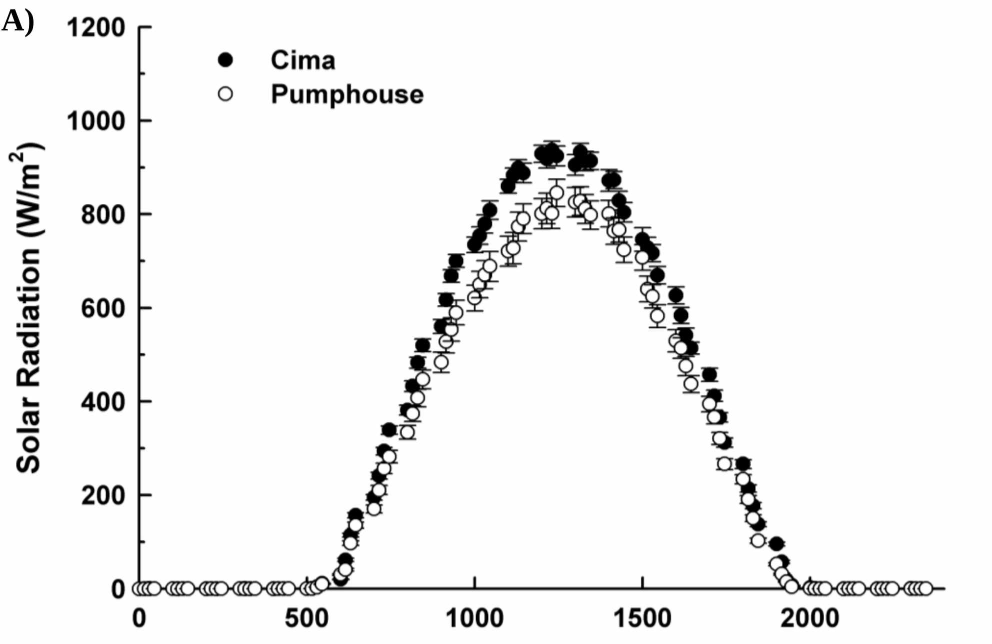
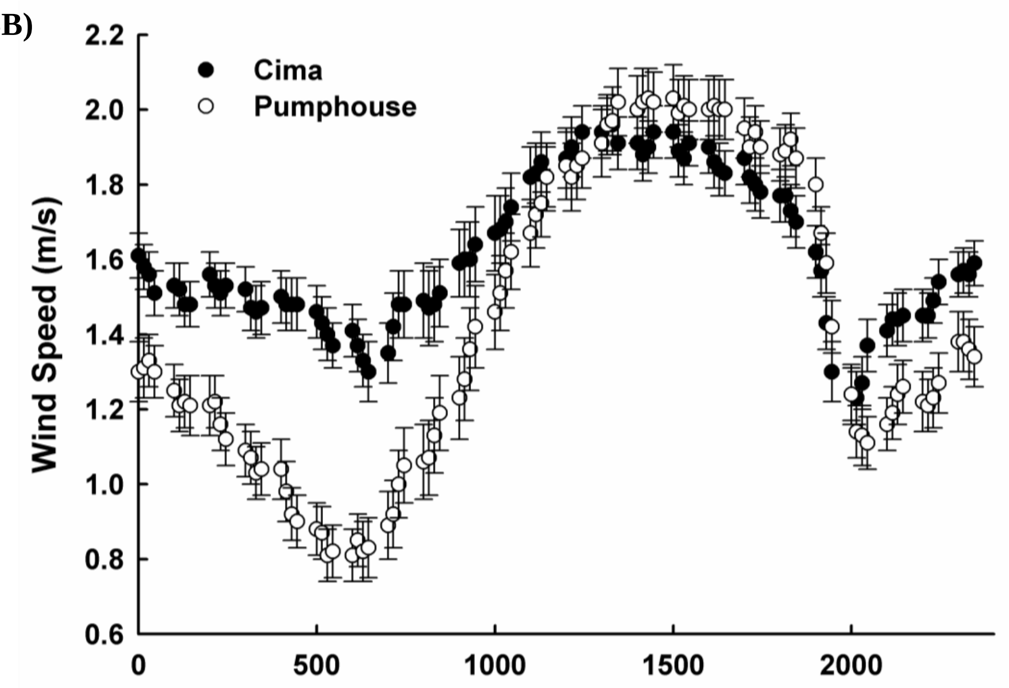


Figure 14. Map of Ivanpah Valley, Eastern Mojave Desert, California, USA. Proposed location of the Ivanpah Valley Solar Energy Generating System is just north of I-15 as it enters the valley.

15A)


Solar Radiation (W/m^2)
1200
1000
800
600
400
200
0
0
500
1000
1500
2000
● Cima
○ Pumphouse

15B)


Cima
Pumphouse
Wind Speed (m/s)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0
500
1000
1500
2000

15C)

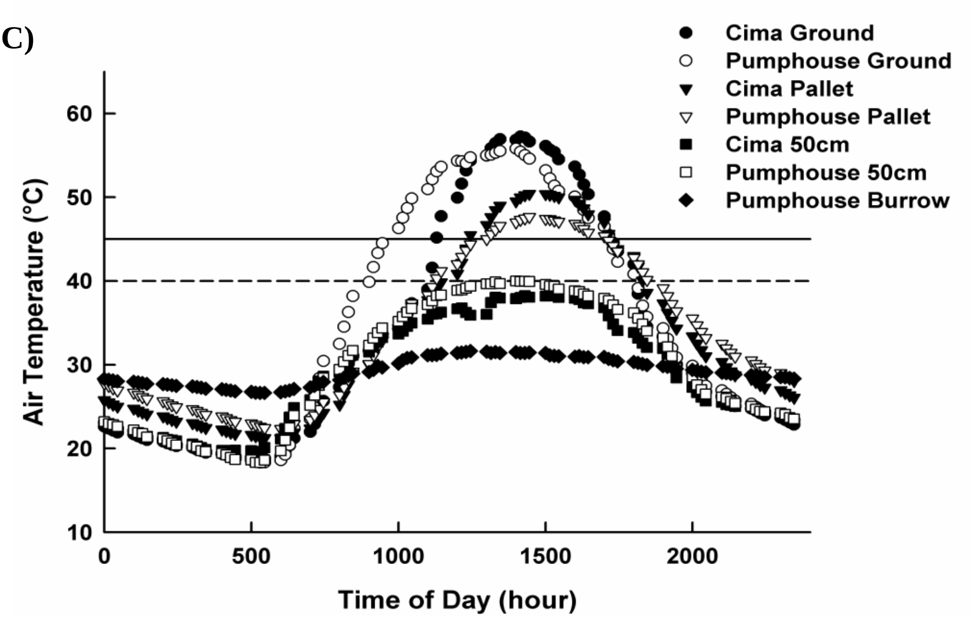


Figure 15. Microhabitat characteristics for desert tortoises in Ivanpah Valley from May to July 2003 measured by meteorological stations in Cima (*N* = 1) and Pumphouse (*N* = 1). **15A)** Incident solar radiation; **15B)** Wind speeds at 50 cm height off the ground; **15C)** Air temperatures at the ground surface, in pallets, in a burrow, and at 50 cm height off the ground. The solid reference line is the mean critical thermal maximum for desert tortoises (45°C, Naegle 1976) and the dashed line is the temperature at which desert tortoises enter burrows (40°C, Zimmerman et al. 1994). All points correspond to mean values ± 1 SEM.

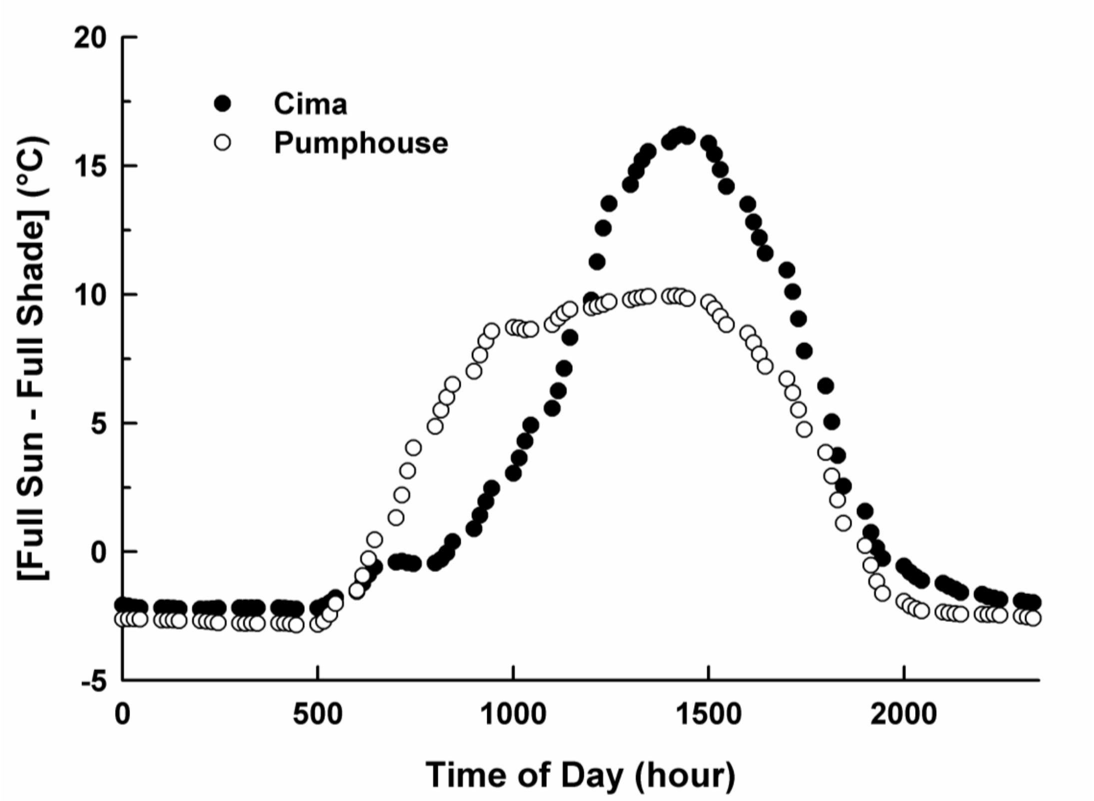
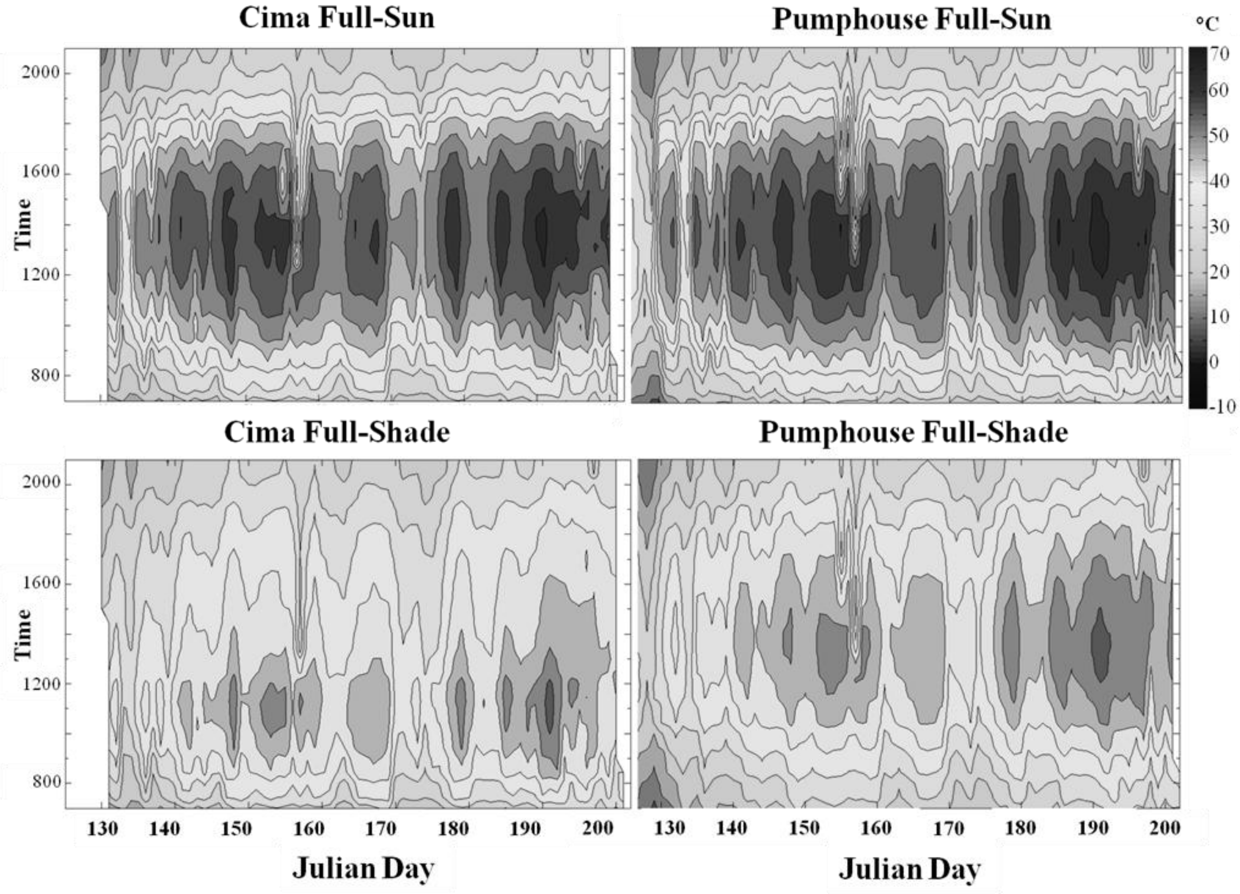
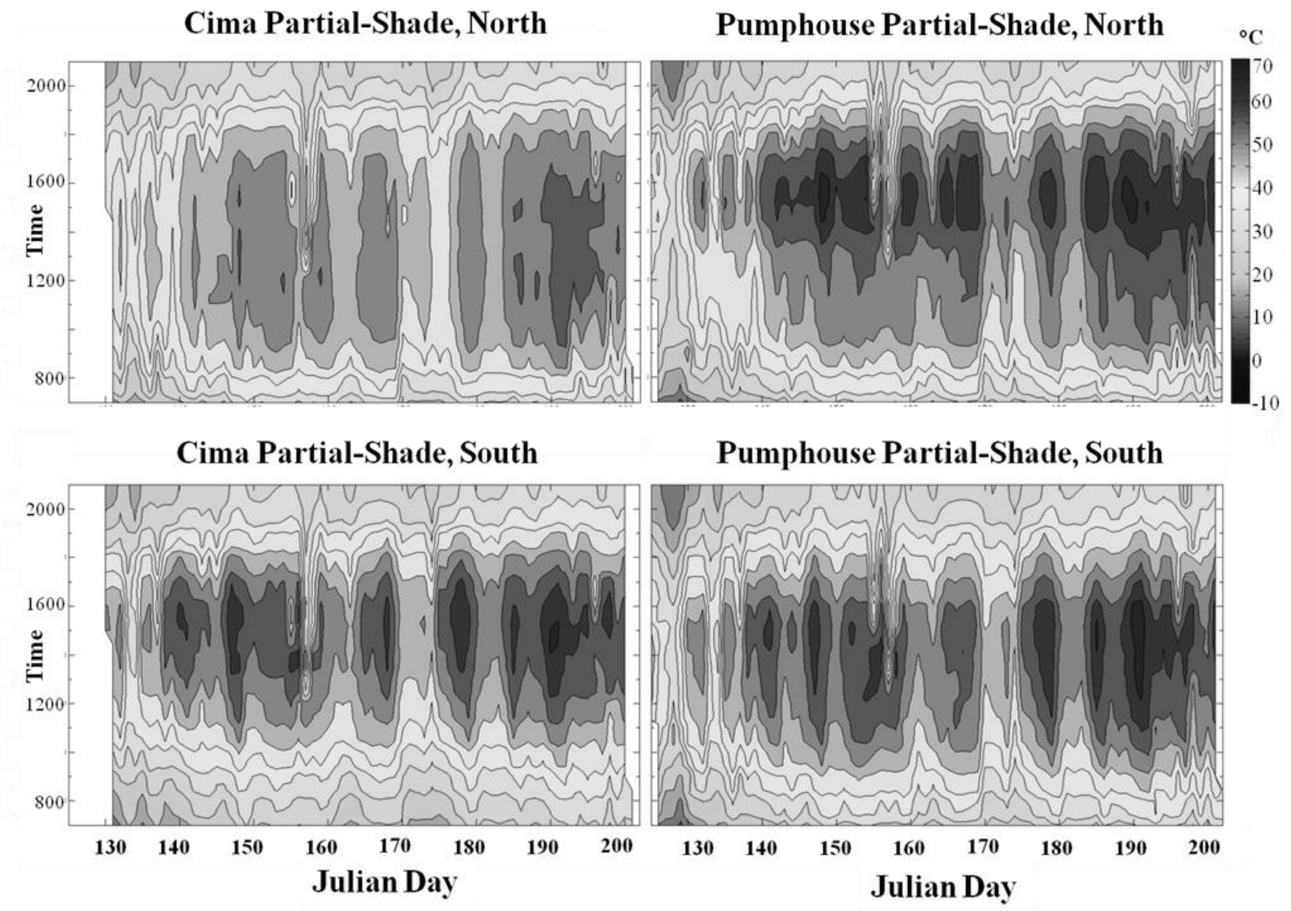


Figure 16. Shade quality in the Cima and Pumphouse plots as assessed by calculating the relative difference between operative temperature in full-sun and in full-shade for each plot (from May to July 2003).

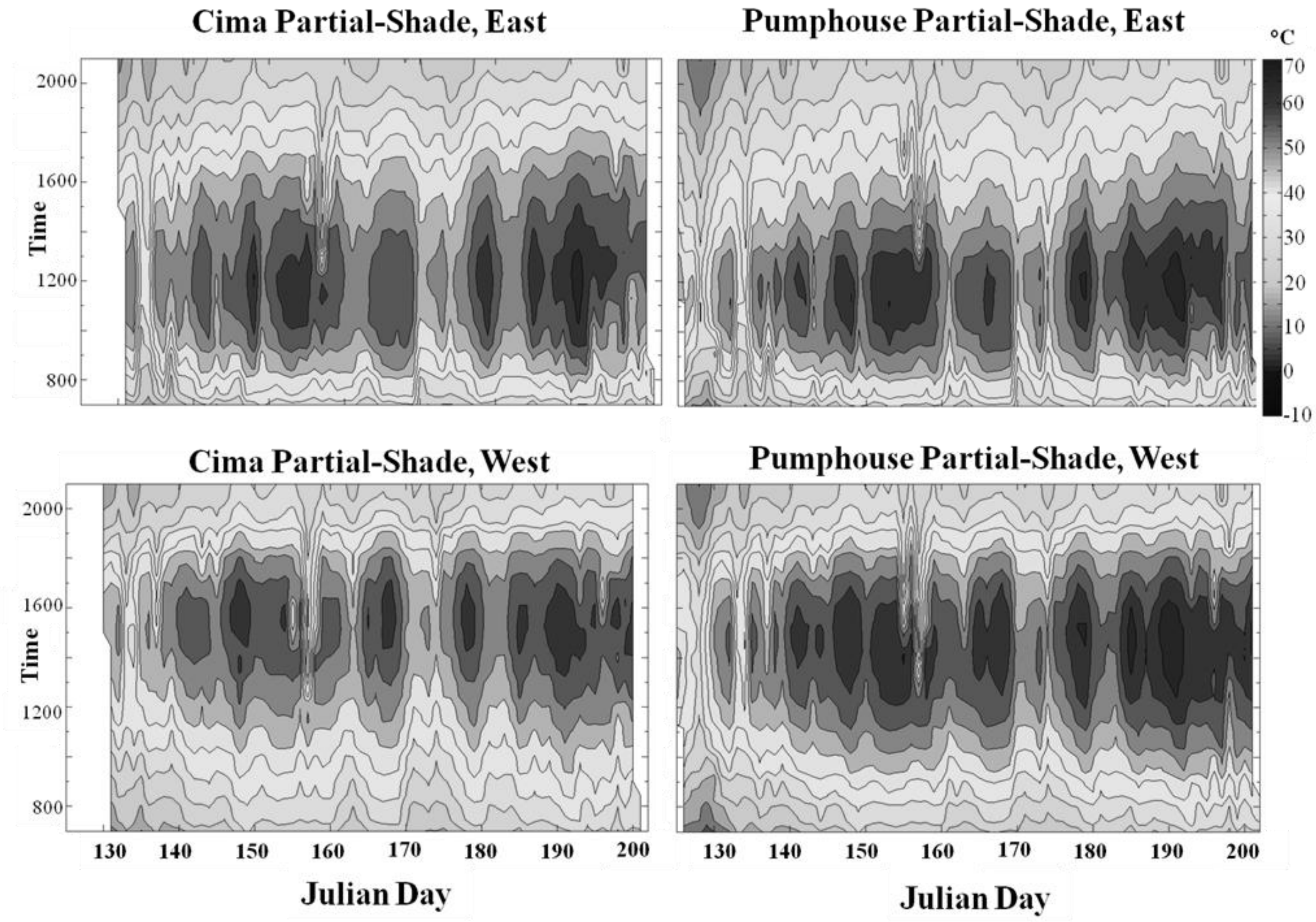

Cima Full-Sun
Pumphouse Full-Sun
°C
70
60
50
40
30
20
10
0
-10
Cima Full-Shade
Pumphouse Full-Shade
Time
2000
1600
1200
800
130
140
150
160
170
180
190
200
Julian Day


Cima Partial-Shade, North

Pumphouse Partial-Shade, North

Cima Partial-Shade, South

Pumphouse Partial-Shade, South



Cima Partial-Shade, East

Pumphouse Partial-Shade, East

Cima Partial-Shade, West

Pumphouse Partial-Shade, West

Figure 17. Daytime (0700 to 2100 hours) operative environmental temperatures (°C) measured in Ivanpah Valley from May through July (Julian Day). **Cima Full-Sun** and **Pumphouse Full-Sun**, with no nearby shrubs or succulents; **Cima Full-Shade** and **Pumphouse Full-Shade**, directly underneath a shrub or succulent; and **Cima Partial-Shade** and **Pumphouse Partial-Shade**, on the **North**, **South**, **East**, and **West** side of a shrub or succulent.

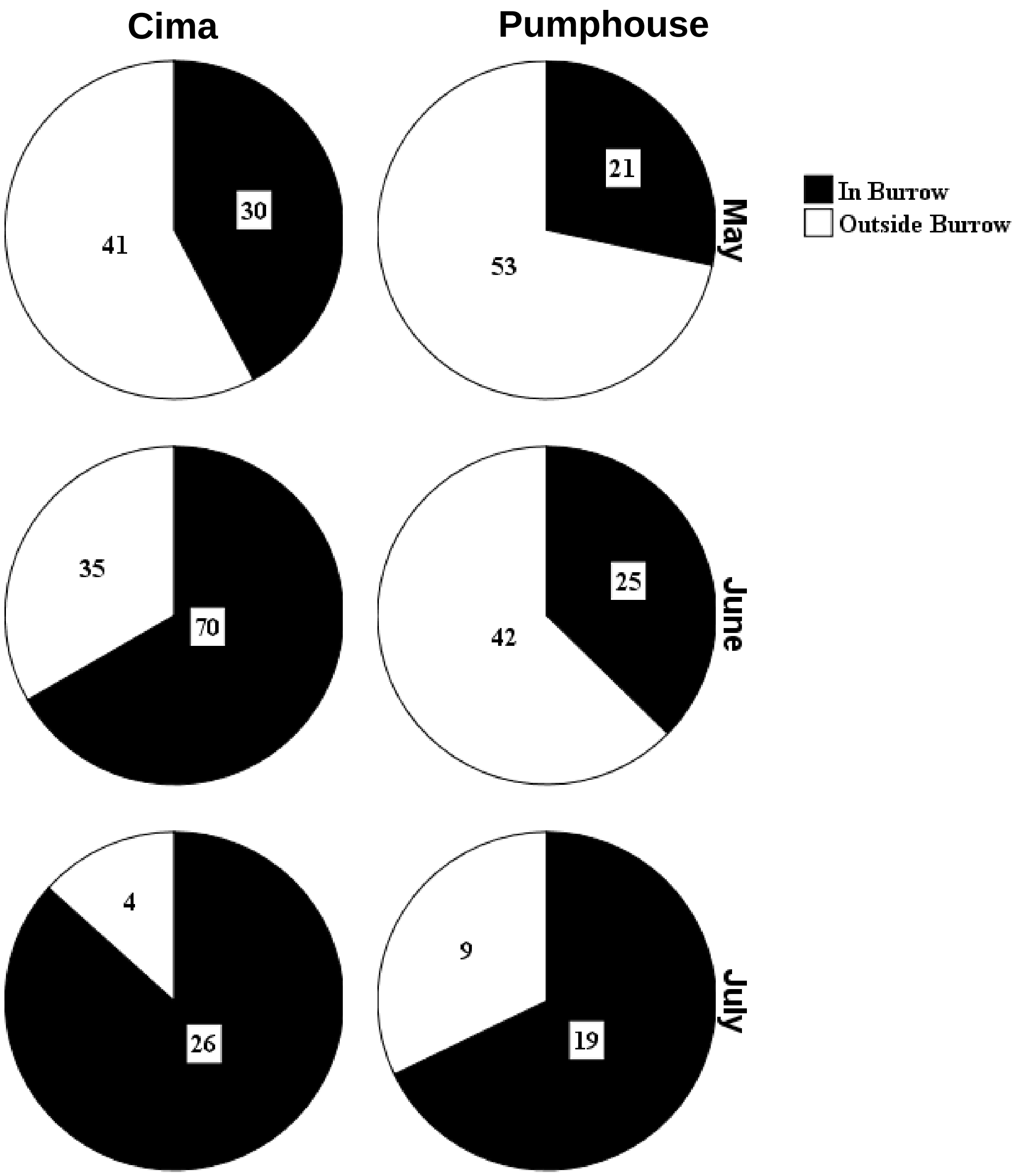
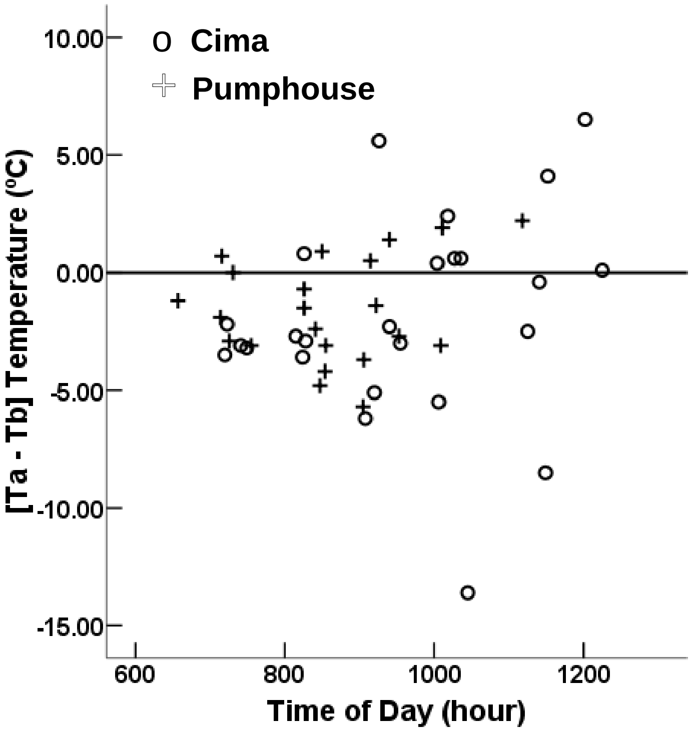


Figure 18. Desert tortoise activity during morning hours (700 – 1200) in the **Cima** and **Pumphouse** plots. Sizes of pie slices correspond to percent of total captures with individuals found outside versus inside a burrow at the time of capture. Numbers within pie slices are sample sizes (*N*).

19A)


o Cima
Pumphouse
10.00
5.00
0.00
-5.00
-10.00
-15.00
[Ta - Tb] Temperature (ºC)
600
800
1000
1200
Time of Day (hour)

19B)

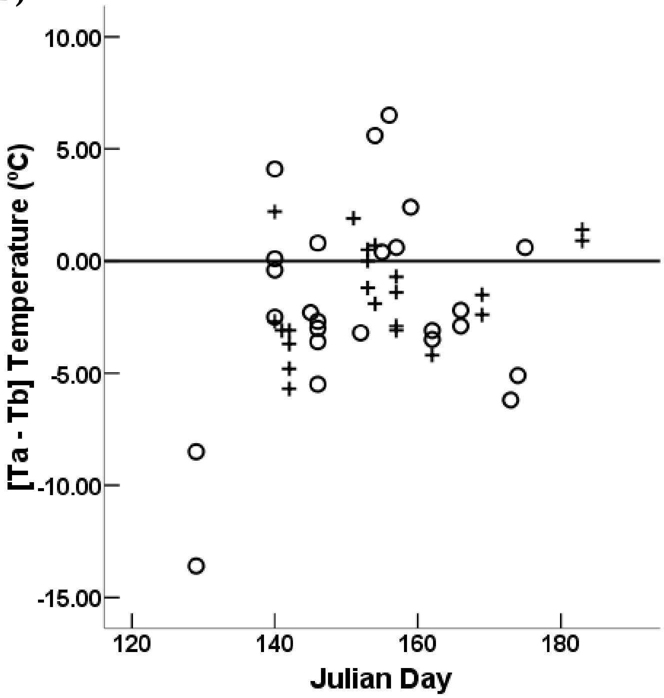


Figure 19. Difference between shaded air temperature and body temperature at the **19A)** time and **19B)** date of capture in the Cima and Pumphouse plots. The reference line at 0°C indicates no difference between ambient and body temperature.

CHAPTER 5: Climate, not conservation, controls leatherback turtle primary sex ratios in Pacific Costa Rica

ABSTRACT

Reports of worldwide declines in sea turtle nesting colonies are often unsupported by long-term data needed to distinguish human impacts from natural variability in reproductive life history traits. Sea turtles exhibit temperature-dependent sex determination. Their primary sex ratios could be affected by climate variability and by the conservation practice of translocation of doomed-eggs (at risk of inundation) to an artificial nest in a beach hatchery. We monitored incubation temperatures of eastern Pacific leatherback turtle (*Dermochelys coriacea*) hatchery translocated and *in situ* egg clutches at Playa Grande, Costa Rica from 1998 – 2007. *In situ* clutches were 90% female, whereas hatchery clutches (9% of clutches) were 64% female. The overall sex ratio was 83% female. We identified natural trends in sex ratios by establishing a correlation between hydroclimate and incubation temperature. Then, using precipitation records from 1950-2007, we determined that sex ratios at Playa Grande were naturally around 88% female, and that boom-bust cycles occurred for male hatchling production: fewer than 10% of hatchlings were males in most years, but occasional pluvial years had greater than 25% male production due to La Niña events and near-shore Atlantic tropical storms. The effects of doomed-egg translocation on overall sex ratios were minimal compared to natural sex ratio fluctuations due to climatic variability. Climatic effects should be assessed in other sea turtle conservation programs and incorporated into future

population viability analysis, particularly because global warming will influence regional climate phenomena at all sea turtle nesting beaches.

INTRODUCTION

Many reptiles exhibit temperature dependent sex determination (TSD) where incubation temperatures experienced by developing embryos determines their sex (Bull 1980). For species of conservation concern with TSD, understanding natural variation in offspring sex ratios is critical to conservation efforts that aim to increase the production of hatchlings through managed egg incubation (Morreale et al. 1982).

Sea turtles are oviparous reptiles and they are threatened with extinction in many parts of the world (Hilton-Taylor 2000). They exhibit a common pattern of TSD defined by males produced at low temperatures, and females produced at higher temperatures with a narrow range of temperatures producing both sexes (reviewed by Wibbels 2007). Like other sea turtles, gonadal differentiation in leatherback turtles is determined by the majority exposure temperature during the middle-third of incubation (Bull 1980; Standora and Spotila 1985). Egg clutch incubation temperatures, and therefore hatchling sex ratios, are influenced by a variety of biotic and abiotic factors (e.g. egg position within nest, Standora and Spotila 1985; vegetational shading, Janzen 1994; sand albedo, Hays et al. 2001; number of metabolizing embryos, Wallace et al. 2004). Many nesting beaches, have established doomed-egg translocation programs to reduce mortality due to predation, poaching, beach erosion and/or tidal inundation (reviewed by García et al. 2003; Pfaller et al. 2009). Egg clutches may be relocated to artificial incubation chambers, other sections of the nesting beach, or to hatcheries (Morreale et al. 1982). Because the incubation microenvironment experienced by developing embryos can vary between natural and artificial nests, egg relocation could potentially alter sex ratios and other aspects of embryonic development (Mrosovsky 2006, 2008; Pike 2008).

Climate change has the potential to exacerbate global sea turtle population declines via direct ecological impacts or through its effects on large-scale climate phenomena that are correlated with sea turtle population dynamics (reviewed by Chaloupka et al. 2008; Hawkes et al. in press). The potential effects of climate change induced oceanic warming on egg incubation and sex ratios includes sea level rise and inundation of nesting habitat (Fish et al. 2005), alterations in adult remigration intervals (Solow et al. 2002; Saba et al. 2007) and nesting phenology (Weishampel et al. 2004), latitudinal shifts in nesting beach selection (Baptistotte et al. 1999; Hawkes et al. 2007), and increased susceptibility to storm surges due to increased frequency and/or intensity of tropical cyclones (Pike and Stiner 2007). Indeed, climate change is predicted to alter climate phenomena such as Atlantic tropical cyclone activity (Webster et al. 2005) and the El Niño-Southern Oscillation (Trenberth and Hoar 1997), although there is a lack of consensus about the exact outcome (Latif and Keenlyside 2008).

Unfortunately, assessments of how regional climate (e.g. hydroclimate, ambient temperatures) affects sea turtle egg clutch incubation conditions have often been limited to just one or two seasons of incubation temperature measurements (Godfrey et al. 1996; Binckley et al. 1998; Matsuzawa et al. 2002; Houghton et al. 2007). Short-term studies frequently fail to capture the often complex and temporally variable associations between local climate and ecological processes (Hallett et al. 2004). One of the most important rookeries for the critically endangered eastern Pacific leatherback turtle (*Dermochelys coriacea*) is Playa Grande, Costa Rica (Santidrián Tomillo et al. 2007), and this population, along with beach sand and egg clutch incubation temperatures, has been extensively monitored since 1993 (Steyermark et al. 1996; Binckley et al. 1998; Reina et al. 2002). Sex ratios from this beach are likely the major determinant of future sex ratios of the eastern Pacific leatherback population, so this long-term dataset represents a valuable opportunity for improving estimates of this input parameter for population modeling of eastern Pacific leatherbacks.

The endangered status of leatherbacks precludes widespread direct assessment of hatchling sex using histological examination of gonadal morphology because that requires sacrificing the hatchling (reviewed by Broderick et al. 2000). Instead, sex ratios are usually estimated by comparing incubation temperatures with experimentally determined relationships between temperature and hatchling sex from incubation of otherwise ‘doomed’ eggs in controlled laboratory settings (e.g. Standora and Spotila 1985). The relationship between hatchling sex and incubation temperatures in leatherback turtles was determined before widespread recognition of breeding colony declines (Rimblot et al. 1985; Rimblot-Baly et al. 1987; Binckley et al. 1998). In this study, we determined the effects of climate and doomed-egg translocation on leatherback turtle sex ratios at Playa Grande. These efforts are aimed at improving our conservation efforts and enhancing population projection models by linking both large-scale climatic phenomena and local scale management with sex ratios of leatherback hatchlings.

METHODS

Playa Grande (3.6 km) is located on the Northern Pacific coast of Costa Rica, and has distinct wet (May – November) and dry (December – April) seasons. The leatherback turtle nesting season at Playa Grande runs from October through February with an approximately Gaussian distribution (Reina et al. 2002).

Monitoring in situ *and translocated egg clutch temperatures*

We collected egg clutches from doomed natural oviposition locations at or below the high tide line and translocated the clutches to the beach hatchery on Playa Grande where eggs were reburied mimicking natural deposition (Wallace et al. 2004). We monitored incubation temperatures in 408 hatchery relocated egg clutches and 776 natural egg clutches over 9 nesting seasons from 1998-2007.

We put a copper constantan thermocouple (± 0.05°C) into the center of the egg mass of every third clutch in the hatchery. Readings were taken with a BAT 12 thermocouple meter (Physitemp, Clifton, NJ) every other day throughout incubation. Temperatures were similarly monitored in *in situ* (sensu Eckert and Eckert 1990) egg clutch locations. We also monitored daily sand temperatures at nest depth (STND; 75 cm depth) in the hatchery and on the beach with thermocouples placed centrally at each site (i.e. one in each site). Because of the lack of spatial replication of STND measurement within the hatchery and on the beach, we performed a bootstrapped two-way analysis of variance (ANOVA) on mean 10-day STNDs with site (hatchery, *in situ*) and nesting season as fixed effects.

Estimating sex ratios

Based on an average total incubation period of 60 days, we calculated the mean middle-third temperature (MMT) for each monitored egg clutch from days 20 – 40. We estimated sex ratios based on the relationship between incubation temperature and sex ratio determined for Playa Grande leatherback turtles by Binckley and others (1998) who determined that the pivotal temperature (temperature producing 50:50 male to female sex ratio) was 29.4 °C, the transitional range of temperatures (TRT) producing a mixture of males and females was from 29°C to 30°C, eggs incubated above 30°C were 100% female, and below 29°C they were 100% male. For egg clutches with mean incubation temperatures within the TRT, we applied the percentage female (and male) observed by Binckley et al. (1998) at the tested incubation temperature that corresponded most closely to that in the egg clutch. Diel variation within Playa Grande egg clutches was less than 0.5ºC (Binckley et al. 1998), and therefore field thermal exposure could be considered similar to that experienced by eggs incubated in laboratory conditions (van de Merwe et al. 2006).

In any given month, a subset of *in situ* egg clutches was monitored for temperature, and these egg clutches spanned the entire coastal axis of Playa Grande. Monthly MMT data from monitored egg clutches was considered to be representative of all egg clutches going through their MMT in a given month. The actual number of *in situ* and hatchery egg clutches was known from saturated beach monitoring (Santidrián Tomillo et al. 2007). February and March were beyond the *in situ* egg clutch incubation temperature monitoring period in a couple of seasons, but the last monitored month (January or February) always exhibited sand and egg clutch incubation temperatures above the TRT and thus subsequent months were considered 100% female. We considered the potential contribution of egg clutches going through their MMT outside of October-March to be negligible, as roughly 7% of all nesting activity occurs outside of that period (Binckley et al. 1998; Reina et al. 2002). We corrected for the difference in relative numbers of *in situ* versus hatchery egg clutches by weighting the mean sex ratio each month, in each location, by the number of egg clutches. Sex ratios at 100% female-producing temperatures in *in situ* egg clutches were ground-truthed histologically in 1994-1995 (Binckley et al. 1998).

A repeated-measures ANOVA assessed the pattern of temperature increase during the middle-third of incubation. The dependent variable consisted of the mean temperatures in each of the 3 one-week intervals within the middle-third of incubation (Early = first-third of the middle-third of incubation, Middle = second-third, and Late = third-third). We tested for significant sex ratio differences between sites (hatchery versus *in situ* egg clutch locations) by having site as a fixed effect and nesting season as a random effect in the model. We further tested for differences in metabolic heating, or the difference between MMT and STND due to metabolizing embryos, at each site using an analysis of covariance (ANCOVA). The ANCOVA tested the hypothesis that metabolic heating was affected by annual precipitation levels, the month when the MMT occurred, and the egg clutch site.

Correlating sex ratio estimates with climate variables

We obtained monthly precipitation levels and air temperatures (1998-2007) from the Daniel Oduber International Airport in Liberia, Costa Rica (55 km straight-line distance from Playa Grande) which experiences the same regional climate and wet and dry seasons as Playa Grande. Air temperature explained only 5% of the variation in MMTs and was excluded from further analyses. An ANCOVA tested the hypothesis that MMTs were affected by annual precipitation levels, the month during which the MMT occurred, and the egg clutch site. The interaction terms were highly correlated with the main effects, and we restricted the ANCOVA to just main effects. We also regressed annual sex ratio estimates on precipitation levels from 1993 – 2007 (this study; Binckley et al. 1998) using logistic regression. We used the regression equation to estimate sex ratios from annual precipitation records from the Liberia airport going back to 1950. Analyses were performed using SAS 9.1 and considered significant at an alpha level of 0.05.

RESULTS AND DISCUSSION

In situ *and translocated egg clutch sex ratios*

Sex ratios in the hatchery and in *in situ* egg clutches were strongly female biased in all nesting seasons except 1999-2000 (Fig. 20). Hatchery egg clutches were substantially less biased (64.5%) than *in situ* sex ratios (89.8%). Indeed, ranges of monthly MMTs were 0.9 (SE 0.1°C) in hatchery egg clutches versus 1.3 (SE 0.2°C) in *in situ* egg clutches. Monthly numbers of hatchery and *in situ* egg clutches varied, with a median 9% of egg clutches translocated to the hatchery. Weighting each monthly sex ratio by the relative number of egg clutches in each location (hatchery versus *in situ*) yielded an overall sex ratio of 83.2% female. Highly female skewed sex ratios at Playa Grande are consistent with earlier estimates from 1993-1996 of 74.3 – 100% female (Binckley et al. 1998). Leatherback sex ratios from one of the largest leatherback rookeries in the Atlantic Ocean are also female biased: 69.4% female (Godfrey et al. 1996) and 60.5% female (49.0 – 67.8%; Mrosovsky et al. 1984). Highly female biased sex ratios are also commonly observed in other sea turtle species (Godfrey et al. 1999; Broderick et al. 2000; Hawkes et al. 2007, in press; Wibbels 2007).

There were significant effects of egg clutch location ($F_{1,8} = 10.52$, $P = 0.012$) on incubation temperature within the middle-third of development. Incubation temperatures in the hatchery followed the same trajectory of increase throughout the middle-third of incubation as in *in situ* egg clutches, only hatchery egg clutch temperatures were consistently less than those in *in situ* egg clutches by ≈ 0.7ºC ($P = 0.012$, Fig. 21). The reduced hatchery incubation temperatures occurred without significant differences between site-specific STNDs as there were no significant effects of nesting season (i.e. year) or site on mean STNDs (Fig. 22a, b). The hatchery was not shaded by nearby vegetation, which can reduce incubation temperatures (Janzen 1994; Carrasco et al. 2000). Systematic differences in clutch depth or dimensions within the hatchery might have decreased incubation temperatures, but attempts are consistently made to closely recreate natural nest dimensions in hatchery nests (Wallace et al. 2004).

The most parsimonious explanation was that lower numbers of metabolizing embryos per clutch in hatchery egg clutches decreased the metabolic heating contribution to incubation temperature and, thus, depressed incubation temperatures relative to those in *in situ* egg clutches at Playa Grande (Broderick et al. 2001; Wallace et al. 2004). Indeed, ongoing research suggests that hatching success in hatchery egg clutches is approximately 10% less than in *in situ* egg clutches (Santidrián Tomillo et al., unpublished data), similar to the pattern observed at the St. Croix leatherback turtle rookery (Eckert and Eckert 1990; Boulon et al. 1996). Furthermore, metabolic heating was significantly greater in natural egg clutches than in the hatchery ($P < 0.0001$; Fig. 23a, b), it was generally less than 1ºC in both sites, it decreased through the season ($P<0.0001$) and it was significantly positively correlated with precipitation (+0.064; $P = 0.001$). Thus, metabolic heating was most pronounced in potentially male-producing conditions, specifically in early season *in situ* egg clutches in the wettest years, but it was significantly less overall in hatchery egg clutches. The relationship between metabolic heating and precipitation was not recognized in previous studies that incorporated a metabolic heating increase with indirect measurements of incubation temperatures to estimate sex ratios (e.g. Hays et al. 2003; Hawkes et al. 2007).

Translocation of egg clutches is a conservation tool that can enhance embryo survivorship. This practice is unlikely to select for poor leatherback nest site selection because repeated ovipositions below the high tide line by individual females do not occur at Playa Grande (Nordmoe et al. 2004). Despite decreased incubation temperatures in the hatchery, egg clutches were still female biased, and the effect overall did not markedly decrease the female bias at Playa Grande.

Abiotic correlates with sex ratios

Location in the hatchery versus in natural nest sites, annual precipitation levels, and seasonal progression explained nearly 50% of the variation in MMTs, and there were significant effects of month, precipitation, and nest site on MMTs. Hatchery MMTs were significantly lower than those in *in situ* egg clutches ($P < 0.0001$), MMTs were negatively correlated with annual precipitation (-0.40; $P < 0.0001$, $R^2 = 0.50$), and MMTs increased with progression through the season ($P < 0.0001$; Fig. 22a, b). Furthermore, the logistic regression between annual precipitation and concurrent *in situ* egg clutch MMTs (Fig. 24a; $R^2 = 0.69$, $\chi^2_1 = 147.1$, $P < 0.0001$) yielded natural sex ratio estimates from 1950 to 2007 of 12.3% male: 87.7% female (Fig. 24b).

At Playa Grande, in every season except 1999-2000, hatchery and *in situ* egg clutch MMTs were above the TRT from December through the end of the nesting season. This coincided with the distinct regional shift in ambient conditions from the wet to the dry season driven by the Inter-Tropical Convergence Zone shifting south of Central

America from around December to April (Coen 1983; Kessler 2006). The El Niño-Southern Oscillation (ENSO) alters the intensity of regional wet and dry seasons by decreasing rainfall during El Niño and increasing rainfall during La Niña (Waylen and Harrison 2005; Poveda et al. 2006). The ENSO also changed leatherback turtle *in situ* egg clutch incubation conditions: 2002-2003 was a moderate El Niño year (NOAA Oceanic Niño Index) with 99.8% female, and 1999-2000 was a strong La Niña year with a male bias (47.7% female).

However, 1998-1999 was also a strong La Niña year and there was a female bias of 95.0%. In September and October the '*temporales del Pacifico*' which occur regardless of ENSO, bring moisture in from the Pacific because of pressure differences resulting from Caribbean tropical depressions near the Costa Rican Caribbean coast that generate westerly winds (Coen 1983; Waylen and Harrison 2005). Tropical depressions, storms and hurricanes that pass within 1300 km of the Liberia airport account for approximately 15% of annual rainfall on the northern Pacific coast of Costa Rica (Waylen and Harrison 2005). For example, stochastic events such as Tropical Storm Katrina in 1999 and Hurricane Michelle in 2001 added significant rainfall to Playa Grande. Egg clutch incubation temperatures in the first week of November 2001, when Hurricane Michelle neared Costa Rica, were approximately 5ºC less than temperatures in the preceding week (see Wallace et al. 2004), and sex ratios for this period were extremely male biased (15.6% female) even though the year overall was 87.3% female in *in situ* egg clutches. Historically, female bias was greater than 65% in all years except 1955, one of the strongest La Niña years on record (Trenberth 1997) and the year that Hurricane Katie came close to the northern Panamanian Caribbean coast in October

(NOAA Oceanic Niño Index).

Rain cools beach sand by the direct transfer of cold water, evaporation, and by changing the specific heat of the sand (Standora and Spotila 1985; Spotila et al. 1987). Periodicity, rate, and the total amount of rainfall, combined with its timing relative to the nesting season and the total rainy season length can affect thermal characteristics of the nest chamber, the respiration of developing embryos, and survivorship (reviewed by Houghton et al. 2007). With the vast majority of leatherback nest sites in the un-shaded, open sand above the high tide line (Nordmoe et al. 2004), some male hatchling are predictably produced at Playa Grande in early season nesting (the end of the rainy season) and in La Niña years. However, truly male biased nesting seasons (> 50% male) require stochastic inputs of precipitation, and the ephemeral effects of Atlantic tropical cyclone activity on Playa Grande may add precipitation and cool incubation temperatures without negatively impacting survivorship.

Global warming is increasing the frequency and intensity of Atlantic tropical cyclone activity, and also increases storm surge flooding and sand displacement on sea turtle nesting beaches worldwide (reviewed by Pike and Stiner 2007). On Playa Grande, amplified Atlantic cyclone activity could greatly increase production of male hatchlings (barring loss of egg clutches from inundation or beach destruction) which is an uncommon observation within the literature on sea turtle sex ratio responses to climate change (e.g. Hays et al. 2003). However, climate change-related warming of ambient air may eventually increase beach sand temperatures, although we did not observe a strong influence of this climatic factor on MMTs. This could lead to shifts either in the timing of the nesting season (i.e. earlier nesting within the rainy season) or shifts of the nesting population to higher latitude nesting beaches. Although nesting phenology has yet to be assessed, sex ratio gradients among nesting beaches at different latitudes have been observed in western Atlantic loggerhead turtles (*Caretta caretta*, Baptistotte et al. 1999; Hawkes et al. 2007). Currently, the eastern Pacific leatherback turtle population nests on beaches as far north as Baja California, Mexico, but most of these are already highly female biased (Sartí Martínez et al. 2007). Thus, it is unlikely that eastern Pacific leatherback turtles could enhance male production via location adjustments without drastically shifting their rookeries to higher latitude areas.

Tempering the common female bias at this beach, as well as many others (Godfrey et al. 1999; Broderick et al. 2000; Wibbels 2007), is the fact that sex ratio estimates typically have not incorporated intra- or inter-seasonal differential mortality in egg clutches (Godfrey and Mrosovsky 1999). The strong positive correlations we observed between seasonal progression, beach sand temperatures, and leatherback egg clutch incubation temperatures suggest that differential mortality due to environmental factors (e.g. extreme temperatures, desiccation) might have led to overestimation of Playa Grande female bias via inferred sex ratios (Matsuzawa et al. 2001). Intensive study of hatching success and emergence success (proportion of eggs that result in emerged hatchlings) from 2004 – 2007 indicates that there is a significant negative correlation between these factors and seasonal progression (Santidrián Tomillo 2007). If we incorporate monthly natural emergence success measured from 2004 – 2007 (Santidrián Tomillo et al., unpublished data) into the inferred sex ratio estimates reported above, then the estimated number of female hatchlings produced in *in situ* egg clutches was 18,132 (out of 21,648 hatchlings) giving a sex ratio of 83.8% female hatchlings. Thus, our *in situ* female bias for 2004 – 2007 was overestimated by 4.5%. This difference would not impact the overall conclusions of our analysis. Furthermore, hatchery translocation at Playa Grande has been minimal (9%) compared to many other sea turtle nesting beaches (reviewed by Chan and Liew 1995; Mrosovsky 2006, 2008). For Playa Grande, translocation of clutches laid below the high tide line is warranted because hatching success would otherwise be zero and changes in overall sex ratio on a beach would be minimal. However, widespread clutch relocation would not be justifiable, absent a strong threat such as rampant egg harvest. Because alterations of sex ratios, as well as of hatching and emergence success may occur with egg clutch translocation, we recommend that use of this technique be avoided whenever possible in favor of protection of egg clutches in their natural sites where imminent threats to embryonic survival are absent.

Implications

Complications for management of eastern Pacific leatherback turtles and numerous other threatened species arise from the reliance of population viability analyses on accurate assessments of primary (and adult) sex ratios (see Ewen et al. 2001). The Playa Grande beach hatchery, while boosting hatchling production overall, has consistently decreased the natural female bias. However, natural Playa Grande sex ratios are strongly influenced by variable annual precipitation levels. Conceptually similar to the “boom and bust” cycles of reproduction in amphibians (Pechmann et al. 1991; Semlitsch et al. 1996), the long-lived leatherback turtle exhibits boom and bust years for the production of male hatchlings. At the population level, boom years for production of male hatchlings are probably amplified by increases in hatching success and hatchling emergence (Santidrián Tomillo 2007), and increases in the probability of adult female remigration (e.g. 1999, Saba et al. 2007; Reina et al. 2008) that also coincide with large increases in annual precipitation levels. The lesson from boom and bust cycles in amphibians is that short-term studies fail to capture important natural life history trait dynamics which can lead to erroneous conclusions about population growth versus decline (Pechmann et al. 1991). Current population projections for Playa Grande leatherback turtles do not incorporate variability in this or other climatically related life history traits (Santidrián Tomillo et al. 2007, 2008; Wallace and Saba 2009). Finally, a comprehensive analysis of sand and nest temperatures on leatherback beaches along a latitudinal gradient in the eastern Pacific would be valuable to identify patterns in sex ratio contributions by individual rookeries to the overall population, and could provide insights for changes in nesting distribution of leatherbacks in this region under scenarios of future climate change (Hawkes et al. 2007).

CONCLUSIONS

Playa Grande, like many other sea turtle nesting beaches, is highly female biased (83% female). Our results indicate that female biased primary sex ratios have occurred regularly over the past 57 years at Playa Grande and thus, are a natural aspect of eastern Pacific leatherback population dynamics. However, occasional years of more than 50% male hatchling production occurred, and variation in climatic conditions, specifically hydroclimate, was the primary driver of fluctuations in sex ratios. A shorter term study might have misdiagnosed this situation if it happened to include one or two rainy years. Our long-term monitoring further revealed that translocation of doomed-eggs to the beach hatchery lessened female bias of those eggs perhaps by decreasing the number of metabolizing embryos. With this knowledge of natural trends in leatherback primary sex ratios, managers can more accurately assess population growth rates and the use of doomed-egg translocation in their evaluation of appropriate conservation efforts in response to climate change. Natural sex ratio fluctuations due to climatic forcing should be assessed in other sea turtle conservation programs and incorporated into future population viability analysis, particularly since global warming will influence regional climate phenomena at all sea turtle nesting beaches.

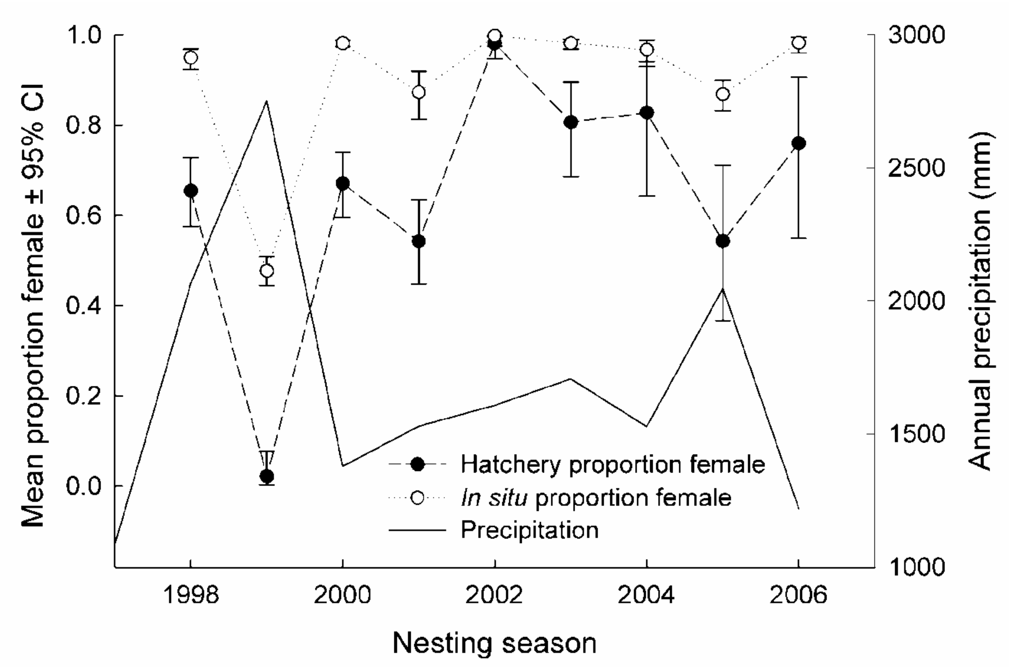


Figure 20. Relocation to the hatchery and large increases in annual precipitation (e.g. 1999) decreased the female-bias of Playa Grande leatherback turtle sex ratios. Error bars are binomial 95% confidence intervals (Clopper and Pearson 1934).

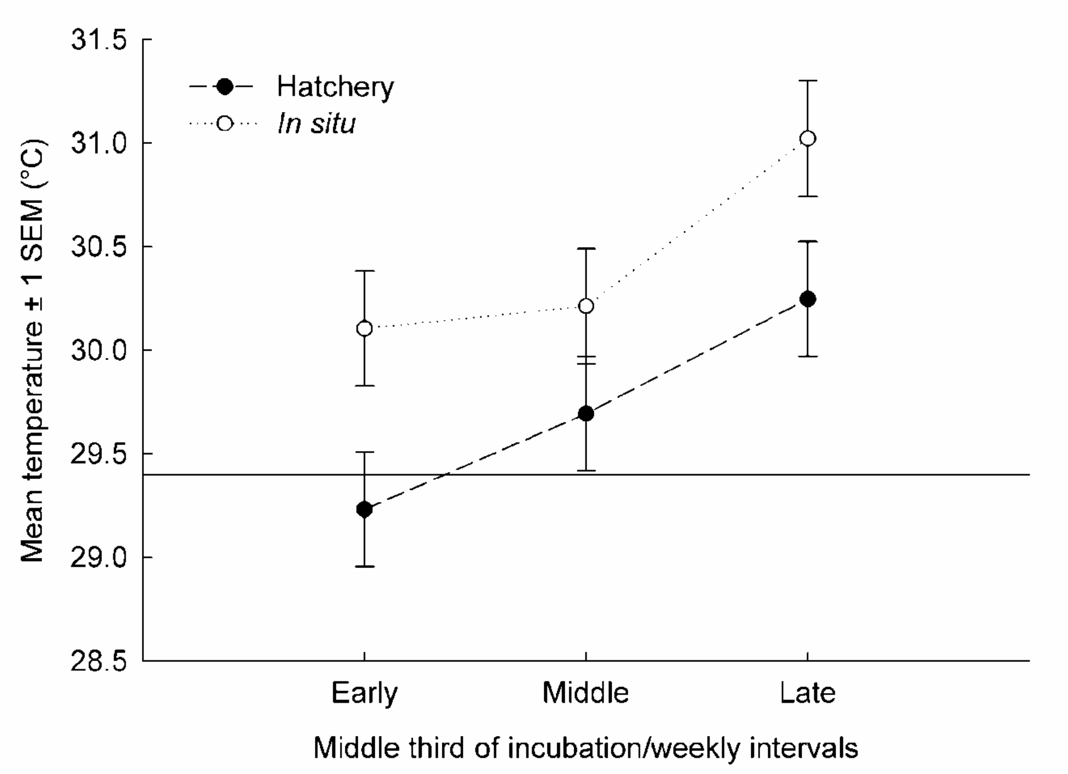
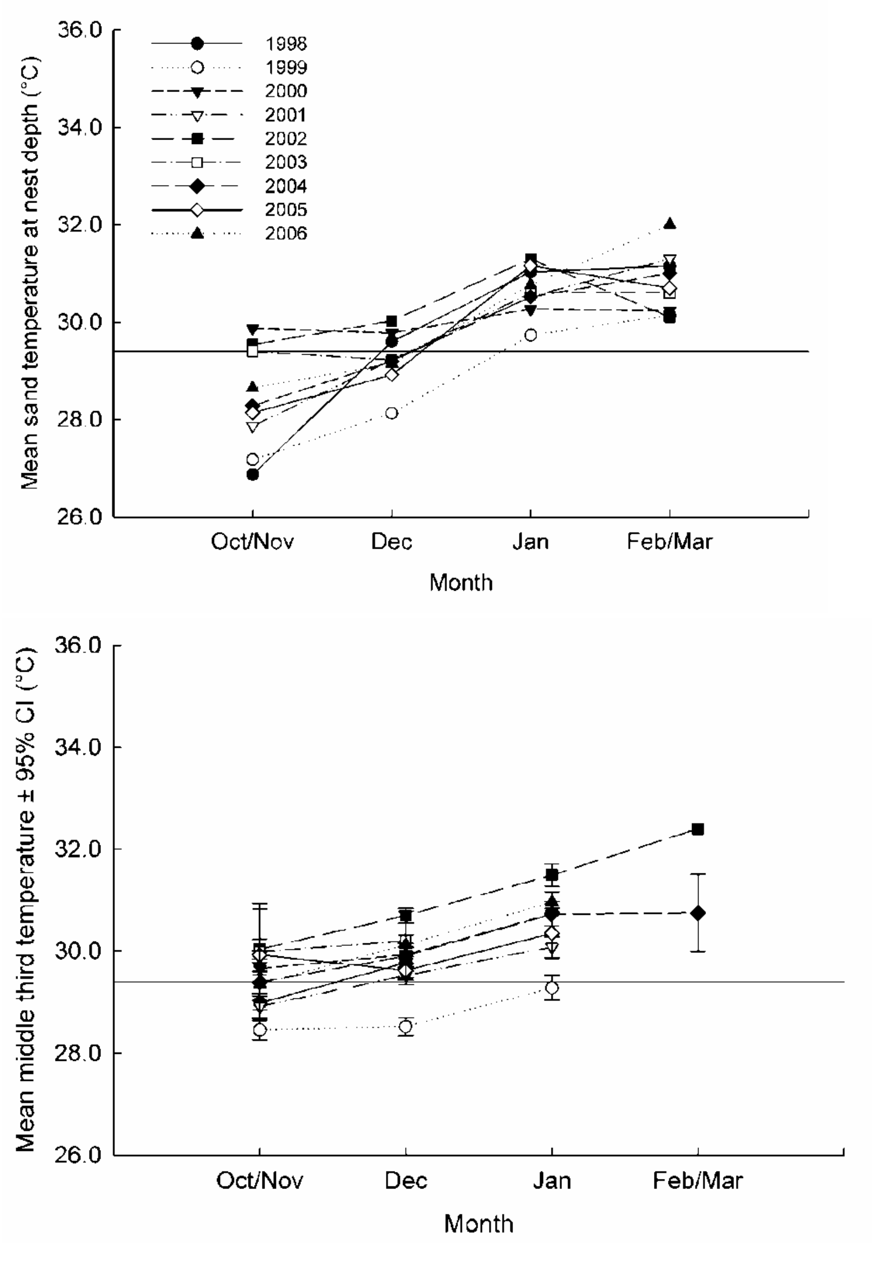


Figure 21. The pattern of temperature increase during the middle-third of incubation was consistently depressed in hatchery egg clutches. Mean temperatures for 1-week intervals within the middle third of incubation in hatchery and in *in situ* egg clutches were above the pivotal temperature (reference line = 29.4 °C) except in the earliest part of the middle-third in hatchery egg clutches.

22A) Hatchery egg clutches



22B) ***In situ*** **egg clutches**

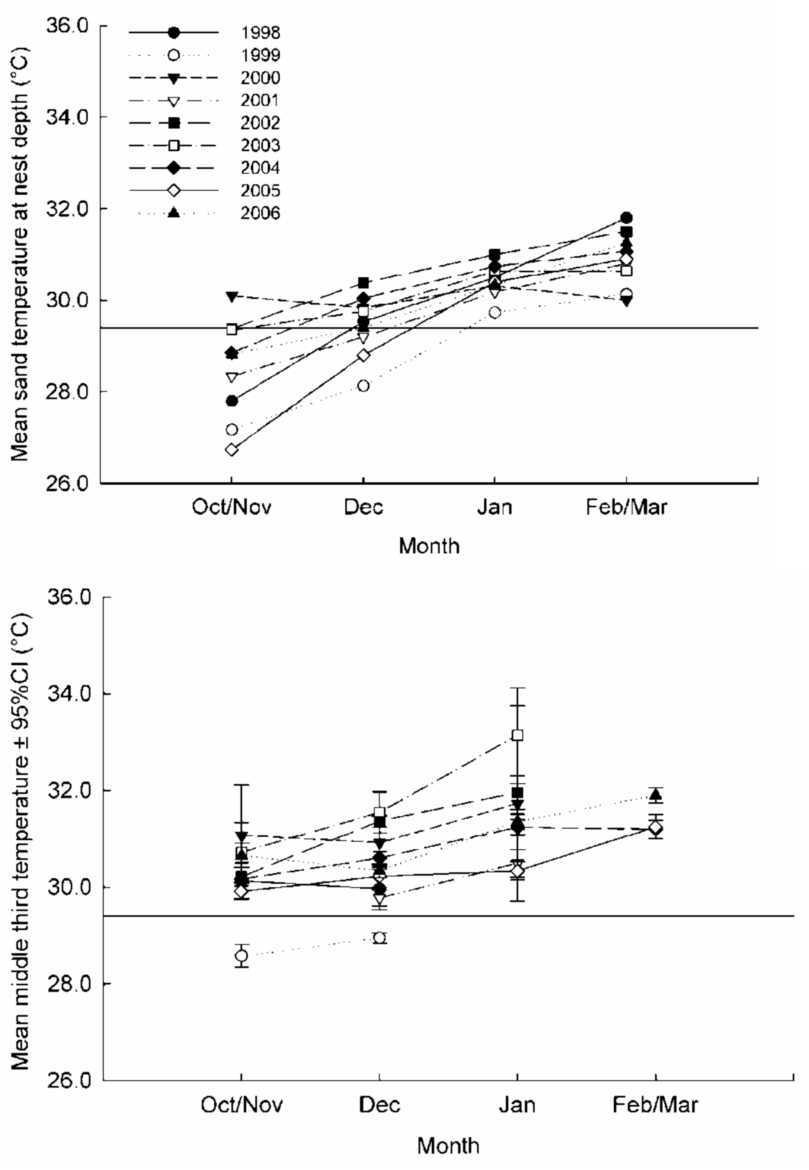
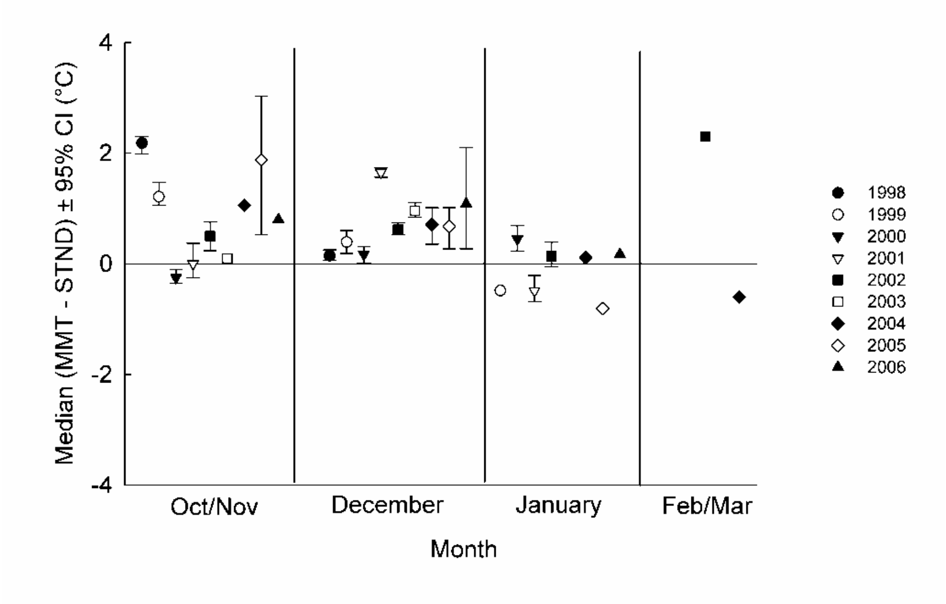


Figure 22. 22A) Hatchery and **22B)** *in situ* egg clutch mean middle-third temperatures are elevated relative to ambient sand temperatures at nest depth. Hatchery incubation temperatures are above the pivotal temperature (reference line = 29.4 °C) by December while *in situ* incubation temperatures are above it throughout each season except 1999-2000.

23A) Hatchery egg clutches



23B) ***In situ*** **egg clutches**

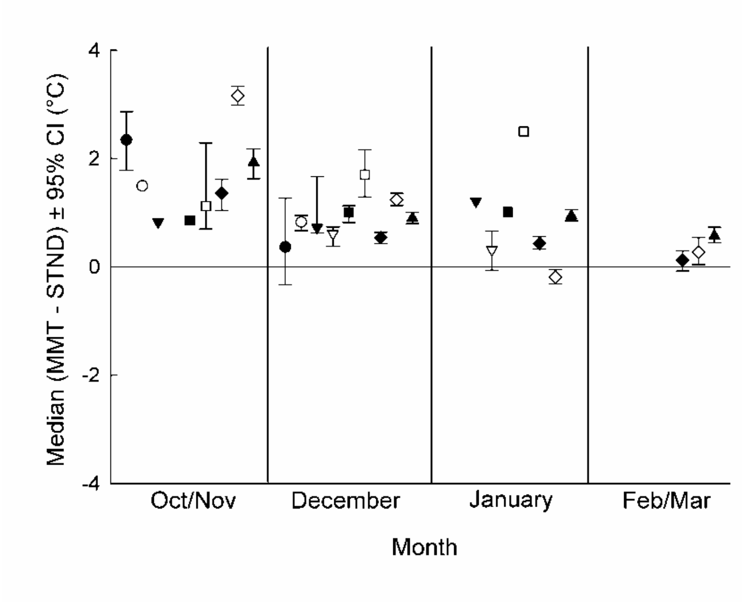


Figure 23. Metabolic heating was generally less than 1°C in all egg clutches during the middle third of development. Metabolic heating was negatively correlated with month (i.e. seasonal progression), positively correlated with annual precipitation, and greater in **23A)** *in situ* egg clutches as compared to **23B)** hatchery egg clutches

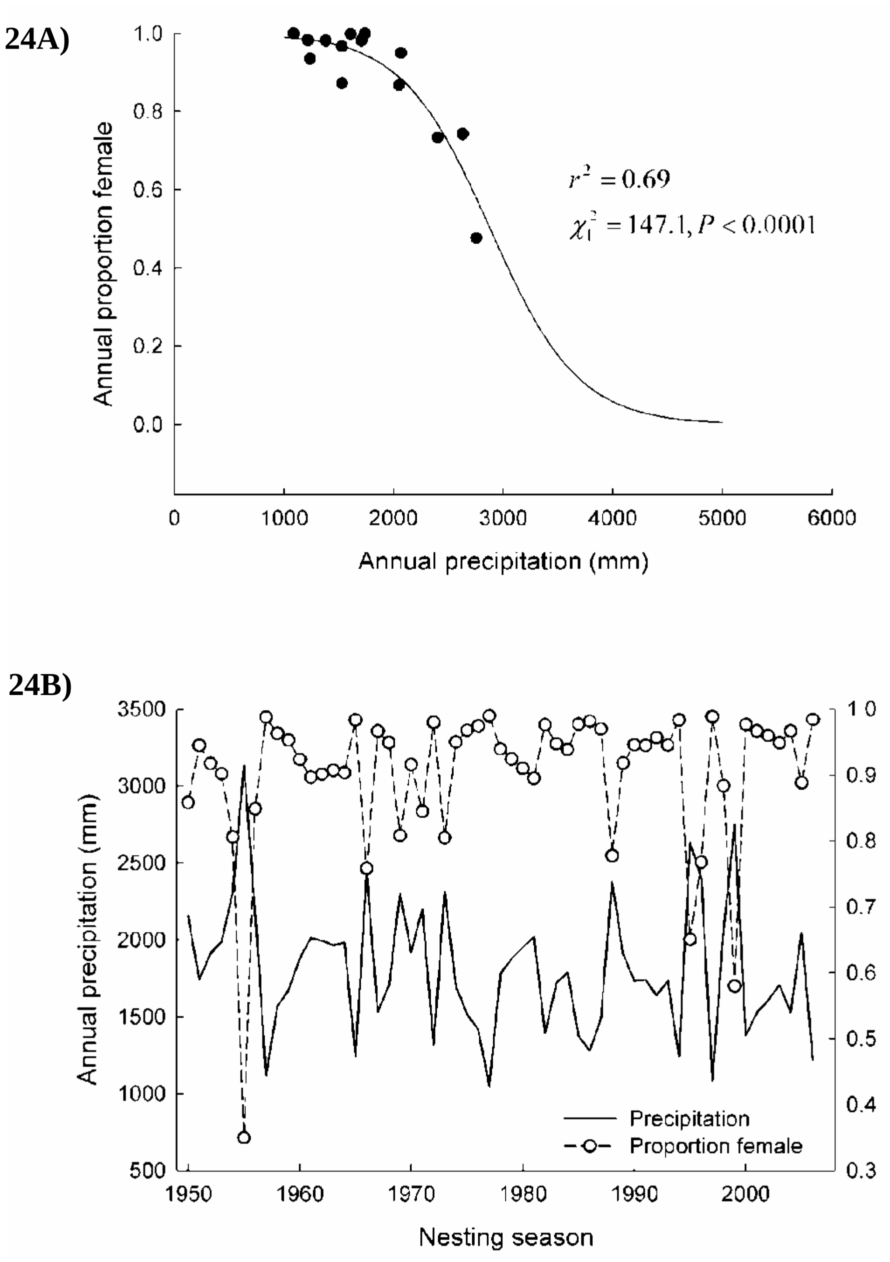


Figure 24. Historical leatherback sex ratio estimates from 1950 to present. **24A)** Logistic regression relating annual precipitation to sex ratios estimated from direct measurements of incubation temperatures from 1993 – 2007; **24B)** Precipitation levels and proportion female estimates based on the logistic regression relationship are plotted versus nesting season.

CHAPTER 6: Mammalian metabolic allometry: do intraspecific variation, phylogeny, and regression models matter? (*American Naturalist* 174: 720 – 733)

ABSTRACT

Power scaling relationships between body mass and organismal traits are fundamental to biology. Compilations of mammalian body masses and basal metabolic rates date back over a century, and are used both to support and to assail the universal quarter-power scaling invoked by the Metabolic Theory of Ecology. However, the slope of this interspecific allometry is typically estimated without accounting for intraspecific variation in body mass or phylogenetic constraints on metabolism. We returned to the original literature and culled nearly all unique measurements of body mass and basal metabolism for 695 mammal species, and (1) phylogenetically corrected the data using the fullest available phylogeny, (2) applied several different regression analyses, (3) re-sampled regressions by drawing randomly selected species from each of the polytomies in the phylogenetic hypothesis at each iteration, and (4) ran these same analyses independently on separate clades. Overall, 95% confidence intervals of slope estimates frequently did not include 0.75, and clade-specific slopes varied from 0.5 to 0.85 depending on the clade and regression model. Our approach reveals that the choice of analytical model has a systematic influence on the estimated allometry, but irrespective of the model applied we find little support for a universal metabolic rate-body mass scaling relationship.

INTRODUCTION

Allometric relationships between body mass and a great variety of organismal traits take the form of power functions. Rubner's empirical work over a century ago effectively launched the field of allometry with the discoveries that metabolic rates scale non-isometrically with body mass in dogs, and that indirect calorimetry is well correlated with direct calorimetry (Rubner 1883, 1894). Since that time, empirical scaling relationships between mass, metabolism and numerous other traits have been demonstrated (Peters 1983; Calder 1984; Schmidt-Nielsen 1984), but a tenable mechanistic explanation for these patterns continues to elude us.

The study of allometry has been reinvigorated by the lively debate surrounding the Metabolic Theory of Ecology (MTE) (West et al. 1997; Brown et al. 2004; Clarke 2004; Cyr and Walker 2004; Kozlowski and Konarzewski 2004). Briefly, MTE posits that minimization of transport costs of metabolites in the quasi-fractal distribution networks that supply metabolically active tissues requires a scaling exponent of 3/4 for metabolism which, in turn, requires the scaling of various other traits to be multiples of 1/4 (West et al. 1997, 1999; Brown et al. 2004). MTE's putative mechanism has been rebutted on theoretical (Dodds et al. 2001; Chaui-Berlinck 2006; Painter et al. 2006; Apol et al. 2008) and functional grounds (reviewed in O'Connor et al. 2007b), and the existence of a single explanatory mechanism for allometry is generally considered implausible (Dodds et al. 2001; Cyr and Walker 2004; O'Connor et al. 2007b). The generality of MTE has also been pared down by findings that allometric exponents across the major kingdoms of life broadly diverge from universal quarter power (or even third power) scaling (Bokma 2004; Makarieva et al. 2005; Reich et al. 2006; Downs et al.

2008; Makarieva et al. 2008). As a result, the empirical foundation on which MTE now rests is restricted to the allometry for which its proposed mechanism was primarily designed in the first place: the relationship between body mass and basal metabolism in vertebrates.

Publication of large-scale meta-analyses of metabolic allometry data has risen sharply in recent years (reviewed in White et al. 2007) just as publication of new measurements on mammal species has fallen to pre-1960 levels and sobering declines in mammal species have come to light (Schipper et al. 2008). The mammalian metabolic allometry data, in particular, have been the subject of extensive re-analysis (reviewed by Dodds et al. 2001; White and Seymour 2003; Savage et al. 2004). Issues that remain largely unresolved in these analyses include how well the metabolic data satisfy the strict definition of basal metabolism, which regression model is appropriate, and whether the data should be corrected for phylogenetic relatedness (Glazier 2005).

Numerous studies have excluded measurements on all animals with ruminant digestive systems on the grounds that they fail to satisfy the definition of basal metabolic rate (White and Seymour 2003, 2004, 2005; White et al. 2006). It has also been argued, however, that most resting metabolic rate measurements should be included, provided the animal regulates its body temperature (McNab 1997). With regard to statistical methodology, allometry data are usually analyzed with ordinary least-squares regression despite clear violations of the statistical assumptions of that technique and the fact that several other, more appropriate techniques are available. Use of ordinary least-squares regression is usually justified by an assertion that variation in the quantity treated as a dependent variable (e.g. basal metabolic rate) is much greater than that in the quantity treated as an independent variable (e.g. body mass), and/or that the regression r^2 is high enough (> 0.9) that use of an alternative regression model that properly accounts for variation in both quantities is unwarranted (Enquist et al. 2003; Savage et al. 2004; Makarieva et al. 2005; Makarieva et al. 2008; Moses et al. 2008). But rarely is either assertion supported with compelling evidence. Moreover, McNab (1988) has pointed out that r^2 is a biased estimate of the overall fit of the regression because it is positively correlated with the range in basal metabolic rate and body mass. Finally, with regard to statistical problems created by phylogenetic relatedness, many studies have found that phylogenetic correction does not significantly change the value of the estimated slope (reviewed in Glazier 2005). However, Duncan et al. (2007) and Clarke and Rothery (2008) have recently found a significant phylogenetic signal in mammalian allometric data with significant differences in scaling at the ordinal level.

The purpose of this paper is to address these three unresolved issues by assembling an updated mammalian metabolic allometry dataset that includes original measures of variation. Using information in this new dataset, we address how well the data satisfy the strict definition of basal metabolic rate, the appropriateness and utility of several different regression models, and the need for phylogenetic correction. We hope to encourage more careful consideration of analytical techniques applied to allometry data, and to highlight the need for new measurements of metabolic rates for additional mammalian species.

METHODS

Dataset

The relationship between body mass (m) and whole-organism metabolic rate (MR) is generally assumed to take the form of a power function,

$$MR = a \cdot m^{b} \quad (1)$$

(reviewed by LaBarbera 1989), in which scaling is determined jointly by the coefficient a and mass exponent b. For statistical analysis and visual comparison with data, it is traditional to log-transform the nonlinear equation (1) to the linear equation,

$$\log(MR) = \log(a) + b \cdot \log(m). \quad (2)$$

Here, $\log(MR)$ is a linear function of $\log(m)$, and the two parameters are the slope b and intercept $\log(a)$.

Two important factors are often overlooked in studies of physiological allometry when fitting equation (2) to data. First, the purpose of the analysis is to estimate parameters for the theoretical relationship between the true values of $\log(m)$ and $\log(MR)$, not to predict the true value of $\log(MR)$ given an observed value of $\log(m)$. And second, parameter estimation is being performed based on observed values of $\log(m)$ and $\log(MR)$, both of which are random variables subject to both measurement error and intrinsic variation. These factors are important because ignoring either can lead to biased estimates of the slope. Specifically, ignoring the error in $\log(m)$ causes systematic underestimation of the slope (LaBarbera 1989) (except when the purpose of the analysis is to predict the true value of $\log(MR)$ given an observed value of $\log(m)$; Draper and Smith 1998). Special cases defined by the ratio of error variances of $\log(MR)$ and $\log(m)$ are also known where this bias will be negligible (e.g. Draper and Smith 1998). Thus, the validity of regression techniques commonly applied to metabolic allometry data rests on implicit assumptions about relative error variances. Yet previous compilations of data do not include information required for calculating these variances (Lovegrove 2000, 2003; White and Seymour 2003; Savage et al. 2004). One of our objectives in building the new dataset was to include this information.

We obtained original papers cited in the compilations of Savage et al. (2004), White and Seymour (2003), Lovegrove (2000, 2003), and Muñoz-Garcia and Williams (2005)—which are themselves to varying degrees based on other compilations (Hart 1971; Hayssen and Lacy 1985; Elgar and Harvey 1987; Geiser 1988; McNab 1988; Heusner 1991)—and performed literature searches for new papers since 2004. We thereby obtained nearly all unique measurements for 695 mammalian species. Measurements that were reported in the text of an original paper as a mean with some stated measure of variation (standard deviation, standard error, confidence interval, or range) were taken directly from the text. If raw data were presented in a published figure, we extracted the values using Matlab routine digitize2.m (available from The MathWorks website). Using multiple extractions of sample figures by different investigators, we estimated that error in these extracted values is approximately 5%.

We standardized the measures of variation to standard deviations, and converted all units for mass to grams and for metabolic rates to milliliters of oxygen consumption per hour. For conversions requiring a respiratory quotient, that value was taken directly from the paper if available or assumed to be 0.8 otherwise. In a few papers, ranges had to be transformed into standard deviations by applying a correction based on a Monte Carlo simulated relationship between sample size, range, and standard deviation. We discarded reports of standard deviations if they were based on multiple measurements of only one individual. For species for which we had multiple papers or multiple sets of measurements (e.g. in different years), we calculated an overall mean body mass and basal metabolic rate weighted by sample size.

The extracted data satisfied the strict definition of basal metabolism to varying degrees. The most common violations were with respect to absorptive state and consciousness. These types of violations were often hard to identify with certainty and questionable data were therefore left in the dataset with comments about suspected problems. Likewise, animals that had been captive bred, long-term acclimated to laboratory conditions, or had recent minor surgery performed (e.g. insertion of a probe) were also left in the dataset. However, animals in torpor, juveniles, reproductive females, obviously active animals (e.g. exercising), or non-normothermic animals were discarded from the extracted dataset. The species, genus, family, and order identifications were corrected to reflect their listing in the third edition of *Mammal Species of the World* (Wilson and Reeder 2005). Finally, body temperature data from White and Seymour (2003), supplemented with body temperature data extracted from the original literature, are also included in the dataset. Our complete dataset on 695 species with references and comments can be found in the online appendix (available online at: http://hdl.handle.net/10255/dryad.713).

We $\log_{10}$-transformed our data prior to regression analysis in all cases except where body temperature was included as a predictor variable. In that case, a $\log_e$ transformation was applied to mass, resting metabolic rate, and body temperature (which was also inverse transformed) because of the Boltzmann factor in the Arrhenius equation relating body temperature to metabolic rate (Gillooly et al. 2001; Downs et al. 2008). These transformations yielded a linear allometric relationship of the form,

$$\log_{10}(MR) = \alpha + \beta \cdot \log_{10}(m),(3)$$

with slope β and intercept α estimated using generalized linear models.

Mammal phylogeny

Quantitative assessment of relationships between traits in comparative studies is often confounded by phylogenetic influences on those traits. Phylogenetic autocorrelation violates statistical assumptions of independence, artificially inflates degrees of freedom, and can lead to erroneous findings of functional relationships as a result of constraints on trait values due to evolutionary history (Felsenstein 1985; Harvey and Pagel 1991; O'Connor et al. 2007a). The fullest available mammalian phylogeny (Bininda-Emonds et al. 2007) bases its taxonomy on *Mammal Species of the World* (second edition). For the phylogenetic correction, we matched 628 of the species in our dataset directly (there were a few misspellings), identified 57 synonyms, and had to leave out 2 species, Grant’s golden mole (*Eremitalpa granti*) and Abert’s squirrel (*Sciurus aberti*) because a synonym could not be identified. There were also 7 terminal taxa in Bininda-Emonds et al. (2007), each of which is now recognized as 2 or more separate species for which there are measurements in the dataset. If the original species was retained in the new edition, measurements for just that species were included and the “daughter” species was discarded. In one case, the Hamadryas baboon (*Papio hamadryas*), the original species was not retained, and we instead used the “daughter” species with the best available data, the Chacma baboon (*Papio ursinus*), based on the sample size for the measurements. This resulted in a grand total of 685 included species.

Statistical analysis

Regression analysis of the allometric relationship requires assumptions about the trait variation (measurement error and random variation) in body mass (*m*) and metabolic rate (*MR*). Ordinary least-squares (OLS) regression assumes that log(*m*) is an independent variable whose values are known without error (Sokal and Rohlf 1995). Reduced major axis (RMA) regression assumes that the ratio of error variance and intrinsic variation in log *m* and log *MR* equals a constant (LaBarbera 1989) and minimizes the distance of each point perpendicular to the fitted regression line. An orthogonal regression technique, least-squares variance-oriented residuals (LSVOR), weights the importance of variance in *m* and *MR* by their relative magnitudes and does not require residuals to be normal to the regression line (O'Connor et al. 2007a).

In order to compare the effects of the type of regression analysis on estimates of the slope, we performed OLS, RMA, and LSVOR on each subset of our data. LSVOR requires the specification of an overall variance ratio (θ; O'Connor et al. 2007a) which we determined for each species (*p*) using the ratio of the squared coefficients of variation for resting metabolic rates (*y*) and body masses (*x*):

$$\theta_{cv} = \left(\frac{\sigma_{y\cdot p}/\mu_{y\cdot p}}{\sigma_{x\cdot p}/\mu_{x\cdot p}}\right)^2 \quad (4)$$

This largely removed the confounding effects of correlation with mass in both variables, although θ_{cv} was still weakly, but significantly, correlated with mass (Figure 25a; $R^2 = 0.029$, $F_{1,521} = 15.587$, $P < 0.01$). The relative frequency distribution of θ_{cv} was centered about 1.0, with 95% confidence intervals extending from approximately 0.3 to 3.0 (Figure 25b). We therefore applied LSVOR with these three variance ratios (i.e. 0.3, 1.0, and 3.0) in addition to conventional OLS and RMA regressions. We bootstrapped our regressions on native data 2,000 times and present mean parameter estimates for scaling relationships with 95% confidence intervals.

We used Felsenstein's method of creating phylogenetically independent contrasts (PICs) with hypothetical reconstructed ancestors, untransformed branch lengths, and a Brownian-motion process of evolution (Felsenstein 1985). Since the mammal phylogeny is less than 50% resolved at the species level (Bininda-Emonds et al. 2007), we took a re-sampling approach to deal with polytomies. We constructed PICs using a randomly selected representative from each of the polytomies (see Figure 26). We re-sampled the tree selections 50,000 times, and at each iteration: (1) we selected a full complement of representatives from each of the polytomies as well as all of the species from fully resolved taxa, (2) we constructed PICs based on that tree, (3) we performed regression analyses on those PICs, and (4) we bootstrapped the regressions 2,000 times. A previous attempt to resolve the large polytomy within the Rodents by inserting a more resolved phylogeny from Steppan et al. (2004) into the Bininda-Emonds et al. (2007) supertree, and proceeding with PIC construction, did not significantly differ from the results obtained by random selection of taxa within polytomies (data not shown).

We also used the method of phylogenetic generalized least-squares (PGLS) regression to estimate the parameters of the allometric scaling relationship (Grafen 1989). The variance-covariance matrix was determined by the length of the shared portion of the phylogenetic tree between two species (i.e. covariance for pairs of species) and the length of the total path through the phylogenetic tree from root to tip for each species (i.e. specific variance) (Grafen 1989). This method ends up being equivalent to constructing

PICs from the full phylogeny (Rohlf 2001). The covariance matrix was computed using standard equations (Garland and Ives 2000), assuming Brownian motion evolution and scales branch lengths within the variance covariance matrix by the standard deviation, or square root of the sum of the branch lengths for each paired species (Garland et al. 1999; Garland and Ives 2000). We used PGLS to fit scaling exponents and intercepts to our allometric relationships.

Finally, we applied these same analyses to allometry data separated by clade. Clades were chosen as separated regions (i.e. sub-trees) of the full mammalian tree that altogether spanned a majority of the full tree (>90%), were regions with a single common ancestor, and that did not exclude any measured taxonomic groups descending from that common ancestor. Only the most populated clades (in terms of species measured) were analyzed: Rodents, Chiropterans, Primates, Marsupials, Soricids, and Carnivore/Ungulates/Pangolins (Fereuungulata; (Springer et al. 2005; Waddell et al. 1999)). We first tested for homogeneity of clade-specific intercepts and slopes using an ANCOVA. We then re-sampled OLS, RMA, and LSVOR regressions performed on native data and PICs in each of the separate clades, and we compared the cumulative frequency distributions of the slope estimates using the Kolmogorov-Smirnov test. We also performed PGLS on the clade-specific data.

Computations

All of our analyses were performed in Matlab 7.0 (Release 14; MathWorks, Natick, MA). Matlab routines are available from the authors upon request. Bootstrapped parameters are presented as means with 95% confidence intervals (CI), and generalized linear model results are mean ± 1 SEM.

RESULTS

Full native dataset

The dataset contains mean body masses and basal metabolic rates (BMR) for 695 species, body temperatures for 535 species, and complete information on variation in mass and metabolic rate measurements for 529 species. Using OLS without phylogenetic correction, there was a highly significant relationship between mass, body temperature, and metabolic rate:

$$\ln(MR) = 35.267 + 0.676 \cdot \ln(m) + (-10.455 \cdot 1000/T_b)$$

($R^2 = 0.957$; $F_{2,479} = 5217.3$, $P < 0.001$) where the inverse transformed T_b had a small, but significant, negative relationship with ln (m):

$$1000/T_b = 3.24 + (-0.001) \cdot \ln(m)$$

(Figure 27; $R^2 = 0.013$, $F_{1,479} = 6.243$, $P = 0.013$). This yields an overall linear relationship between ln (MR) and ln (m) with a small estimated effect of temperature correction ($0.0104 \cdot \ln(m)$):

$$\ln(MR) = 1.42 + (0.676 + 0.0104) \cdot \ln(m)$$

Results of bootstrapped OLS, RMA, and LSVOR with $\theta_{cv} = 0.3$, 1.0, and 3.0 on $\log_{10}$ transformed native body masses and metabolic rates are presented in Table 8. OLS had the shallowest slope, LSVOR with $\theta_{cv} = 0.3$ had the steepest, LSVOR with $\theta_{cv} = 3.0$ was roughly equivalent to OLS, and LSVOR with $\theta_{cv} = 1.0$ was roughly equivalent to RMA which was intermediate in steepness.

Full dataset contrasts

In general, phylogenetic correction via the formation of PICs increased the slope of the regressions slightly, but significantly. Results of bootstrapped OLS, RMA, and

LSVOR on PICs were again that OLS had the shallowest slope and LSVOR with $\theta_{cv} = 3$ was roughly equivalent to OLS, LSVOR with $\theta_{cv} = 0.3$ had the steepest slope, and RMA and LSVOR with $\theta_{cv} = 1.0$ were intermediate and roughly equivalent. The PGLS slope estimate for the full tree was even shallower than OLS with a highly variable intercept.

Clade-specific analyses of full dataset

The ANCOVA revealed that there was a significant difference between clade-specific slope estimates ($F_{5,614} = 10.693$, $P < 0.01$). The ANCOVA further indicated that there were no significant differences between clade-specific intercepts ($F_{5,619} = 0.2795$, *n.s.*), although this result should be viewed cautiously because there are significant differences in the clade-specific slopes. The predictive power of the phylogenetic effects is demonstrated via the mean model having a root mean square error (RMSE) of 0.0792, the fraction of variance explained by the regression model is $R^2 = 0.756$ (RMSE = 0.0392), with the effect of the clade intercepts $R^2 = 0.757$ (RMSE = 0.0393) and clade slopes $R^2 = 0.780$ (RMSE = 0.0375). The shallowest relationship was for the Soricids (intercept = 0.990 ± 0.224, slope = 0.527 ± 0.077) and the steepest was in the Chiropterans (intercept = 0.297 ± 0.219, slope = 0.872 ± 0.049). Rodents also exhibited a shallow slope (intercept = 0.970 ± 0.207, slope = 0.553 ± 0.024) while Fereuungulates (intercept = 0.427 ± 0.181, slope = 0.766 ± 0.027), Primates (intercept = 0.323 ± 0.225, slope = 0.775 ± 0.055), and Marsupials (intercept = 0.340 ± 0.287, slope = 0.757 ± 0.016) were close to ¾-power scaling.

Clade-specific PGLS regressions yielded virtually identical parameter estimates to those from the ANCOVA in terms of slope estimates (Table 8). Intercepts in clades were highly variable and tied to the slope values, with larger intercepts for shallower slopes (e.g. Soricids, see Figure 28).

Analyses of separate clade-specific datasets

The distribution of clade-specific slope estimates from regressions on PICs (and native data, not shown) shifted based on the particular regression analysis applied (see Figure 29): LSVOR ($\theta_{cv} = 0.3$) > RMA and LSVOR ($\theta_{cv} = 1.0$) > LSVOR ($\theta_{cv} = 3.0$) > OLS. This pattern was similar to that of the different regression analyses applied to the full native and contrast datasets. The cumulative frequency distributions of the slope estimates were also significantly different between regression analyses in each of the separated clades ($D \geq 0.190$, $P < 0.001$). In contrast to the ANCOVA and clade-specific PGLS slope estimates, (1) Fereuungulate and Rodent slope estimates were much more variable than other clades, and (2) the pattern of slope estimates changed with Chiropteran, Primate, and Marsupial slopes tightly centered about 0.75 and Rodents exhibiting steeper slope estimates than Soricids. A randomization test of the placement of trait pairs (mass and metabolic rate) on different terminal branches of the clade-specific subtrees prior to PIC construction and subsequent regression analysis demonstrates a phylogenetic signal: the jagged distribution of estimated slopes in the original analyses, especially in the Rodents (Figure 30a) and Fereuungulates (Figure 30b), are smoothed out over a broader range after randomization.

DISCUSSION

The analyses we have presented are based on the largest available mammalian metabolic allometry dataset and the best available phylogeny (Bininda-Emonds et al. 2007). Our dataset is also unique in that it includes measures of intraspecific variation that are necessary for checking the assumptions of alternative regression models. We found that estimates for the slope of the allometric relationship between log(*m*) and log(*MR*) diverge from predictions of the MTE (West et al. 1997; Brown et al. 2004). Both the choice of regression technique and phylogenetic correction affect estimates of allometric slopes and intercepts. We argue that there probably is not a canonical approach to analyzing allometric data, and that our results stand in contrast to the existence of universal scaling of metabolic allometry in mammals.

Meeting the criteria for BMR

Since our results make clear that decisions made on analyses to be applied to data should be based on the data themselves, we start with a discussion of the many instances where our data are less than optimal. There is widespread pseudoreplication of metabolic rate measurements which may be more problematic in large and/or rare animals. Failure to reach postabsorption, activity, and measurements while sleeping are also common problems. We excluded measurements on reproductive females and animals that were clearly active throughout the metabolic measurements (i.e. field and maximal metabolic rates). We also excluded measurements on most domesticated species from our new dataset, due to potential changes in body composition and size that occur due to artificial selection (McNab 1988), although a few such species (e.g. aurochs, *Bos taurus*) have been retained because they were included in recent compilations (Heusner 1991;Savage et al. 2004). We included, with comments, animals we suspected were not post-absorptive, sleeping, that later entered torpor, hibernation, or died, that had mass values not definitively given for just the individuals with measured metabolic rates, and that were reported in non-English papers.

There are numerous physiological issues that may affect the clade-specific data. For instance, it is commonly noted that ‘basal’ metabolic measurements in the smallest shrews may be unattainable because they are physiologically incapable of reaching postabsorption without adverse effects, they increase activity levels in response to periods of fasting, or their body size dictates metabolic rates that do not conform to ‘typical’ basal metabolic rate scaling (Speakman et al. 1993). However, care has been taken in the inclusion of measurements, and clearly active measurements on shrews were excluded (e.g the Asian house shrew, *Suncus murinus*; Oron et al. 1981). Examination of the native data in the smallest shrews (and rodents and bats) also demonstrates that their allometries are not obviously different than those of their larger bodied clade-conspecifics (separate scatterplots of data not shown).

Approaches to dealing with these issues have previously consisted of the exclusion of measurements on animals with ruminant digestive systems and Q_{10} adjustment of metabolic rates to correct for differences in body temperature and measurements performed in the sleep part of the circadian cycle (White and Seymour 2003, 2004, 2005; White et al. 2006). However, the effect of circadian rhythm on metabolic rate is small in mammals above 50g (Clarke and Rothery 2008), ruminant digestion is largely anaerobic although it does provide some amount of thermogenesis (Blaxter 1967), and most animals, including many shrews, can be brought to basal metabolism by careful researchers (McNab 1997). Furthermore, there is no consistent pattern across phyla (e.g. Marsupials, Artiodactyls, and Lagomorphs) in the influence on body temperature of heat from gut fermentation (Clarke and Rothery 2008). Instead of selecting only the metabolic rate measurements deemed as most closely matching BMR, or with the greatest sample size, or with the least amount of time in captivity, etc., we have left the resulting variability in our dataset and tried to address it analytically with regressions that incorporate different error variance structures and corrections for body temperature and phylogeny.

Regression analysis

Regression analyses adapted to different relative variances in each trait and/or different assumptions and minimization criteria yield consistently different slope and intercept estimates. OLS estimates were consistently shallower than RMA and LSVOR, estimates from LSVOR adjusted for 3-times greater intraspecific variation in metabolic rate than body mass were significantly steeper than OLS, estimates from LSVOR adjusted for equal intraspecific variation in both variables were slightly shallower than RMA, and estimates from LSVOR adjusted for 3-times less intraspecific variation in metabolic rate than body mass were significantly steeper than all other regressions. Each of these types of intraspecific variance ratios applies to part of the dataset, but the dependent variable does not invariably have variation that is much greater than, equal to, or less than the independent variable.

Overall slope estimates differed significantly between regression methodologies, estimated intercepts were negatively correlated with estimated slopes, and high R^2 values did not indicate immunity from these differences. LSVOR regression requires measurements of intraspecific variation (both biological and measurement) to select the angle along which residuals are measured (O’Connor et al. 2007a), and without these inputs, the direction of the measurements of residuals has to be made independently of the data just as in OLS and RMA regressions (O'Connor et al. 2007a; Warton et al. 2006).

Indeed, LSVOR generally outperforms both OLS and RMA: simulations bear out the superior performance of LSVOR under conditions in which RMA and OLS mis-estimate slopes, and the equivalent performance of LSVOR under conditions in which RMA and OLS perform well (O'Connor et al. 2007a). We therefore advocate the use of LSVOR for allometric analyses of physiological traits when the intraspecific variance is known although there is perhaps no one correct regression analysis for these data.

Phylogenetic signal

There is a significant phylogenetic signal in our mammalian metabolic allometry dataset: steeper slope estimates were obtained in analyses of PICs as compared to analyses of native data, significantly different clade-specific slopes were obtained via ANCOVA, and randomization of the location of trait values on the clade-specific sub-trees smoothed out histograms of slope estimates. Calculation of phylogenetic contrasts alleviates overestimation of the strength of the relationship between traits caused by phylogenetic correlations or constraints (Martins and Garland 1991; O'Connor et al. 2007a). PGLS and ANCOVA (with phylogenetic least-squares) are also important phylogenetic correction methods, especially in dealing with different types of evolutionary processes (Grafen 1989; Diaz-Uriarte and Garland 1996; Hansen and Martins 1996; Hansen 1997; Martins and Hansen 1997; Butler and King 2004). However, these methods employ scaled branch lengths, assume that variation in the ‘independent’ variable is negligible, and impose an OLS-style fitting procedure that specifies regressors and response variables (Rohlf 2001; O'Connor et al. 2007a). Finally, Symonds and Elgar (2002) have also demonstrated sensitivity of mammalian metabolic allometry slope estimation to evolutionary trees based on molecular versus morphological data. While the supertree we used is an amalgamation of evolutionary data (Bininda-Emonds et al. 2007), in simulations where the exact timings of evolutionary divergences (ancestral nodes) and character states were known, and different rates of evolution were imposed, the un-scaled Felsenstein (1985) method of phylogenetic independent contrast formation was found to correlate most closely with the true contrast values (O'Connor et al. 2007a).

A significant phylogenetic signal has previously been observed in mammalian allometries at the ordinal level with similar observations of steeper slopes upon phylogenetic correction (Hayssen and Lacy 1985; Glazier 2005; Duncan et al. 2007; Clarke and Rothery 2008). The shallower slopes of Soricids have also been alluded to in Duncan et al. (2007) and Glazier (2005) although these were within the outdated designation of Insectivora. The phylogenetic effects incorporated in the ANCOVA explained statistically significant variation in metabolic rate and indicated significant clade-specific differences in slopes. The jaggedness of our resampled slope estimates due to clades with outlying trait combinations (e.g. Fereuungulates, possibly due to Pangolins) also demonstrates the importance of the phylogenetic signal through the heterogeneity of slope estimates that results from different phylogenetic tree selections prior to contrast calculation. We acknowledge that there is still uncertainty in each of the phylogenetic hypotheses herein. However, our results indicate that the overall allometric slope should not be interpreted as a general description of metabolic allometry in mammals.

Physiological and ecological factors

Among mammals within the same clade or having the same body size, metabolic rates are highly variable due to a diverse array of factors such as body temperature, environmental temperature and precipitation, latitude, altitude, food availability, behavioral strategy, and diet (McNab 1995; McNab 1997; Mueller and Diamond 2001; Lovegrove 2003; McNab 2003; White and Seymour 2004; Careau et al. 2009). General differences between larger mammals (with steeper scaling) and smaller mammals (with shallower scaling) have also been described (reviewed in Glazier 2005). Proponents of MTE have argued that the preponderance of small mammal measurements in metabolic allometry (with consistent deviations toward higher metabolic rates) artificially drives overall slope estimates to be shallower, and that this is supportive of MTE (Savage et al. 2004). We found that this is not consistently true within Rodents that span the small to intermediate body sizes of the overall dataset, in small Chiropterans, Rodents, and Shrews, or in overall regression analyses of the full dataset with slope estimates that are shallower, equivalent to, and steeper than 0.75.

The only physiological factor we incorporated was body temperature, which had values that were highly variable and weakly negatively correlated with body mass despite the small overall range of body temperatures of animals within their thermoneutral zones during BMR measurements. Incorporation of the body temperature variable in regression analysis of our dataset has a small, but significant effect on the estimated allometric relationship. This statistically significant effect appears to be derived from the large sample size of measurements ($n = 535$) and is unlikely to be biologically significant since it explains very little additional variation ($R^2 = 0.016$) compared to that explained by the body mass variable ($R^2 = 0.939$). There are also significant differences in the scaling of body temperatures with body masses in mammals at the ordinal and higher order (e.g.

Marsupialia, Ferae, and Ungulata) levels of taxonomy (Clarke and Rothery 2008) which may relate to the clade-specific scaling differences we observed.

Our clade-specific slope estimates ranged from 0.5 to 0.85, which is a broader range than those observed previously at the ordinal level (Glazier 2005; Duncan et al. 2007). Each of the clades also had well over a 200-fold span of body masses (lowest in Chiropterans with (maximum m / minimum m) = 277). These clade-specific differences cannot be tied to any one behavioral, procedural, physiological or ecological factor even within a particular clade, although no doubt some factors apply to some of the data.

Metabolic allometry theory

We applaud the attention to allometry that has been rekindled by MTE. Our research herein was prompted by this recent activity especially with regard to ‘universal quarter-power scaling’ (West and Brown 2005). In that vein, the focus of our analyses has been slope estimation, but we have also demonstrated variable intercept estimates (i.e. ‘normalization constants’) primarily in relation to the estimated slope. Proponents of MTE readily admit that their model does not predict normalization constants (Allen and Gillooly 2007), and maintain that variation in the observed slope of a particular allometric relationship is in keeping with predictions of MTE (Moses et al. 2008).

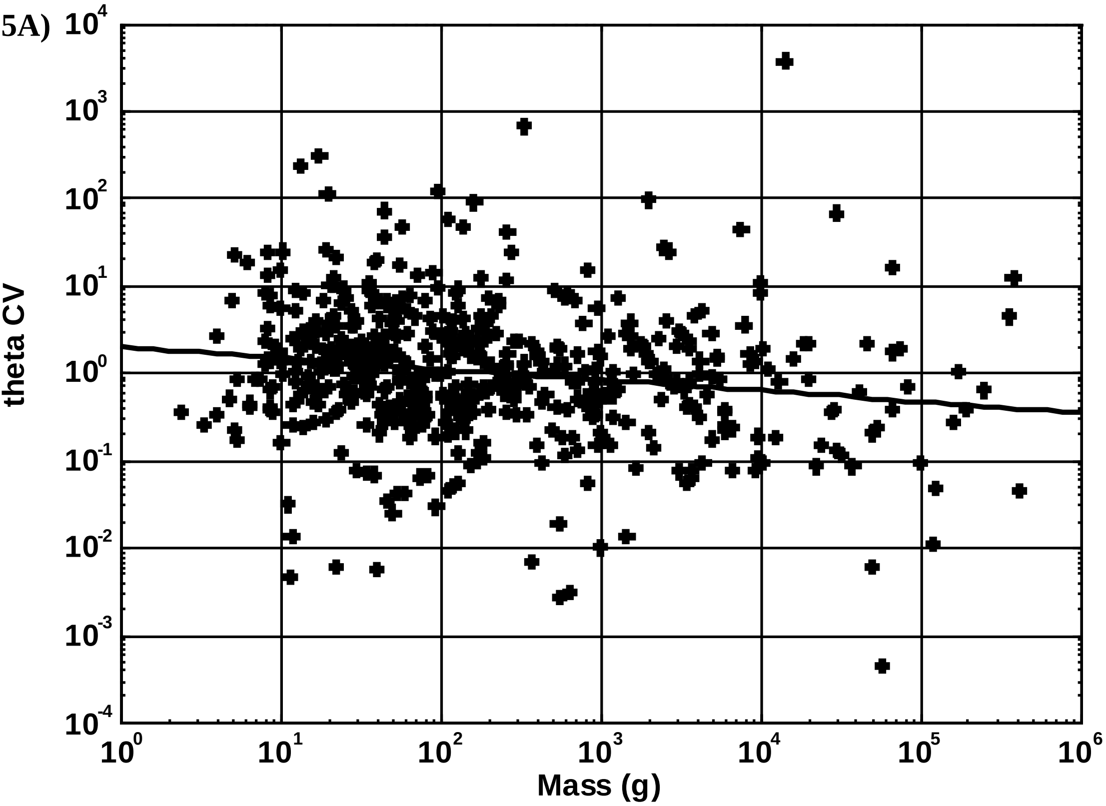
The issue at hand is the extremely limited predictive power of MTE. It predicts neither the slope nor the intercept of mammalian metabolic allometry. We found that slope estimates are tied to the dataset and the analytical model applied (with few instances of 95% confidence intervals on slope estimates including 0.75 in the overall scaling relationship) and that intercepts are tied to the slopes. Downs et al. (2008) also recently demonstrated that MTE fails to prescribe metabolic responses to body temperature in a variety of organisms including mammals. In moving forward we hope these results encourage new measurements of mammalian basal metabolism and careful data-based decisions about the application of particular analytical models to allometry data.

Table 8. Mammal metabolic allometry parameter estimates from regression analyses on native and phylogenetic independent contrast data.

		Native Data					
		OLS	RMA	LSVOR $\theta_{cv} = 0.3$	LSVOR $\theta_{cv} = 1.0$	LSVOR $\theta_{cv} = 3.0$	PGLS*
Rodents	Intercept	0.696 (0.636–0.759)	0.614 (0.558–0.668)	0.628 (0.571–0.684)	0.582 (0.525–0.638)	0.665 (0.607–0.724)	--
	Slope	0.671 (0.642–0.699)	0.714 (0.689–0.739)	0.707 (0.681–0.733)	0.730 (0.704–0.756)	0.687 (0.660–0.714)	--
Fereuungulates	Intercept	0.233 (0.017–0.429)	0.106 (-0.117–0.311)	0.116 (-0.110–0.324)	0.048 (-0.185–0.262)	0.117 (-0.045–0.379)	--
	Slope	0.822 (0.774–0.873)	0.854 (0.805–0.907)	0.852 (0.802–0.905)	0.869 (0.818–0.924)	0.836(0.788–0.889)	--
Chiropterans	Intercept	0.448 (0.368–0.530)	0.390 (0.308–0.469)	0.396 (0.312–0.477)	0.364 (0.275–0.447)	0.423 (0.342–0.505)	--
	Slope	0.779 (0.730–0.831)	0.820 (0.769–0.877)	0.816 (0.764–0.873)	0.838 (0.784–0.901)	0.797 (0.746–0.850)	--
Primates	Intercept	0.416 (0.201–0.648)	0.324 (0.113–0.537)	0.335 (0.123–0.553)	0.286 (0.065–0.502)	0.378 (0.169–0.602)	--
	Slope	0.758 (0.682–0.823)	0.788 (0.723–0.851)	0.785 (0.717–0.848)	0.801 (0.736–0.865)	0.771 (0.699–0.834)	--
Soricomorphs	Intercept	1.052 (0.926–1.173)	0.990 (0.872–1.109)	1.011 (0.886–1.134)	0.976 (0.856–1.099)	1.035 (0.909–1.157)	--
	Slope	0.472 (0.388–0.551)	0.516 (0.438–0.592)	0.501 (0.418–0.580)	0.526 (0.444–0.605)	0.484 (0.400–0.563)	--
Marsupials	Intercept	0.450 (0.344–0.563)	0.419 (0.324–0.519)	0.424 (0.327–0.526)	0.407 (0.315–0.506)	0.438 (0.336–0.547)	--
	Slope	0.722 (0.685–0.757)	0.735 (0.703–0.765)	0.733 (0.700–0.764)	0.739 (0.708–0.769)	0.727 (0.692–0.760)	--
Full Tree	Intercept	0.585 (0.549–0.622)	0.540 (0.506–0.575)	0.547 (0.513–0.582)	0.523 (0.490–0.557)	0.568 (0.532–0.604)	--
	Slope	0.716 (0.700–0.730)	0.735 (0.720–0.748)	0.732 (0.717–0.746)	0.742 (0.728–0.756)	0.723 (0.708–0.737)	--
		Phylogenetic Independent Contrast (PIC) Data**					
Rodents	Intercept	0.018 (-0.013–0.050)	0.013 (-0.018–0.045)	0.014 (-0.017–0.046)	0.011 (-0.020–0.043)	0.016 (-0.015–0.048)	2.234 (0.280)
	Slope	0.640 (0.621–0.657)	0.681 (0.663–0.698)	0.673 (0.654–0.689)	0.695 (0.677–0.715)	0.655 (0.636–0.671)	0.553 (0.024)
Fereuungulates	Intercept	0.015 (-0.026–0.055)	0.013 (-0.028–0.054)	0.013 (-0.028–0.054)	0.013 (-0.029–0.054)	0.014 (-0.027–0.054)	0.984 (0.395)
	Slope	0.769 (0.719–0.801)	0.816 (0.764–0.851)	0.811 (0.758–0.847)	0.837 (0.783–0.874)	0.789 (0.737–0.823)	0.766 (0.029)
Chiropterans	Intercept	0.057 (0.005–0.108)	0.059 (0.007–0.111)	0.059 (0.007–0.110)	0.060 (0.008–0.112)	0.058 (0.006–0.109)	0.683 (0.220)
	Slope	0.728 (0.725–0.730)	0.760 (0.758–0.763)	0.756 (0.754–0.758)	0.774 (0.772–0.776)	0.741 (0.739–0.743)	0.872 (0.035)
Primates	Intercept	0.034 (-0.037–0.104)	0.020 (-0.058–0.094)	0.022 (-0.055–0.095)	0.014 (-0.070–0.091)	0.028 (-0.045–0.099)	0.743 (0.274)
	Slope	0.708 (0.705–0.710)	0.772 (0.769–0.775)	0.764 (0.761–0.766)	0.800 (0.797–0.802)	0.734 (0.731–0.736)	0.774 (0.033)
Soricomorphs	Intercept	0.053 (-0.008–0.112)	0.043 (-0.024–0.105)	0.045 (-0.021–0.107)	0.039 (-0.033–0.104)	0.050 (-0.013–0.109)	2.281 (0.238)
	Slope	0.520 (0.516–0.523)	0.617 (0.613–0.621)	0.594 (0.590–0.598)	0.652 (0.647–0.657)	0.552 (0.548–0.556)	0.527 (0.043)
Marsupials	Intercept	0.049 (0.008–0.091)	0.049 (0.008–0.091)	0.049 (0.008–0.091)	0.049 (0.007–0.092)	0.049 (0.008–0.091)	0.783 (0.270)
	Slope	0.711 (0.709–0.713)	0.750 (0.749–0.752)	0.745 (0.743–0.746)	0.766 (0.764–0.768)	0.726 (0.725–0.728)	0.757 (0.025)
Full Tree	Intercept	0.017 (-0.001–0.035)	0.015 (-0.004–0.034)	0.015 (-0.003–0.034)	0.014 (-0.005–0.033)	0.016 (-0.002–0.035)	1.263 (0.531)
	Slope	0.707 (0.698–0.713)	0.745 (0.735–0.751)	0.739 (0.729–0.745)	0.759 (0.750–0.766)	0.722 (0.712–0.728)	0.687 (0.014)

Table 8 Note – Regressions are Ordinary Least-Squares (OLS), Reduced Major Axis (RMA), and Least-Squares Variance-Oriented Residuals (LSVOR) with three different variance ratios (θ_{cv}). Parameter estimates are means with 95% confidence intervals in parentheses. Phylogenetic Generalized Least-Squares (PGLS) are performed on native data corrected for phylogeny with a variance covariance matrix of branch lengths for species pairs scaled by the square root of the sum of the branch lengths.
*PGLS parameter estimates with the calculated standard error in parentheses.
**Slope estimate confidence intervals for PICs are mean upper and lower bounds for the bootstrapped estimates.

25A)


10^4
10^3
10^2
10^1
10^0
10^-1
10^-2
10^-3
10^-4
theta CV
10^0
10^1
10^2
10^3
10^4
10^5
10^6
Mass (g)

25B)

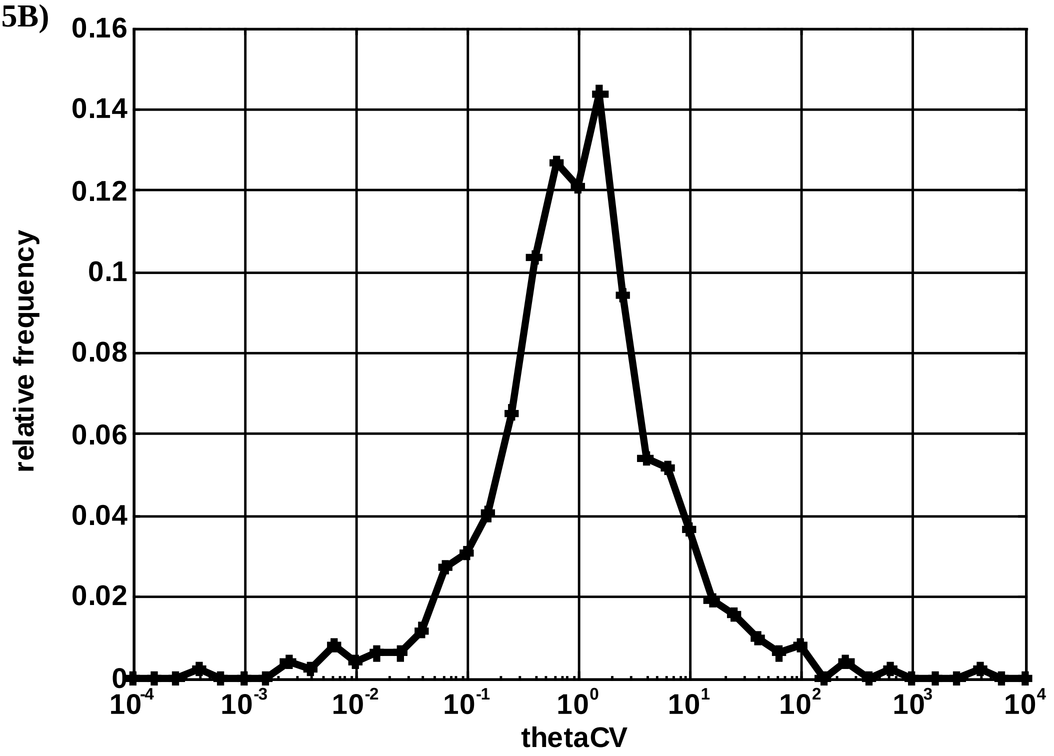


Figure 25. Intraspecific variance ratios of basal metabolic rate to body mass are used to select the slope along which the residuals of least-squares variance-oriented residuals regression are measured. **25A)** Theta CV is the ratio of the squared coefficient of variation for basal metabolic rate to that of body mass for each species. There was a weak, negative relationship between Theta CV and $\log_{10}$ transformed body mass. **25B)** A histogram of Theta CV values is centered about 1, or variance equivalence, with a majority of values falling between 0.1 and 10.

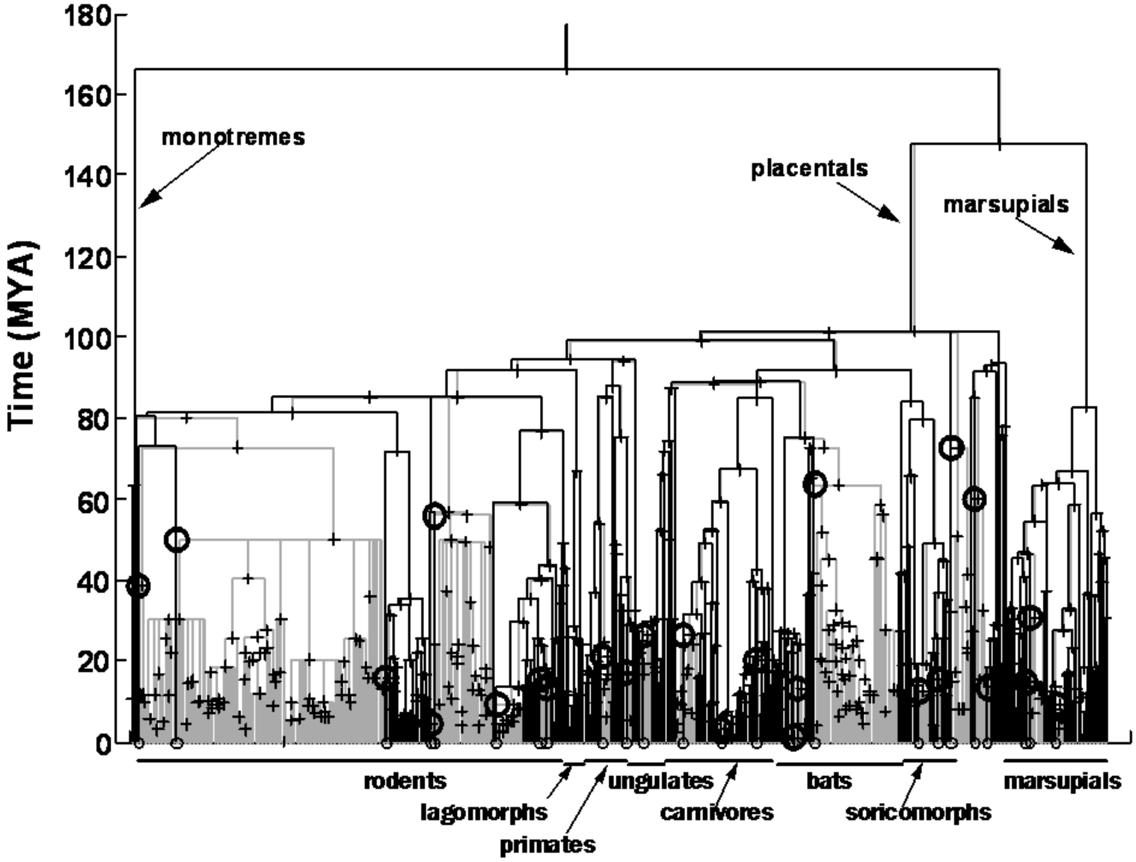


Figure 26. Full mammalian phylogenetic tree (Bininda-Emonds et al. 2007) with branch lengths corresponding to Time, in millions of years ago (MYA), crosses at each ancestral node, and oriented so that tips for extant species are located at Time = 0. The figure depicts one iteration of tree selection in the calculation of phylogenetic independent contrasts: black lines are the included branches of all fully resolved taxa and of the randomly selected representative for each polytomy (indicated by a large black circle at the node of divergence of the selected taxon from the rest of the polytomy). Gray lines are polytomous portions of the full mammal tree not selected in the exemplar iteration.

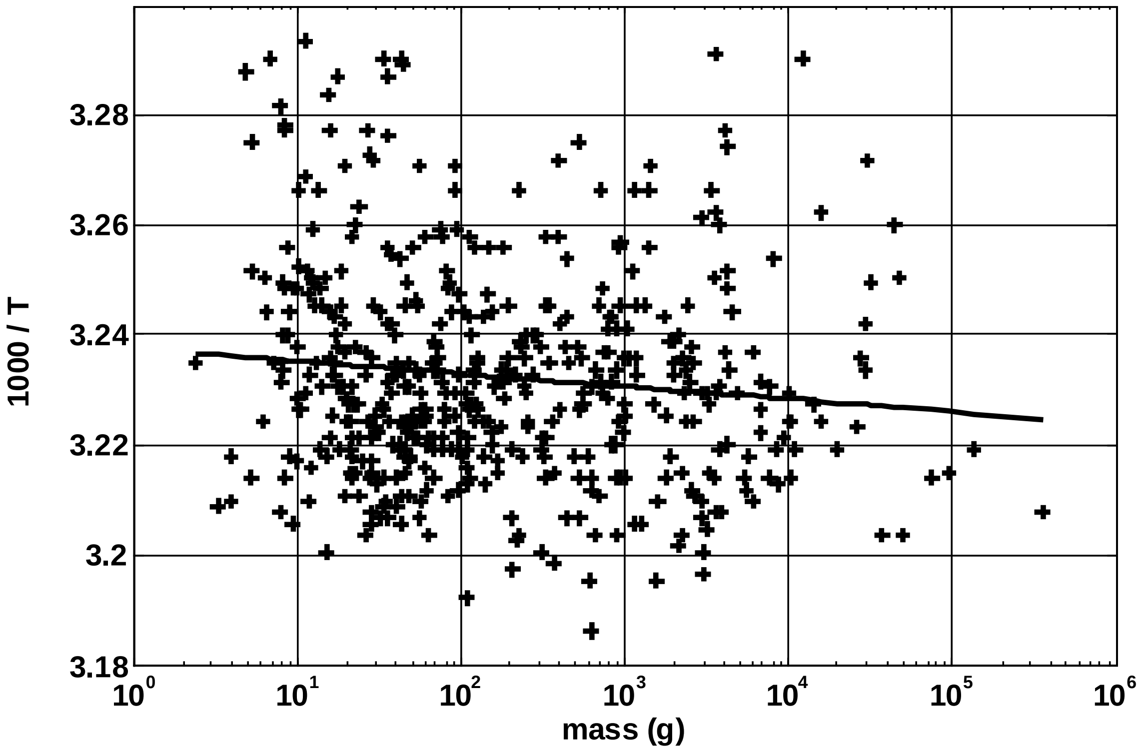


Figure 27. Weakly significant negative relationship between body temperature and body mass in mammals. Body temperatures (T_b, Kelvin) have been inverse transformed and body masses are shown as $\log_{10}$ transformed.

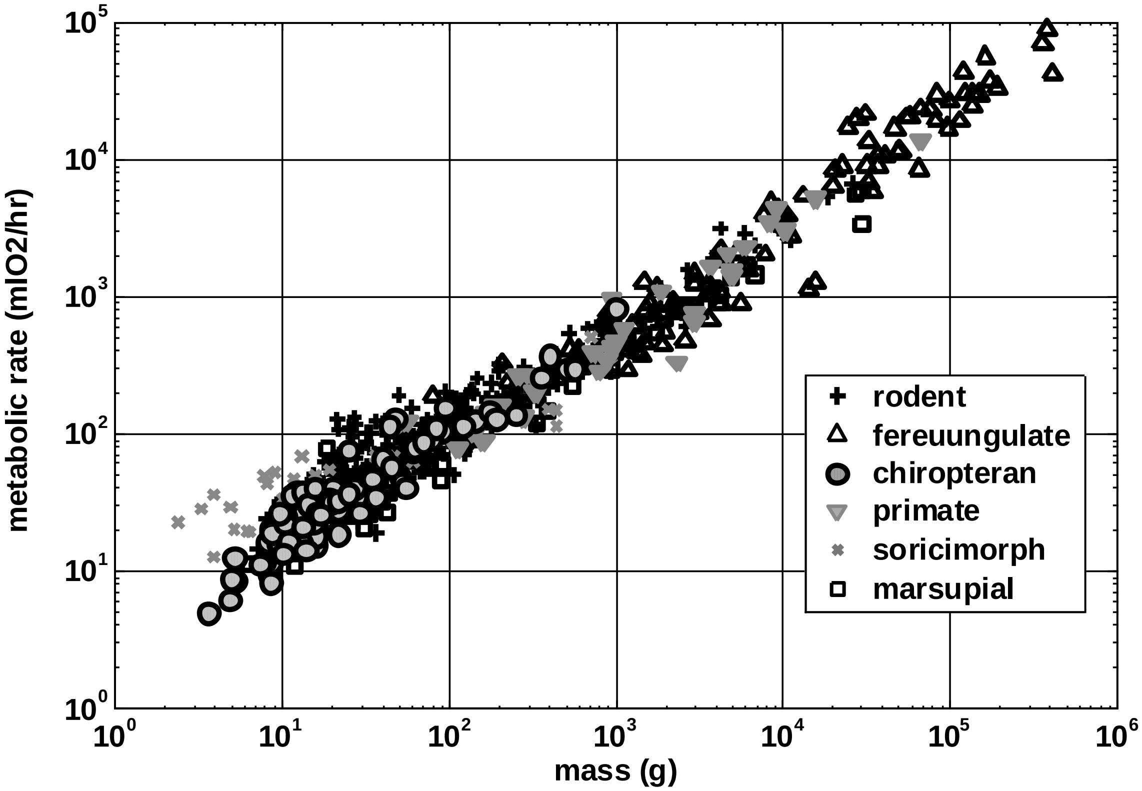


Figure 28. Clade-specific scatterplot of mammalian metabolic allometry data. Basal metabolic rates and body masses have been $\log_{10}$ transformed, and the plot does not include data from clades excluded in the clade-specific analyses (e.g. *Monotremata*).

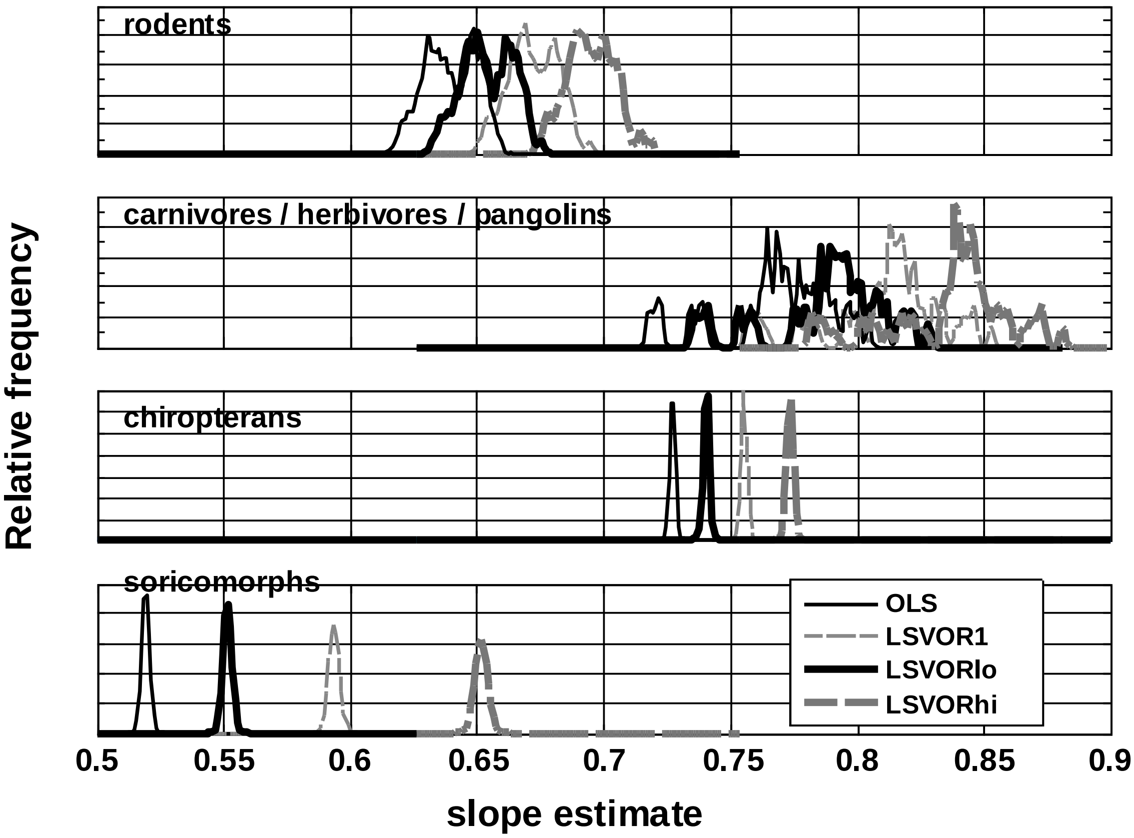
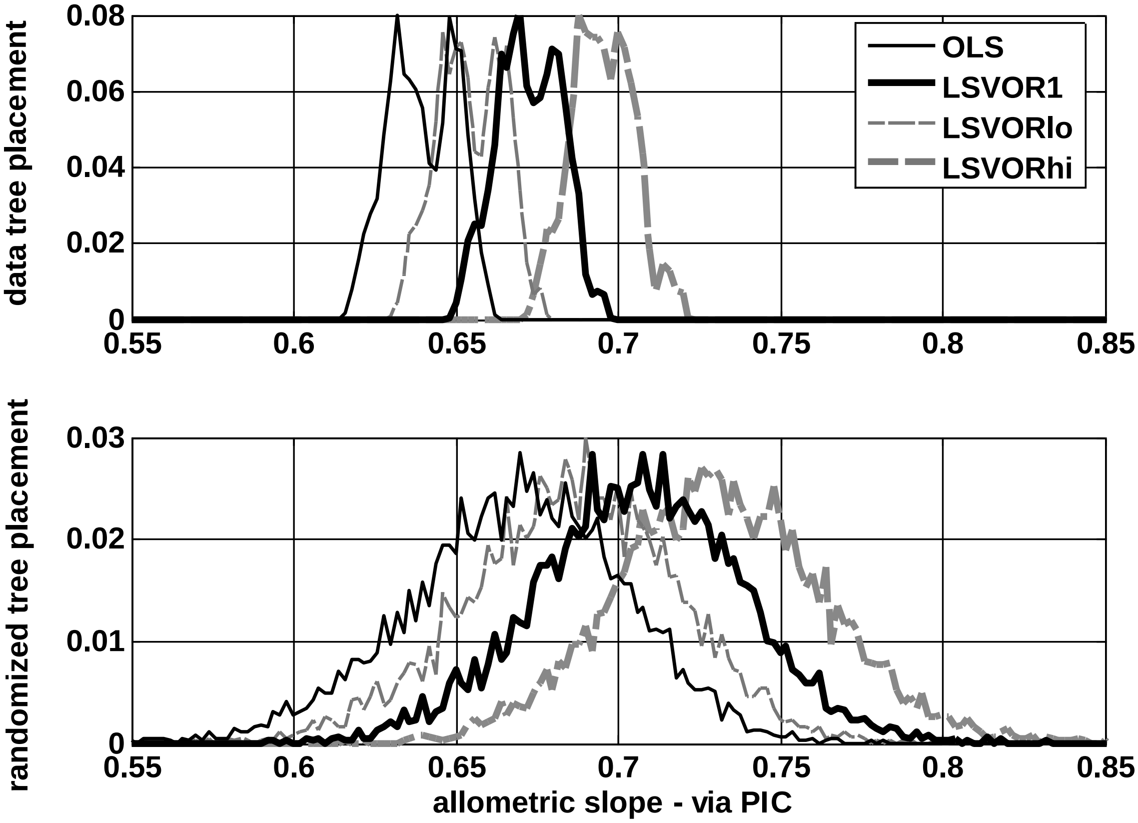


Figure 29. Clade-specific histograms of mammalian metabolic allometry slope estimates. The relative frequency of estimation of a particular slope value is shown for just four clades, Rodents, Carnivores/Herbivores/Pangolins (Fereuungulates), Chiropterans, and Soricomorphs since results for Marsupials and Primates are extremely similar to those for Chiropterans. For clarity, just parameter estimates from ordinary least-squares (OLS) and least-squares variance-oriented residuals (LSVOR) regressions with $\theta_{cv} = 1$, 0.3 (“lo”), and 3 (“hi”) are shown because results for LSVOR with $\theta_{cv} = 1$ are almost identical to those for reduced major axis.

30A) Rodents


0.08
0.06
0.04
0.02
0
data tree placement
0.55
0.6
0.65
0.7
0.75
0.8
0.85
OLS
LSVOR1
LSVORlo
LSVORhi
0.03
0.02
0.01
0
randomized tree placement
0.55
0.6
0.65
0.7
0.75
0.8
0.85
allometric slope - via PIC

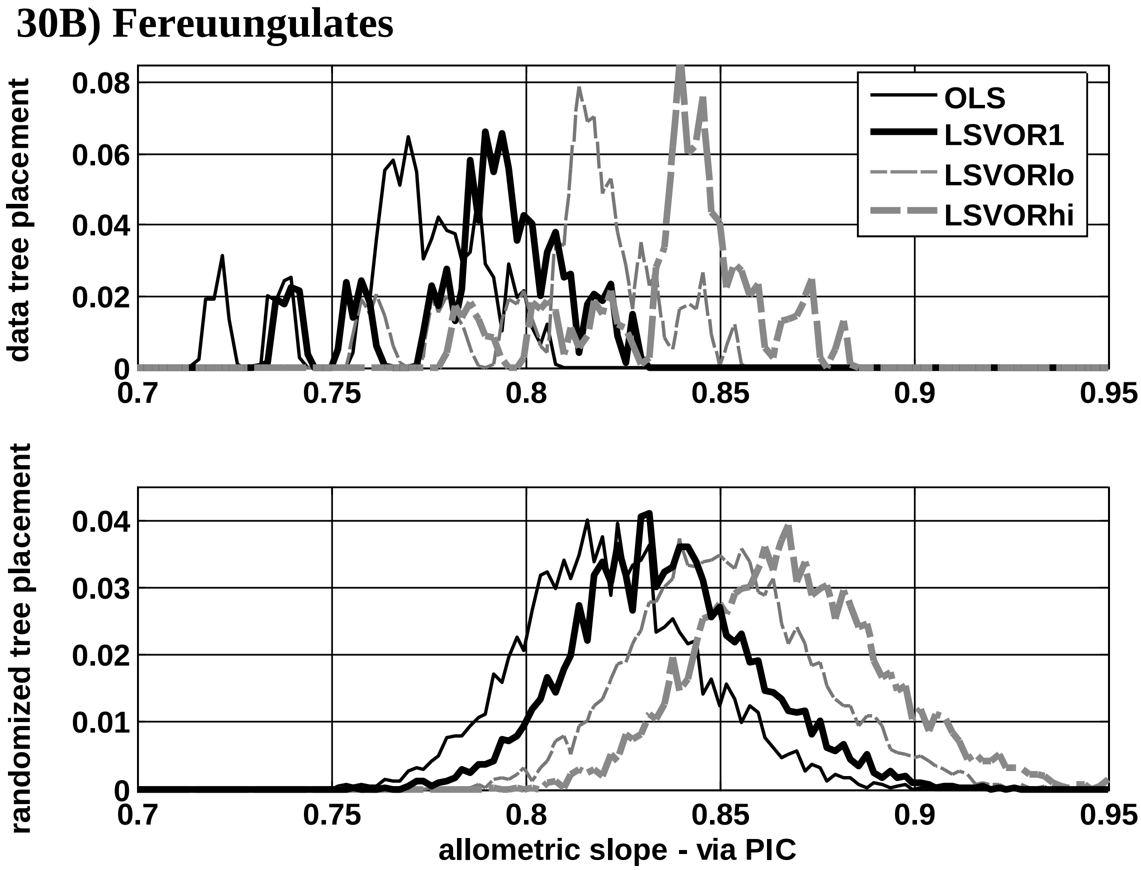


Figure 30. Histograms of allometric slope estimates in **30A)** Rodents and **30B)** Fereuungulates based on phylogenetic independent contrasts (PIC) constructed using native (top) and randomized (bottom) trait placement on the phylogenetic clade-specific sub-trees. Applied regression models shown are ordinary least-squares (OLS) and least-squares variance-oriented residuals assuming equal error variance in both the *x* and *y* variables (LSVOR1; similar to reduced major axis), assuming three-times greater error variance in the *y* variable (LSVORhi), and assuming three-times greater error variance in the *x* variable (LSVORlo).

CHAPTER 7: Linking physiological effects on activity and resource use to population level phenomena (*Integrative and Comparative Biology* 46: 1093-1109)

ABSTRACT

We present an approach to delineating physiological effects on population level processes by modeling the activity and resource budgets of animals. Physiology and its environmental forcing functions are assumed to affect both the total time available for activity and foraging and the resource budgets by affecting resource acquisition, costs, and handling. We extend the earlier model of Dunham *et al*. (1989) and translate it into a computational algorithm. To satisfy conservation needs for accuracy, wide applicability, and rapid deployment, the model is relatively simple, uses as much data on the focal organism as possible, is mechanistically driven, and can be adapted to new organisms by using data for the new species, or the best available approximations to those data.

We present two applications of the modeling approach. First, we consider a system with substantial information available, canyon lizards (*Sceloporus merriami*) studied by Dunham and colleagues in west Texas. In this case the focus is on integration of numerous inputs and the ability of the model to produce predictions that approximate counterintuitive empirical patterns. By using the wealth of specific data available, the model outperforms previous attempts at explanation of those patterns. Next, we consider a system with much less available information (forest-dwelling semi-fossorial frogs). The question here is how hydric conditions can become limiting. A model of evaporation from frogs buried in leaf litter was incorporated and demonstates how rainfall patterns can both supply water and put the frogs at risk of critical dehydration.

INTRODUCTION

In some ways, a symposium asking how physiology can and has contributed to conservation biology should seem like posing a rhetorical question. The papers in this symposium document some of the ways in which physiology, in general, and energetics, in particular, have contributed to an understanding of conservation problems. Further, most biologists would agree that physiological challenges can constrain an animal's ecology and physiological adaptations can affect the range of habitats that an organism can occupy.

In what sense then, are the contributions of physiology and energetics to conservation not a foregone conclusion? Perhaps the most obvious procedure is to develop approaches that allow physiological theory and data to be methodically incorporated into conservation assessments and action plans. Limits on the utility of physiological data arise both from differences in the focus of the two fields and from differences in the approaches of applied and basic scientists. Physiology and physiological ecology focus on organism-level questions that potentially influence the population biology of the animals. Conservationists, on the other hand, tend to focus on the population and community levels of organization. In general then, physiological data must be integrated through one or more levels of ecological organization to make predictions of immediate use to conservation biology. As we will argue below, this integration is both important and difficult. Without a clear integration at the population level, physiological predictions and approaches can be difficult to incorporate into conservation plans.

Differences in research approaches between physiologists and conservationists stem both from the differences in the focal levels of organization listed above and from differing research traditions. Most comparative physiologists and physiological ecologists are trained in an academic, basic-science tradition with its emphases on detailed examination and complete explanation. Many conservation biologists must work within a much more applied tradition. Table 9 lists differences between these two traditions. We suspect that the first two differences drive the others. Conservationists in many cases, are responding to threats to species and/or biomes which imbue the questions asked with an urgency that shortens all time scales and leaves inadequate time for testing hypotheses unless they are immediately and undeniably related to the population biology of the species of interest. Furthermore, the complicated matrix of intraspecific and interspecific influences within which all species invariably live requires that integration at the population level, discussed above, be easily performed for any factor considered. This complication and the compressed time frames for decisions can restrict attention to established approaches (Primack 1998).

In this setting, how can physiological data and analysis be framed so that they translate easily to conservation assessments and plans? No single approach will invariably succeed. The arguments above suggest that physiological ecologists would do well if: (1) physiologically based predictions are translated as closely and concretely as possible to the population biology of the animal in question, (2) physiological models are relatively easy to use, without mounting huge research programs, (3) it is recognized that physiology dictates aspects of the focal animal’s ecology, but in many cases not all aspects of that ecology, and (4) the conditions under which physiological predictions might be seriously wrong are clarified. We offer an approach that adheres as closely as possible to these conditions while remaining adaptable and, hopefully, broadly applicable.

Physiological factors will translate most directly to the population level under three scenarios: (1) when some environmental conditions lead to lethal, pathological, or otherwise disabling physiological conditions and one of the animal's main tasks is to avoid such conditions (e.g., Grant and Dunham 1988); (2) when some resource (e.g., energy, water, activity time) or combination of resources is critical to the animal's survival, growth, and/or reproduction and physiological factors alter either access to the resource (e.g., foraging time), handling of the resource (e.g., capture rate or digestion), or resource costs (e.g., metabolism) (e.g., Kingsolver 1983, 1989; Dunham and Overall 1994); or (3) when any of the conditions above dictate interactions with conspecifics, competitors, predators, prey, pathogens, or parasites (Christian and Tracy 1981).

In this paper, we offer a model-based approach to deal with the first of these scenarios. It can be extended to handle interactions with other organisms. The model attempts to integrate physiological effects over time to predict fitness and demographic correlates, using what information is available on a species of interest and allowing substitution of related data as needed. We argue that it also makes clear on which assumptions predictions depend and points out which data are needed to refine predictions when needed. We use the model to address questions of potential conservation importance, then discuss the pro's and con's of such an approach more generally.

MODEL

Our conceptual model is an elaboration of the model presented by Dunham et al. (1989) to describe physiological effects on the life history and ecology of ectotherms. This model asserts that resources (e.g., water, energy) needed for growth and reproduction constitute critical fitness correlates and that accumulation of those resources can be used as proxies for ecological success of individual animals and, by inference, of their parent populations (Dunham et al. 1989, Fig. 31). This approach is consistent not only with current autecological modeling practice (DeAngelis and Gross 1992, DeAngelis et al. 1993, Maley and Caswell 1993, McNair et al. 1998, Kooijman 2001, Grimm and Railsback 2005) but also with life history theory (Stearns 1992, McNab 2002, Sebens 2002, Dahlhoff et al. 2002, Piersma 2002) and physiological ecology (Congdon et al. 1982, Dunham et al. 1989, Dunham 1993, Porter and Tracy 1983, Porter et al. 2000, 2002; Angilletta et al. 2003). Resources are accumulated by activity in an environment from which the resources can be harvested. Both the resources available and the ability of an animal to be active and forage in its habitat are key determinants of resource accumulation (Fig. 31). Physiological and physical factors affect resource accumulation by (1) facilitating or constraining time available for activity, (2) affecting resource harvest rates (e.g., digestion), or (3) affecting handling of harvested resources (e.g., metabolic energy costs and evaporation).

While the conceptual model guides our consideration of physiological effects at the population and conservation levels, conceptual models alone can and have proven unreliable in predicting such effects. Witness the longstanding debate about physiological tradeoffs in life history theory, and the variety of predictions made using similar conceptual models for particular organisms (see Congdon et al. 1982, Stearns 1992). We argue that models for use in conservation must be made as explicit and quantitative as possible.

Figure 32 represents a highly simplified block diagram of such an explicit model limited to one ‘resource’ (e.g., water, energy, heat). For each time step, the current resource state (stored resource), the environment, and potentially other factors (e.g., other resources) influence whether the animal will be active for this time step. If the animal is active, it incurs costs due to that activity (e.g., increased metabolic rate and/or evaporation). Inactive animals incur different, potentially lower costs. Active animals can also forage for resources, and depending on the resource environment, ingest resources as food. Regardless of activity, animals can digest food already in the gut, body temperature permitting, and assimilate resources. Integrating costs and assimilation, we reach a new resource state at which to start the next time step. Activity and stressful thermal, hydric, and other resource states can expose animals to risks of predation and other sources of mortality (Fig. 32).

In order to adapt the model to particular populations, one must (1) determine what resources are important in an animal’s ecology, (2) expand the model to as many potentially interacting resources (e.g., heat, water, energy) as necessary, (3) provide population-specific information on resource availability and handling (e.g., the effect of temperature on digestive rates, tolerated body temperatures, operative environments), and (4) iterate the model over time frames appropriate to the animal’s biology. It may be the case that insufficient data will be available on populations of interest to parameterize such a model and information must be substituted for other populations, species, or habitats (see below). Such substitutions are almost inevitable, and to the extent that the data used fail to accurately represent resource handling in the focal population, the predictions of the model may be inaccurate (see below).

Here we present two very different applications of this model framework to populations in which physiological processes affect population processes. In the first case, we examine variation in life history among populations of *Sceloporus merriami* in Big Bend National Park, TX where they have been studied intensively for over 25 years (Dunham 1978, 1980; Grant and Dunham 1988, 1990; Grant 1990, Dunham 1993, Dunham and Overall 1994). In this case, substantial specific information is available and must be integrated to explain variations in growth rate among populations at different elevations. For the second application, we consider forest-dwelling amphibians in eastern Missouri and ask to what extent a single resource, water, can constrain activity and foraging. Relatively few population-specific physiological data are available, and only tentative conclusions can be reached, but the overall modeling strategy remains important.

CANYON LIZARDS, (*Sceloporus merriami*)

Sceloporus merriami is a small, insectivorous lizard that we treat as a model organism for examining potential effects of global warming. Global circulation models of climatic change predict large shifts (2 - 5.8ºC) in environmental temperatures over the next 100-year time horizon. Prediction and understanding of organismal and population level responses to environmental change will require incorporation of physiological mechanisms into more complex population models (Dunham et al. 1989, Dunham 1993, Ayres 1993, Kareiva et al. 1993, Dunham and Overall 1994). For terrestrial ectotherms, changes in environmental and body temperature profiles may alter individual mass-energy balance relationships by altering metabolism and digestion (Beaupre et al. 1993b, Henen et al. 1998, Porter and Tracy 1983, Zimmerman and Tracy 1989, Porter et al. 2000, Somero 2002, Dahlhoff et al. 2002). In addition, altered time-activity budgets and food availability may influence growth and reproductive potential (Dunham et al. 1989, Dunham 1993, Dunham and Overall 1994, Grant and Dunham 1988, 1990; Grant 1990, Gates 1993, Sebens 2002, Piersma 2002).

Canyon lizards constitute a good test bed for predicted effects of climate change because (1) physiology and (2) population biology of the species have been well studied, (3) both climatic and microclimatic data are available for the populations examined by Dunham et al., and (4) the populations studied constitute a cline in elevation and a series of related environmental variables (Dunham et al. 1989, Dunham 1993, Dunham and Overall 1994, Grant and Dunham 1988, 1990). Extant predictions from physiologically structured models suggest that: (1) temperature and hydric conditions strongly and predictably affect activity, (2) effects of global warming will depend on both changes in opportunities for activity and costs of that activity, (3) increasing tolerated body temperature to extend activity time may be counterproductive because of elevated metabolic costs at higher body temperatures (Dunham 1993, Dunham and Overall 1994).

A problem with using the canyon-lizard system for such predictions, however, is that although the three habitats studied form a monotonic cline in a series of environmental variables (Table 10), the population dynamics (growth rates, adult body size, activity rates) for the three populations tend to reach extremes at the middle elevation (Grapevine Hills). Conceptual models, despite the wealth of available data, have been unsuccessful in mimicking these biotic patterns, presumably because the environmental gradients interact to affect population parameters in ways that are difficult to predict (Dunham et al. 1989). The question we asked was whether a quantitative, physiological model using the physiological rates and characteristics measured by Dunham et al. for these populations could make more biologically accurate predictions. We use this question to illustrate our model-based approach.

Habitat description

Both temperature and water are important to the ecology of canyon lizards (Grant and Dunham 1988, 1990, Dunham 1993, Dunham and Overall 1994), but simple models indicate that dietary water intake rates are sufficient to maintain body-water stores (Dunham unpublished data), suggesting that hydric conditions primarily affect insect prey densities. To describe each of the three study sites thermally, we need descriptions of (1) seasonal temperature variation, (2) diel variation in microhabitat temperatures, and (3) site-specific factors that strongly affect available operative temperatures. Seasonal trends are available from meteorological stations maintained by the United States National Parks Service within 2 km of each of the sites at comparable elevations. We used data for 1976-1991 for which good data were available for all three sites. For each site we extracted precipitation and daily minimum and maximum temperature. We constructed joint probability density distributions of minimum and maximum temperatures for each time of year for each of the field sites using a product-kernel technique (Martinez and Martinez 2002, Fig. 33). This allowed us to simulate daily environments by randomly selecting a maximum air temperature appropriate for the time of year and then selecting the minimum temperature appropriate for that maximum temperature from marginal distributions constructed for each site. This approach ignored day-to-day autocorrelations, but autocorrelations with lags greater than one day were negligible (data not shown). Daily air and ground temperature trajectories were estimated by fitting measured temperatures for each site (Dunham and Porter, unpublished data) to a model of daily temperature variation (Parton and Logan 1981) allowing prediction of trajectories from daily maximum and minimum temperatures. The Parton and Logan model predicts trajectories of environmental temperatures based on maximum and minimum temperatures, day length and time of solar noon (approximately 14:00 in Big Bend during the summer), and three parameters that vary from site to site and with height above the substrate (the time lag of maximum temperature after solar noon, the slope of exponential temperature decay at night, and the time lag of minimum temperature after sunrise). For air temperatures at each of the three field sites, each of these three Parton and Logan parameters was fit by a non-linear least-squares regression to microclimatic data recorded at the site (Dunham and Porter, unpublished data). Substrate temperatures were well modeled by a regression of measured rock temperatures on air temperature and solar radiation (O’Connor and Dunham, unpublished data). Addition of wind speeds and time-lagged temperatures and radiation loads added no significant improvement in predictions. Solar radiation was predicted using clear day models (e.g., Gates 1980) with clouds intermittently limiting radiant fluxes on a schedule estimated from microclimatic measurements made at the sites.

A final complication to be modeled was the shading of the sites by the steep slopes and peaks that abutted each of the field sites. Peaks tended to lie to the east and/or west of the field sites and thus blocked solar warming in early morning and late afternoon (Grant and Dunham 1988). We modeled these effects by transforming the times of local sunrise (when the sun cleared the peaks) and local sunset into solar elevation angles at which direct beam sunshine could reach the site. When the solar elevation angle was too small to clear the peaks (and the solar azimuth was in the direction of the peaks), we set direct-beam solar radiation to zero, and used only diffuse solar radiation.

Grant and Dunham (1988, 1990) described four microhabitat types based on the complex topography of the rocky habitat inhabited by canyon lizards. The microhabitat types differ primarily in the exposure of both the lizard and its substrate to direct solar radiation and wind. Deep rock crevices are also used as nighttime, thermal, and antipredator refugia by the lizards and temperatures in those crevices have also been measured (Dunham, unpublished data). Operative temperatures (Bakken and Gates 1975) measured in each microhabitat (Grant and Dunham 1988) fell within the range of temperatures predicted for the microhabitats. Temperatures for a two-week period in late April and early May for each site and microhabitat simulated for ten years are shown in Fig. 34.

Prey densities at each site have been measured by a variety of techniques (Dunham 1978, 1980, unpublished data). Prey densities vary among sites (Table 10), with rainfall within and between seasons, and with temperature over the course of a day (Dunham 1978, 1980). Diel variation in prey densities as temperature varies closely parallel thermal variation in lizard activity. Feeding strikes by canyon lizards increase with prey densities, but at higher densities the increase in strike rate with increased densities falls off considerably. We estimated resource availability as prey density and alternatively as strike rate.

Physiological characteristics

We were interested in body temperatures, activity, metabolic costs, and food intake to predict (1) avoidance of lethal temperatures and (2) accumulation of energy for growth and reproduction. Canyon-lizard body temperatures are consistent with simultaneous operative temperatures in the same microhabitat (Grant and Dunham 1988, 1990). Thus, animals were considered active in a microhabitat when simulated operative temperatures in the microhabitat were within the selected thermal tolerances of the lizards; otherwise lizards could not be active in that microhabitat. When conditions in none of the microhabitats were favorable for activity, the animal was assumed to retreat to a refugium in a rocky crevice. Voluntary thermal tolerances were estimated in two ways. First, as in previous models, we used limits presented by Grant and Dunham (1988) corresponding to an overall 90% confidence interval for all measured active body temperatures (approximately 32.2 ± 3.3ºC). Grant and Dunham (1990), however, showed that animals at the lower-elevation sites (Boquillas and Grapevine Hills) use substantially higher body temperatures in the afternoon, presumably to extend activity periods. As an alternative model, we allowed the animals at Boquillas and Grapevine Hills to use those higher body temperatures.

Metabolic rates were modeled using rates measured on canyon lizards (Beaupre, Dunham and Overall 1993b) treating the lowest-measured daytime metabolic rates as resting metabolism and assuming that active animals would have metabolic rates 2.2 times resting rates (Nagy 2005).

Food intake was treated as proportional either to prey density or to strike rates (Dunham 1980). Because individuals animals are not followed in this model and gut capacities and contents are not included, we could not incorporate thermal limits on digestion and energy assimilation into estimates of energy accumulation, but did estimate time available in each simulated day for digestive processing. We assumed that digestive processing ceased at body temperatures below 29.5ºC because digestion declines precipitously at 30ºC and canyon lizards at Big Bend do not eat when held at temperatures below 30ºC (Beaupre, Dunham, and Overall 1993a, Beaupre and Dunham 1995, Dunham, unpublished data).

Results - Activity and energy

Using the data-based environmental and physiological parameters listed above we simulated canyon-lizard body temperatures, activity, and energy accumulation over ten years and averaged values for two-week periods throughout the year for each site. Predicted patterns of activity, energy intake, metabolic costs, and net energy accumulation for mid-March through October are presented in Figure 35 for lizards at the low-elevation site (Boquillas). Important patterns include maximum activity rates, intakes, and net energy accumulation in the morning before temperatures get uncomfortably warm, shifts in activity and energy rates around 15:00 h when the sun is obscured by peaks to the west, peaks in metabolic rate in the early afternoon when the animals allow temperatures to drift up (presumably to maintain activity), marginal (but slightly positive) net energy balance in afternoon during the heat of the summer, and slight seasonal changes in available activity and energy accumulation (Fig. 35). As discussed above, we examined two important changes in assumptions from earlier models. First, we incorporated the empirical tendency for animals at the middle and low elevations to use higher body temperatures in the afternoon when operative temperatures would otherwise preclude activity (Grant and Dunham 1990). Second, we modeled intake rates as being proportional to measured feeding rates rather than to density of invertebrate prey (Dunham 1980). Predicted net-energy accumulation depended strongly on these two sets of assumptions (Fig. 36). Estimating intake rates from feeding strikes rather than from prey density had little effect on predicted intakes (and net energy) at the middle and low elevations where prey densities were lower and both density and feeding strikes varied proportionately. At the high elevation (Maple Canyon), however, prey densities increased to over twice the densities at Grapevine Hills, but feeding strikes increased by only 10% from Grapevine Hills to Maple Canyon. Energy intakes estimated using prey densities at Maple Canyon substantially exceeded those at the lower elevations, but those estimated using feeding strikes were more comparable (Fig. 36) consistent both with anecdotal data and measured growth rates (Table 10).

Assuming that lizards at the low elevation site used relatively warm microhabitats (leading to warmer body temperatures) had a very slight effect on predicted net energy accumulation (Boquillas, Fig. 36). The high metabolic rate due to the high body temperatures (Fig. 33) nearly balanced the extended foraging intakes, leading to a marginally positive energy balance in the afternoon (Fig. 35). At Grapevine Hills, where temperatures are slightly lower, the extended activities and higher temperatures increased the net energy accumulation by 10-20% during the summer (Fig. 36) and raised annual, predicted gains in energy at Grapevine Hills above those recorded at Maple Canyon.

Digestive processing of ingested prey was not included in this model because that would require thoroughly individually based models and a gut model that we cannot yet adequately parameterize. However, we used the availability of temperatures consistent with digestion to probe possible prey-processing limitations at all three sites (Fig. 37). As noted above, we assumed that whenever the animal could achieve a body temperature above 29.5ºC, it could digest prey (Beaupre, Dunham, and Overall 1993a). Under this assumption, it appears likely that digestive constraints would vary between the three sites. At Boquillas, refugium temperatures in summer reached the lower end of the permissive range and significantly extended predicted time for digestion (Fig. 37). Conversely, the lower temperatures at Maple Canyon in the summer allowed only about 2/3 of the processing time predicted at Grapevine Hills (Fig. 37). Without a gut model, we cannot yet address the importance of this possible processing limitation, but it suggests that energy availability at Maple Canyon may be limited compared to that at Grapevine Hills, thereby limiting growth at Maple Canyon.

Caveats and limitations

The model presented here matches ecological and life history patterns in canyon lizards more closely than any previous model (Dunham and Overall 1994). As we suggested above, however, an important characteristic of physiological models meant to be used in conservation is the ability to identify critical assumptions and missing data. Figure 36 suggests that the predictions of the model are sensitive both to the body temperatures of the lizards and to estimated prey-intake rates. Although the intake rates used here are based on relatively extensive data (Dunham 1978, 1980, Ruby and Dunham 1987), annual, seasonal, and rainfall-based variation in both prey density and feeding rates are not included in the model and could substantially complicate the predictions of the model. Likewise, Figure 37 suggests that digestive performance, particularly at high elevations, may complicate estimates of energy accumulation. Finally, we assume that energy accumulation is the key fitness correlate to be measured, excluding other resources (e.g., water) and biotic interactions such as predation. A variety of published and unpublished data suggest that neither of these factors are the key to canyon-lizard ecology under most conditions, but these factors will almost certainly play some role, perhaps especially in drought situations.

FROGS: DESICCATION AND ACTIVITY

We now shift focus from a system where substantial, species-specific information is available and the purpose of the model is to integrate that information into usable predictions to a system in which much less information is currently available and the purpose of the model is to explore a much smaller part of the conceptual model in Figure 31. Nonetheless, the approach remains the same. We focus on activity and resource budgets, how the environment can constrain those budgets, and how a mechanistic synthesis of the available information and the animal's biology can allow us to make potentially useful predictions with some idea of the limits of those predictions.

Amphibians are among the most threatened of vertebrate groups and habitat loss/modification and climatic effects are among the most important threats to amphibians (Bylmer and McGinnis 1977, Bury 1983, Dodd and Smith 2003, Stuart et al. 2004). The moist skins of most amphibians and the attendant cutaneous evaporative water losses make water a major environmental and physiological concern for amphibians and hydric physiology has long been recognized as a key controller of habitat use in amphibians (Thorson and Svihla 1943, Lillywhite 1970, Pough and Wilson 1970, Spotila 1972, Tracy 1975, Preest and Pough 1989, 2003).

Here we focus on a particular aspect of the water-ecology relationship that is of conservation interest in a system currently under study. Forest-dwelling amphibians are subject to habitat modification due to logging and forestry-management techniques including clear-cutting. Semlitsch and colleagues are investigating how various forest-management techniques alter habitat use and population dynamics of amphibians, including in particular wood frogs (*Rana sylvatica*), subjected to various forest-management techniques (Raymond and Hardy 1991, Rothermel and Semlitsch. 2002, Rittenhouse et al. 2004, Daszak et al. 2005, Rothermel and Luhring 2005). Salient features of wood-frog ecology at a Missouri study site include: (1) sequential use of different habitats over the course of a year (breeding ponds in late winter, fossorial habitats while migrating away from the ponds in the spring and summer refugia, (2) use of leaf-litter refugia for most of the time as they migrate away from the breeding ponds, emerging to move primarily during and immediately after rains, and (3) vulnerability to desiccation and mortality during droughts (Semlitsch and Rittenhouse, personal communication). Because forestry-management techniques can change the hydric conditions of the forest floor and hence affect wood frogs, it becomes important to understand to what extent frogs can resist desiccation behaviorally and under what conditions they will face injurious or lethal dehydration.

Water exchanges

Evaporative exchanges of water between an amphibian and its environment are simultaneously both simple and complex, and depend critically both on the environment and the activity of the animal (Heatwole, et al. 1969). For most ranid frogs, the resistance to water transfer across the skin is small in comparison to resistances to transfer from the surface of the skin to the environment; hence the rates of evaporative water loss are determined primarily by diffusion and convection (Lillywhite 2006). Unfortunately convective exchanges themselves can be difficult to describe unless the animal is in a low-speed, laminar flow of air without variations in wind speed, air temperature, and humidity. Environmental surfaces (e.g., the ground), refugia, and vegetation can all affect rates of convective heat and mass transfer (O’Connor 1989, Schwartzkopf and Alford 1996). In addition, evaporation cools the frog’s surface, altering evaporation and buffering the animal’s body temperature (Tracy 1976, Spotila, O’Connor and Bakken 1992). Nonetheless, for animals active on the surface, evaporation can be estimated via standard biophysical techniques (Tracy 1976) if one knows the mass of the animal, the wind speed at the animal’s height, and the environmental temperatures and humidities.

For an animal buried in leaf litter, however, we are aware of no models that predict evaporative rates. The litter creates a layer of still air around the animal, impedes diffusion by lengthening the diffusive path length and limiting the cross sectional area through which diffusion can take place, and can absorb or contribute water vapor to the diffusing stream. We constructed a simple model of diffusion through leaf litter that treats the leaves as inert (no absorption or contribution of water vapor), interdigitated baffles (Fig. 38). Water vapor is assumed to diffuse via passive diffusion without convection along a path shown by the dotted line in Figure 38, with a cross-sectional area that depends on the total number of layers of leaves and the density with which the leaves are packed (given by the total thickness of the litter layer). We used Fick’s first law of diffusion to describe the transfer rate.

Habitat description

We used temperatures, wind speeds, humidities, and rainfall from 2003 though

2005 for several locations near the Missouri study site used by Semlitsch et al. During April, when wood frogs are typically migrating from the breeding ponds toward their summer refugia, typical air temperatures were approximately 20ºC, and water vapor densities ranged from 0.0025-0.01 kg/m^3, with wind speeds typically 1-2 m/s at 1-2 m above the ground. For small frogs on the ground in a forest, sitting on leaf litter, we assumed that wind speeds at animal height ranged from negligible to approximately 0.2 m/s.

Precipitation could be rather local at five weather-station locations near the study site with rain falling at one location but missing others. We focused on the interval at each site between rainfall events with a minimum of either 5 or 10 mm of rain (sufficient to wet the forest floor and recharge the litter with water) (Fig. 39).

Time scales for activity imposed by water exchanges

For over 60 years now, it has been clear that frogs vary in their tolerance of dehydration and that dehydration tolerance plays a role in the terrestrial activity of frogs (Thorson and Svihla 1943), the idea being that a terrestrially active frog will inevitably lose water, and that tolerance of more severe dehydration could relax limits on times that frogs could be active. In this sense, the combination of water-loss rates and the minimum tolerated hydration level impose a limit on the time that animals can be active and away from a water source (sometimes called a release time, Tracy 1976, Schwarzkopf and Alford 1996). Dehydration tolerance is usually specified as the fraction of the original, fully hydrated mass that can be lost as water, or conversely the fraction of the fully hydrated mass at which the animal becomes impaired (by any of several criteria). Here we choose 80% of fully hydrated mass (20% of mass lost as water) as the minimum hydration level tolerated by wood frogs because at that level, wood frogs start showing impaired locomotion (O'Connor 1989).

Using this 'critical' hydration level for a 15-g wood frog in typical April conditions, we calculated rates of evaporation and release times for animals active on the surface with a variety of wind speeds and water vapor densities. We also calculated exchanges for animals buried in leaf litter with several assumptions about leaf litter thickness and structure (Table 11). For animals active on the surface, unless wind speeds are very low (still room air often has an air speed of 0.1 m/s) or the air is nearly saturated (vapor density = 0.015 kg/m^3), surface activity will be limited to 90 min or less. On the other hand, when the air is nearly saturated (e.g., when it is raining or has rained in the last hour or so), activity can extend to 4-6 h. Adding solar radiation would significantly shorten the frog's release time, but wood frogs are not typically active in bright sun so we did not simulate those conditions.

Our model suggests that leaf litter provides a significant resistance to evaporation and that, depending on assumptions about the thickness and structure of the leaf litter, it can extend release times for inactive animals to several weeks (Table 11). Assuming that frogs rehydrate with significant rains and use leaf litter refugia between rainstorms to delay dehydration, we calculated the distribution of dehydrations that would be reached before the next rainstorm under one of the scenarios from Table 11 (4 leaf layers, overlap 0.005 m, vapor density 0.005 kg.m^3, Fig. 40). In this case, 15 of 92 intervals would have resulted in minimum hydration levels of 75% or less and 2 of 92 intervals could reach hydrations less than 55% of fully hydrated mass. These simulations suggest that animals faced a significant risk of lethal dehydration despite using leaf litter refugia. These simulations were for rainfall in 2005 which included extended spring droughts for much of the region. The simulations suggest that frogs face two kinds of dehydration risks. The frogs can be active on the surface for only a few hours except in rainstorms (Heatwole 1961). In between rains, the frogs could use refugia, but if extended dry periods occur, they could still dehydrate.

Caveats and limitations

In this case, less information is available than was the case for canyon lizards, and the purpose, rather than precise prediction, is analysis of the risks frogs face. Treating leaves like inert diffusion baffles is a simplifying assumption, and further work is necessary to justify that assumption. Further, the leaf-litter parameters in a large set of simulations (not presented) were used to bracket possible environmental values because actual values for the litter frequented by the frogs are lacking and likely vary in space and time. At this point, perhaps the most important conclusion is the suggestion that frogs must balance two types of dehydration risk, with the balance depending on frog activity, climate and the characteristics of the leaf-litter refugia.

PHYSIOLOGICAL MODELS AS TOOLS

There would be little reason to build, use, or analyze models if empirical data were already available for the hypotheses in which we were interested. Indeed, classical justifications for modeling include the ability to analyze hypotheses that would be impossible, difficult, or impractical to examine empirically, the opportunity to isolate particular factors from confounding variables that are unavoidable in nature, and the ability to strip a complicated system down to its essential features (Levins 1968, Gotelli 1995, Keener and Sneyd 1998, Thieme 2003, Grimm and Railsback 2005). If one needs to explore the effects of conditions that do not yet exist (e.g., the effects of a 5ºC increase in mean air temperatures due to global warming), those abilities are clearly valuable. Alternatively, if one needs to consider processes that extend through numerous years, models can also be helpful. An impressive literature debates the utility of models; we do not propose to reproduce that debate here. We find models useful, and seek to describe how we find them helpful ifor linking physiology to ecology and conservation.

Advantages of models

We argue, however, that the fundamental value of models as tools to connect physiology to ecology and conservation is the ability to reveal assumptions that underlie hypotheses, explore the sensitivities of systems to perturbations and features of the biology, and map complex relationships among variables. Since Descartes, the importance and necessity of assumptions underlying our ideas has been relatively clear. In complex ecological systems, however, unrecognized assumptions can be important and have been at the center of major controversies, e.g., the role of competition in structuring communities (Connell 1983) and the role of optimality in behavior and physiology (Pyke 1984, Weibel *et al*. 1998). In our model of canyon lizard dynamics, two simple (and plausible) assumptions can affect the predicted outcomes of the model, and have affected previous models. First, the assumption that animals at different elevations would tolerate and experience similar body temperatures can strongly affect predicted energy intakes, metabolic costs, and net energy accumulation (Fig. 36). The ability of animals at the warmer, lower elevation sites to tolerate and use higher afternoon body temperatures extended activity times, increased predicted energy intakes, metabolic costs, and net energy accumulation—weakly at Boquillas and more strongly at Grapevine Hills (Fig.

36)—and led to qualitatively different predictions about relative energy accumulation at Grapevine Hills and Maple Canyon (Fig. 36 c, d). The virtue of the modeling process is that it both makes an assumption explicit and allows exploration of the importance of that assumption. Similarly, the assumption that energy intakes are dictated primarily by the availability of food and not by the digestive processing of ingested food could further influence predicted resource accumulation at the Grapevine Hills and Maple Canyon sites (Fig. 37). In building models connecting physiology to population level phenomena, our experience has been that assumptions often involve areas in which potential polymorphisms or adaptations on the part of the animal can affect the animal's population biology, as is the case for both of the assumptions discussed here. Hence, the role of modeling in identifying, dissecting, and evaluating such assumptions is a potentially important contribution to the conservation of the animal.

A sensitivity analysis asks how model outputs vary with changes in model inputs (Caswell 2001, Grimm and Railsback 2005). Mathematically, a sensitivity analysis estimates the derivative of a model's output with regard to some input. Biologically, sensitivity analyses reveal which inputs strongly affect system behavior, and under what circumstances they do so. Here, Figures 36 and 37 and Table 11 present the results of sensitivity analyses. We believe that such sensitivity analyses are critical in linking physiological effects to ecology and conservation.

We argue that the most important obstacle to understanding the mechanisms linking physiology to population ecology is the complexity of the mechanistic linkages. Specifically, we argue that many of the physiological processes affecting animal autecology will be characterized by non-linearities, (e.g., threshold effects, saturable processes, curvilinear relationships among variables, and time lags in processes) and by competitive and synergistic effects between factors (Dreisig 1984). Further, multiple abiotic factors and physiological systems are likely to affect an animal's ecology interactively without a single dominating factor (Porter and Tracy 1983). For instance, desert reptiles must "balance" highly interrelated budgets for thermal energy (thermoregulation), water, chemical energy, and activity (Dunham *et al*. 1989) (Fig. 31). Each of the budgets depends on the others in complicated ways (Nagy *et al*. 1984, Adolf and Porter 1993, Dunham and Beaupre 1998).

To illustrate the complexity of such interdependences, we present sensitivity analyses (Fig. 41) from a predecessor to the canyon-lizard model presented above. In this model, we envisioned a desert-dwelling reptile that needed to avoid lethal temperatures and acquire both water and energy needed for growth and reproduction. Figure 41 presents the sensitivity of a single predicted response variable (available activity time) to changes in the environment (minimum and maximum daily air temperature, burrow [refugium] temperature, and density and caloric and water content of food) and in the animal's physiology (maximum tolerated body temperature, metabolic rate, and cutaneous water-vapor conductivity). Figures 41A and 41B present estimates of activity time as each of the input variables is changed in a stepwise manner from baseline values. In some cases, predicted activity time is not sensitive to the input variable (e.g., minimum daily air temperature, 'Tmin'; caloric content of food, 'Endens'). In other cases, predicted activity time is linearly related to the input (burrow temperature, 'Tburr'). In yet other cases, however, threshold effects (food density, 'fddens'; metabolic rate, 'Mrbase') and sigmoid responses (maximum tolerated body temperature, 'Tblim') are seen. In Figure

41C, we find the simulated activity time for a series of randomly chosen combinations of input parameters, and for the response predicted by adding together the one-at-a-time effects presented in Figures 41A and 41B. Although the two measures are correlated, the one-at-a-time predictions are poor predictors of the simulated activity time, in part because of the non-linearities in Figures 41A and 41B, and in part, because of interactions among the input parameter effects.

Such non-linear, multi-causal relationships are difficult to study and document, and are poorly probed by analytic techniques that consider one factor at a time and/or depend on linear relationships among variables (Dunham and Beaupre 1998). One of the fundamental problems of employing such techniques to probe the relationship between physiological and population data is that the non-linearity of effects and the interaction of multiple processes can produce patterns that are plausible and understandable once discovered, but are non-intuitive and difficult to predict *a priori* (e.g., Dunham *et al*. 1989). Thus, complicated non-linear ecological systems are likely to result in patterns that are difficult to anticipate from the physiological processes alone (Kauffman 1993, Williams 1997).

Given the short time frame sometimes available in conservation assessments, the rapidity with which models can be developed, and the independence of model development from the seasonal and annual activity cycles that affect most organisms in the field is worth noting. Each of the models presented here was developed in under a year.

Disadvantages of models

We find two major disadvantages of models linking physiology to conservation questions. First, if model results are sensitive to input parameters or sets of parameters, then poor estimates of the parameters will lead to poor predictions. This is the equivalent of the old programming aphorism, 'garbage in, garbage out'. The problem, for complicated models that depend on data-based parameter estimates for an animal under consideration (e.g., the canyon-lizard model), is that we may not have data on the physiological or environmental characteristics for the population in which we are interested. We then tend to substitute data from nearby locations or similar species (e.g., the weather data from towns near the wood-frog study sites above). While this is defensible and in many cases necessary, in so doing, we adopt the implicit assumption that the nearby population does not differ from the focal population. For example, previous models (Dunham, unpublished data) of canyon-lizard dynamics used afternoon body temperatures drawn from the morning temperatures of the animals. For the highest elevation, Maple Canyon, this agrees with data (Grant and Dunham 1990). For the other sites, the data differ, and Figure 36 suggests that this would affect predicted energy accumulation.

A second danger results if one forgets that a model is only a model and that all models are deliberate simplifications of complex systems. Simplifying assumptions, like adopted data, can fail to accurately reflect the ecology of the animal in which we are interested. All ecological data, empirical or model-based, can be inappropriately applied, but as we noted above, applying models when their assumptions may not be satisfied has been the basis of numerous debates in ecology. Our preference is to make models as mechanistic as possible in the hopes that assumptions will be clear, and to treat all model predictions as hypotheses that are subject to empirical verification.

SUMMARY

We present resource accumulation models as a tool to link physiology to conservation questions. We give two very different examples - one in a well-described system in which numerous factors needed to be integrated to produce a useful population-level synthesis, another in a system with less available data where the object is explore a system with relatively simple questions. In each case, we used an elaboration of the Dunham, Grant, and Overall (1989) model that picks activity as a way to harvest resources useful in growth and reproduction and, hence, as a useful axis of analysis. We then seek the effects of physiological and environmental processes on activity and resource budgets. We suggest that such an approach is generalizable and easily adapted to situations where physiology may be a key factor in the population-level ecology and conservation of animals.

Table 9. Differences between applied and basic biology, listed as characteristics of more applied research.

–Questions are more immediate and urgent, with short timelines for answers

–Questions are inherently, thoroughly, and adamantly integrative, with numerous confounding variables

–Little utility for answers that are interesting, provocative, and revealing, but in their essential features, wrong or difficult to apply in novel situations

–Because of the above, approaches are systematized

–Complications from non-biological issues sometimes supercede biological considerations

Table 10. Habitat characteristics of *Sceloporus merriami* study sites.

	MC	**GVH**	**BOQ**
Elevation (m)	1609	1036	560
Precipitation			
Annual (cm)	43.6	33.7	24.1
May-Aug (cm)	26.5	18.6	13.5
July T_{ave} (ºC)	23.5	27.1	31.0
Veg. Cover (%)	32.8	23.2	15.1
Prey Density	0.290	0.137	0.086
Active Season (d)	173	203	232

MC = Maple Canyon; GVH = Grapevine Hills; BOQ = Boquillas

Table 11. Predicted evaporative water loss under leaf litter.

			EWL (g/h)				Time to dehydration (h)			
EWL Habitat										
Vapor Density (kg/m^3)			0.0025	0.005	0.01	0.015	0.0025	0.005	0.01	0.015
Relative Humidity (0 – 1)			0.145	0.289	0.579	0.868	0.145	0.289	0.579	0.868
		Wind (m/s)								
Open		0.01	1.137	0.945	0.560	0.175	2.64	3.18	5.36	17.14
Open		0.1	3.596	2.988	1.771	0.554	0.83	1.00	1.69	5.42
Open		0.2	5.086	4.225	2.504	0.783	0.59	0.71	1.20	3.83
Layers Overlap (m)										
Leaves	2	0.0025	0.0565	0.0469	0.0278		53.1	63.9	107.9	
Leaves	2	0.005	0.0282	0.0235	0.0139		106.2	127.9	215.8	
Leaves	2	0.01	0.0141	0.0117	0.0070		212.5	255.7	431.5	
Leaves	4	0.0025	0.0141	0.0117	0.0070		212.5	255.7	431.5	
Leaves	4	0.005	0.0071	0.0059	0.0035		425.0	511.5	863.1	
Leaves	4	0.01	0.0035	0.0029	0.0017		849.9	1023.0	1726.1	

Evaporative water loss rates and release times for a 15-g wood frog under 2 cm of leaf litter predicted using a model treating leaves as inert baffles deflecting diffusive flows

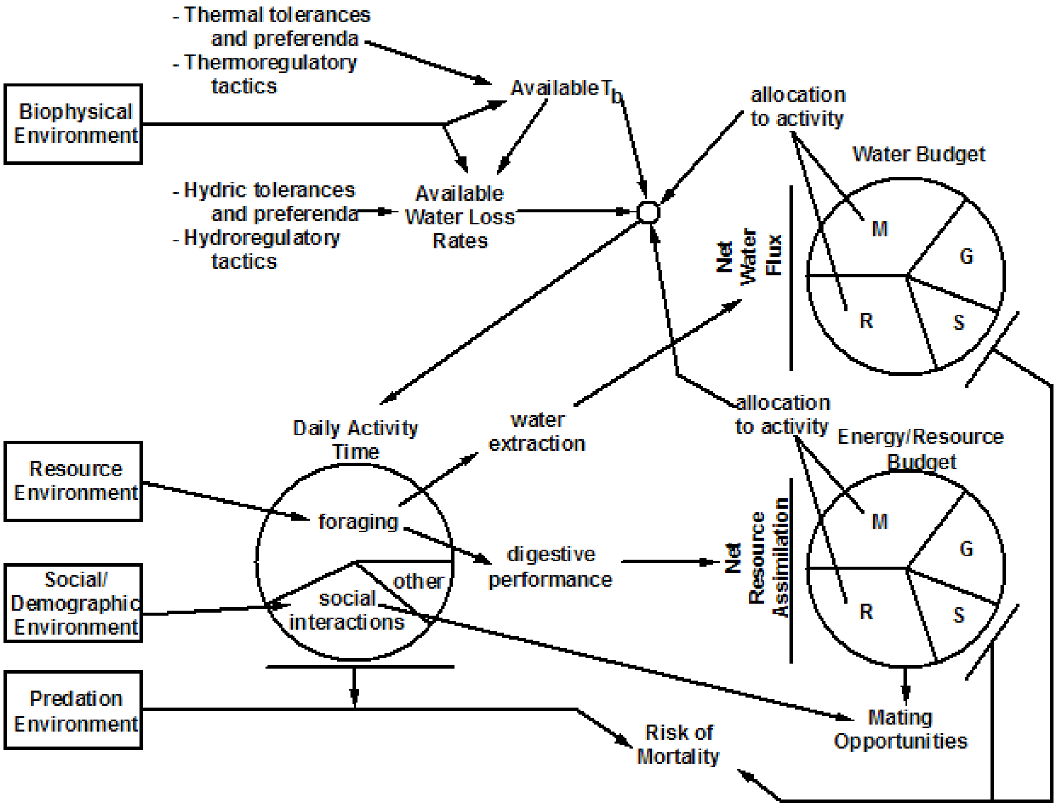


Figure 31. Conceptual model of physiological effects on population level processes via effects on activity and resource budgets. Elaborated from Dunham et al. (1989).

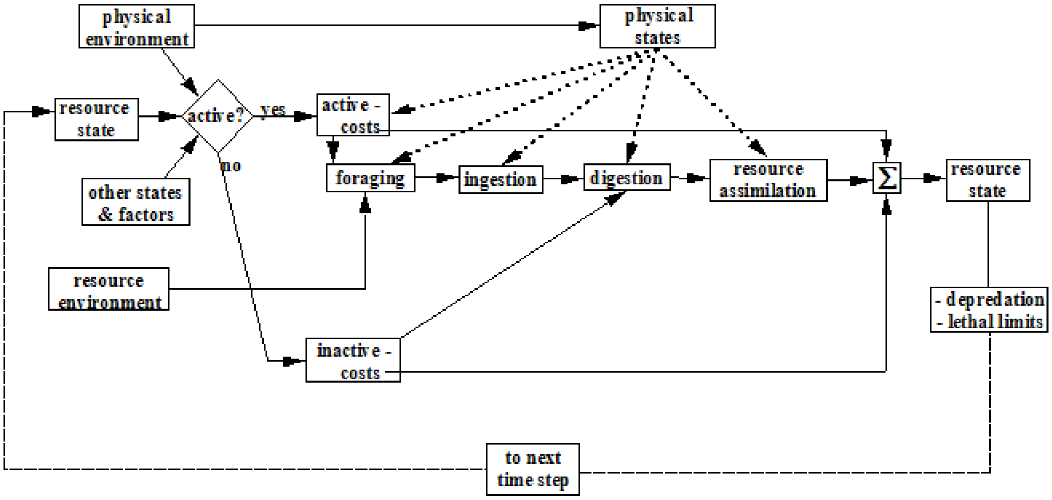


Figure 32. Flow diagram for a computational implementation of the conceptual model in Figure 31. Solid lines represent resource and control flows. Dashed lines represent influence of physical states (e.g., temperature, hydration) on physiological processes that handle and accumulate resources, see text for details.

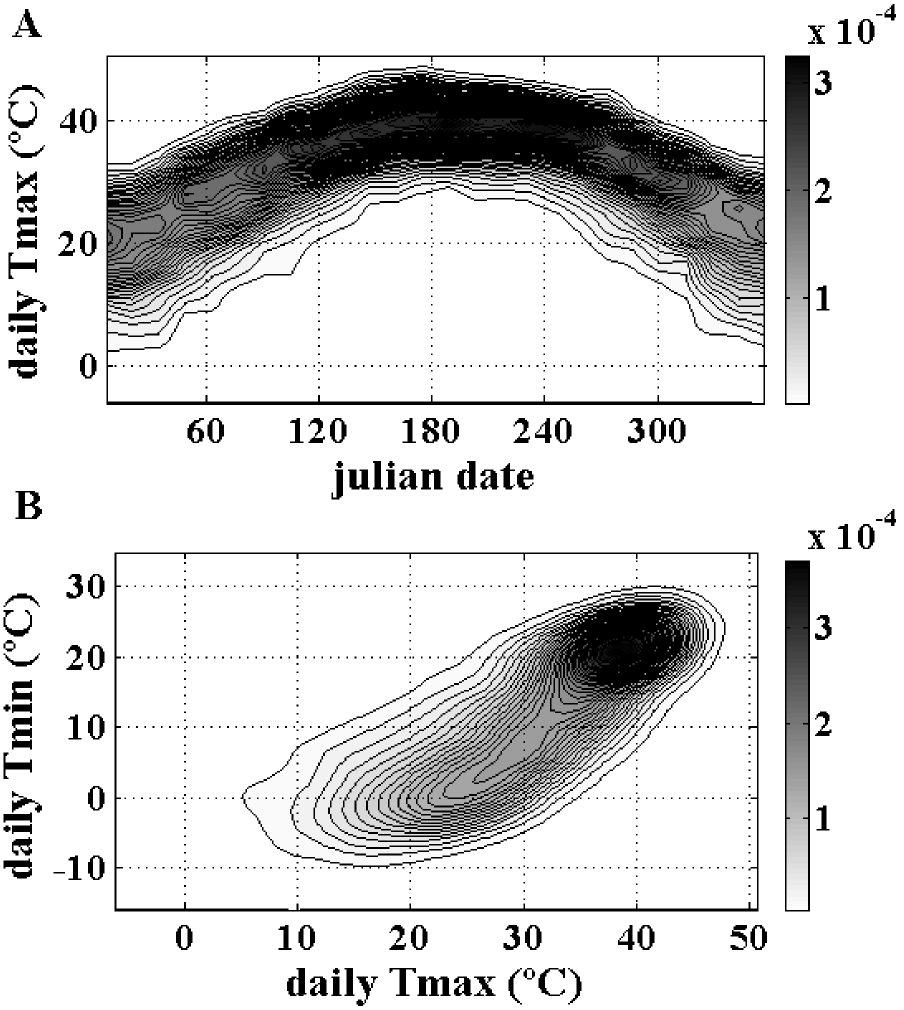


Figure 33. Probability distribution of daily temperatures at Boquillas Canyon, Big Bend National Park, Texas. The distribution describes the simultaneous distribution of maximum and minimum daily air temperatures versus season (Julian date). **33A)** Marginal distribution of daily temperature maxima over the course of the year. Minimum-temperature axis extends into the plane of the paper. **33B)** Marginal distribution of maximum and minimum daily air temperatures summed over all seasons. Julian date axis extends into the paper.

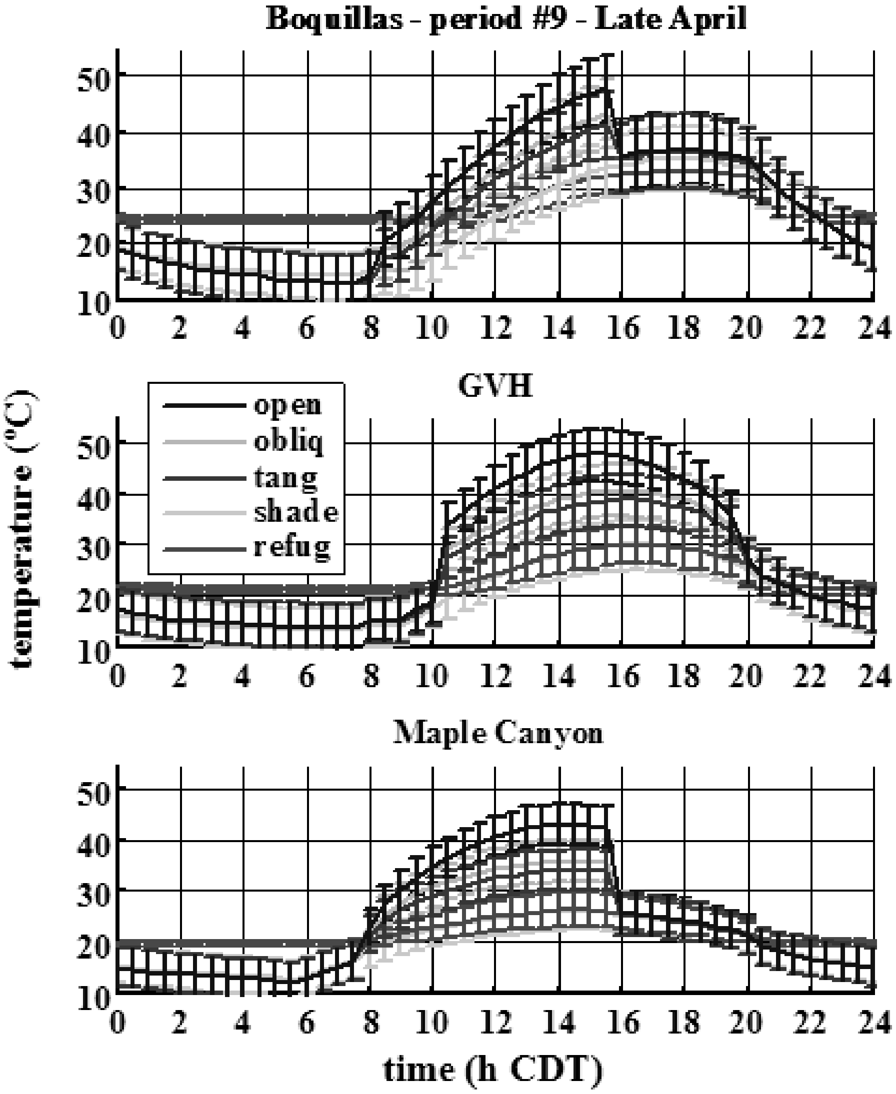


Figure 34. Operative temperatures (± 1 standard deviation) calculated for four surface microhabitats and a deep crevice refugium for each of the sites studied by Dunham and colleagues. Temperatures were simulated for each day in a 10-year span, then averaged for two-week periods. Temperatures shown are for the 9th two-week period (late April into May). Sudden changes in predicted temperatures are due to sun being obscured by (or appearing from behind) surrounding peaks.

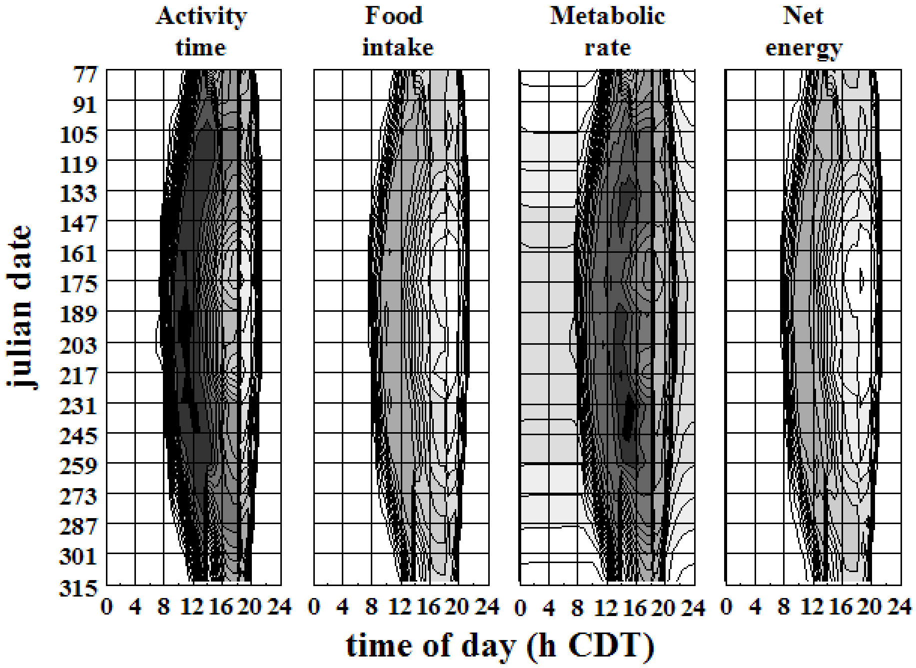


Figure 35. Contour plots of activity and energy transfers predicted for canyon lizards at the low-elevation site (Boquillas) versus time of year and time of day over the activity season. In each case darker shading corresponds to a higher probability of being active or higher energy intake or cost. Shading for activity represents the fraction of temperatures in simulations as in Figure 34, that allow the animal to be more active. Note sudden changes in the afternoon when the sun is obscured by a neighboring western peak.

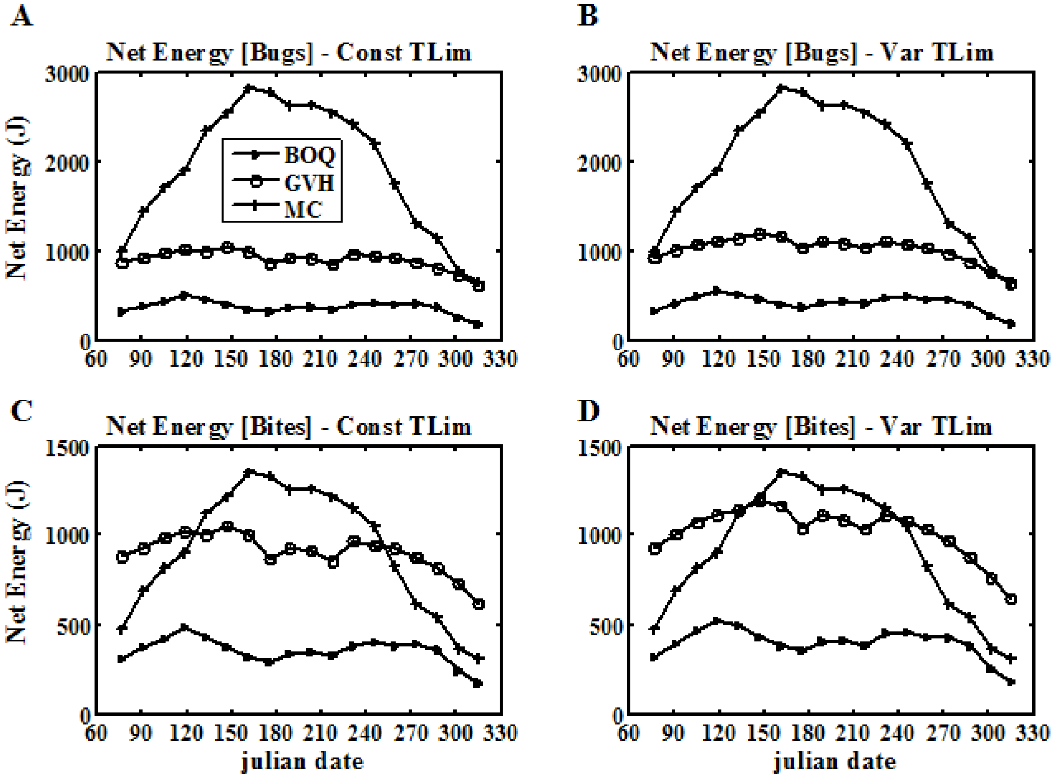


Figure 36. Estimated net energy accumulation for canyon lizards for entire days at each of three sites over the activity season. Intakes were estimated either from invertebrate prey densities (**36A** and **36B**) or from number of feeding strikes (predicted from temperature and prey density, **36C** and **36D**). Activity was calculated either using the same temperature limits for activity all day as in Grant and Dunham (1988), or using higher limits in the afternoon, as in Grant and Dunham (1990).

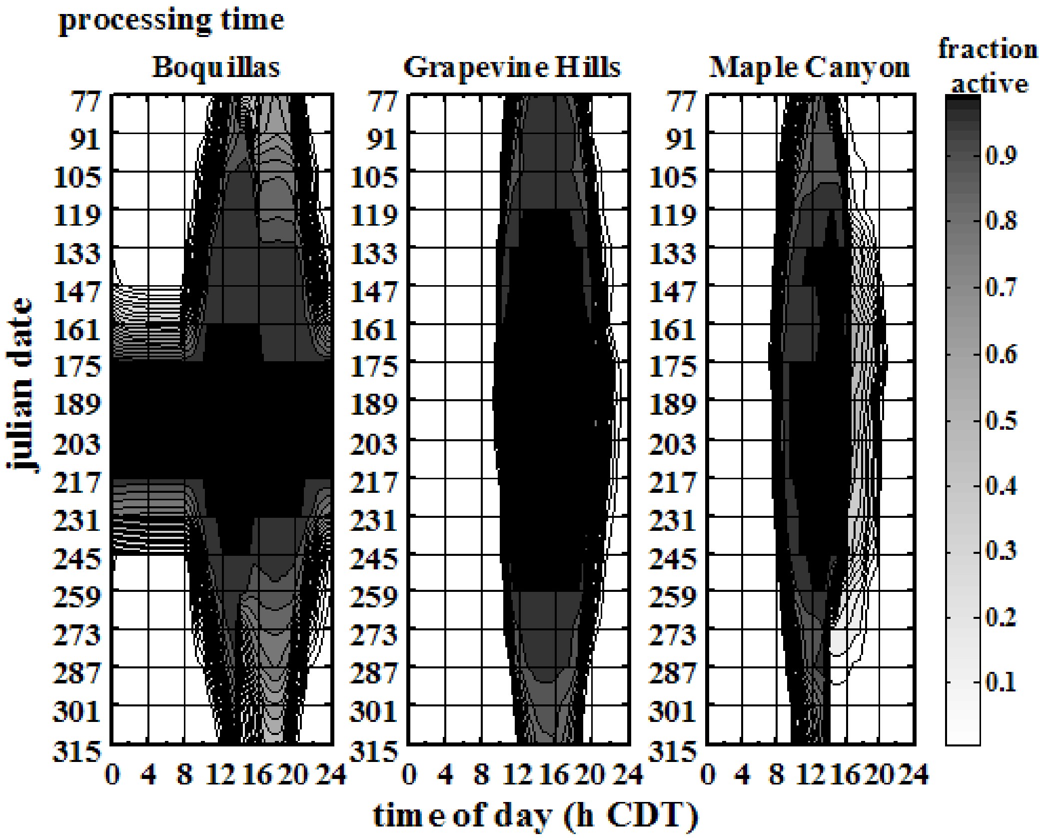


Figure 37. Possible limits on digestive processing in canyon lizards at each of three sites. Darker shading indicates a higher probability that operative temperatures exceeding 29.5°C are available, permitting digestion of prey.

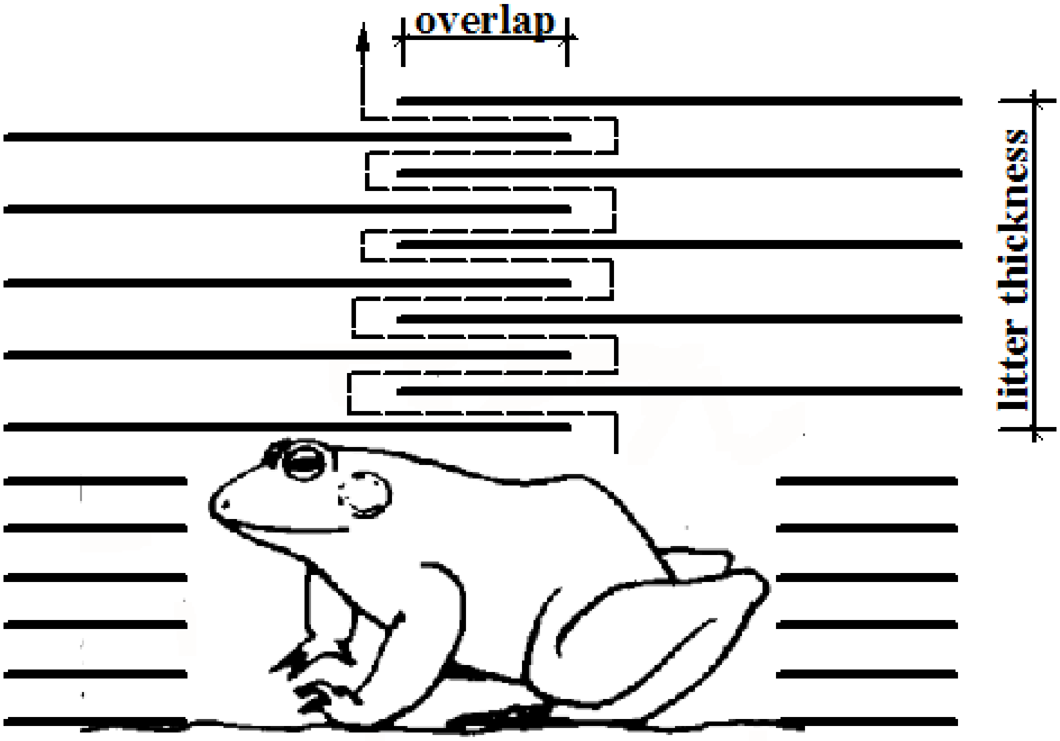


Figure 38. Geometry of model for evaporative water loss from frogs buried under leaf litter with leaves treated as diffusion baffles. Leaves are assumed to prevent any effective convection. Diffusion path length is controlled by number of leaf layers and distance by which leaves overlap. Cross-sectional area for diffusion is controlled by number of leaf layers and total thickness of litter.

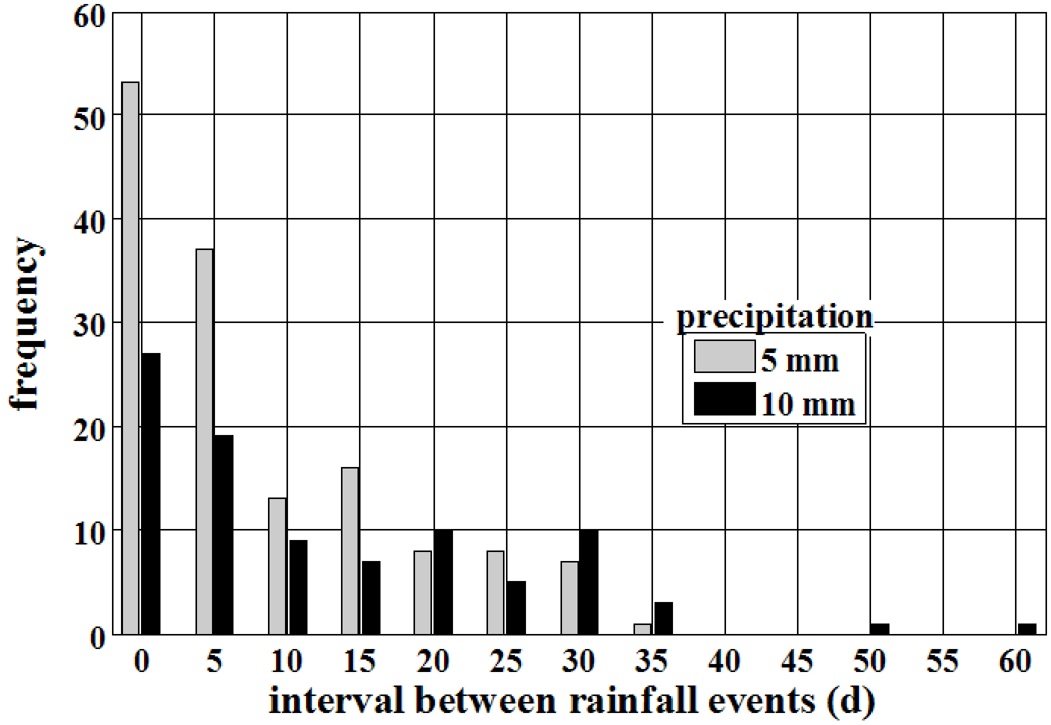


Figure 39. Intervals between rainfall events in 2005 at five sites near wood-frog study site in Missouri. We used two different rainfall amounts as minima needed to recharge the leaf litter with water.

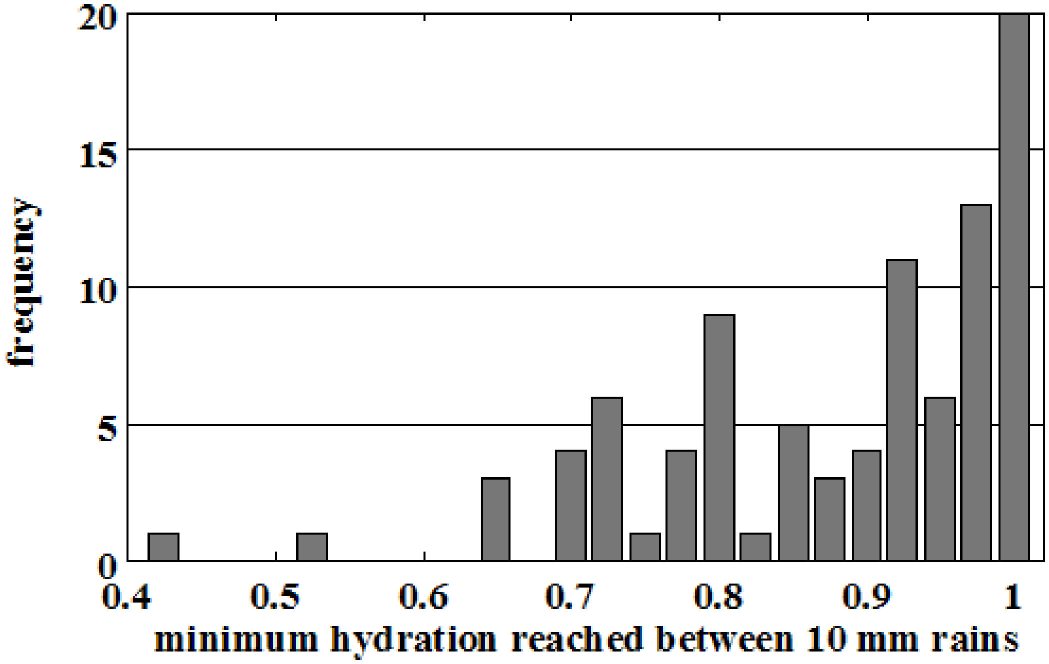


Figure 40. Minimum hydrations predicted for 15-g wood frogs in intervals between successive rain storms using evaporation model (Fig. 38) and intervals between rainfall events of 10 mm or greater (Fig. 39).

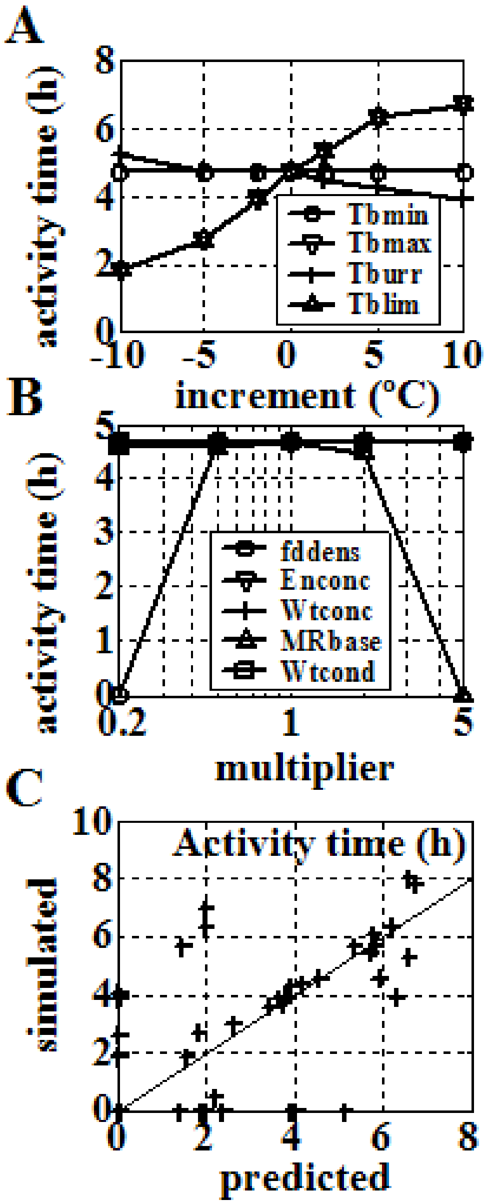


Figure 41. Sensitivity analysis using early, individual-based version of model for canyon lizards. Sensitivity of predicted activity times to changes in environmental or physiological temperatures (**41A**), and energy or water supplies (**41B**). **41C**. Correspondence of activity times simulated using model (vertical axis) to those predicted from sensitivities in **41A** and **41B**. Oblique line indicates perfect agreement.

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