Analyzing Time-Energy Constraints to Understand the Links between Environmental Change and Local Extinctions in Terrestrial Ectotherms

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Abstract: Accelerated extinction rates have prompted an increased focus on the interplay between environmental change and species response. The effects of environmental change on thermal opportunity are typically considered through a climate change context. However, habitat alteration can also have strong effects on the thermal environment. Additionally, habitat alteration is considered a leading factor of species extinction, yet few studies address the influence of habitat alteration on thermal opportunity and time-energy budgets in at-risk species. Here, we show the strong effects that habitat degradation can have on thermal opportunity, time-energy budgets, and life history demographics of local populations. In the Ozark Mountains of northern Arkansas, woody vegetation encroachment has resulted in a shift in life history traits that appears to play an important role in recent extirpations of eastern collared lizards (Crotaphytus collaris). Populations in degraded habitats experienced a decline in thermal opportunity and less time at body temperatures (time at \( T_b \)) suitable for digestion compared with those in intact habitats. We used our data to model the effect of reduced time at \( T_b \) on the net assimilated energy available for growth and reproduction. Our model predicts an \( \sim 46\% \) decline in the annual fecundity of individuals, which is similar to empirical observations of reproduction of \( C. \) collaris populations in degraded habitats (\( \sim 49\% \)). We conclude that \( C. \) collaris in degraded habitats experienced reduced growth and reproduction primarily as a result of constrained thermal opportunity leading to a decline in digestive processing rates. Our study applies an underappreciated approach to identify the biophysical and time-energy effects of habitat alteration.

Keywords: thermal opportunity, net assimilated energy, time-energy constraints, bioenergetic model, mass-energy budgets, conservation physiology.

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Introduction

In the midst of unprecedented extinction rates (Ceballos et al. 2015), the need for effective strategies to ameliorate the negative impacts of environmental change has become paramount to conservation biology. Conservation strategies often require information on cause and effect to successfully slow or reverse population declines and to predict future outcomes associated with environmental change (Carey 2005; Cooke et al. 2013). However, causal links between environmental change and population demographics are typically complex, making identification of leading variables elusive (Tracy et al. 2006; Cooke and O’Conner 2010). A powerful tool to address the effects of environmental change derives from the interactions among the thermal environment and time-energy budgets of organisms. Such interactions can be used to address questions associated with life histories and population vital rates (Dunham et al. 1989; Dunham and Overall 1994), thus establishing a mechanistic basis from which to understand the effects of environmental change on at-risk species (Wikelski and Cooke 2006). Habitat loss and degradation are leading factors resulting in biodiversity loss (Pardini et al. 2017; Horváth et al. 2019). Indeed, habitat alterations can have strong and immediate effects on the thermal environment (Murcia 1995; Tuff et al. 2016; Neel and McBrayer 2018). Studies addressing thermally induced changes in time-energy budgets of ectotherms typically focus on warming temperatures associated with climate change or across broad geographic scales of latitude or elevation gradients (Niewiarowski and Roosenburg 1993; Beaupre 1995a, 1995b; Bale et al. 2002; Hodkinson 2005; Buckley 2008; Sinervo et al. 2010). Far less appreciated are the effects of time-energy constraints as a consequence of habitat alteration on species persistence.
Population persistence is governed by the laws of thermodynamics, which determine organismal mass-energy requirements and conversion efficiencies of food to new biomass (e.g., growth, reproductive effort, and propagules). The total energy available for competing functions of maintenance, storage, growth, reproduction, and activity are dependent on net assimilated energy (NAE; Congdon et al. 1982). Thermodynamics determines climatological limits of species persistence (Porter and Gates 1969; Porter and Tracy 1983; Adolph and Porter 1993) and constrains the allocation of available time to competing behaviors (e.g., foraging, territory defense, mate cycling, inactivity, and thermoregulation) and mass-energy resources to competing functions (Congdon et al. 1982; Dunham et al. 1989). Changes in operational environments (e.g., thermal, hydric, resource, social, or predation environments; Dunham et al. 1989; Beaupre 2002) resulting from climate change or anthropogenic habitat disturbance can alter the dynamic interaction between environment and organism, which may result in significant population-level effects. Of greatest interest from a conservation perspective is when changes in habitat impose constraints on the life history (sensu Dunham et al. 1989). Congdon (1989) described four categories of proximate constraints on mass-energy budgets: “(1) absolute resource availability; (2) harvest rate limitations; (3) process rate limitations; and (4) limitation on harvest or processing resources imposed by risk of predation” (p. 356). Any of these constraints could arise from a change in habitat thermal or hydric properties and/or resource availability and thus ultimately affect the life history traits of individuals (Dunham et al. 1989). Comparative biophysical, bioenergetic, and demographic analysis can potentially differentiate among these possible constraints (fig. 1). An understanding of interactions among the physical resource environments, time-energy allocations and constraints, and life history traits represents a robust foundation for clarifying...
the mechanistic link between environmental change and extirpations.

Variation in the thermal environment can have a strong influence on the body temperatures ($T_b$) of ectotherms, which in turn affect rates of physiological processes such as metabolism, digestion, and evaporative water loss (Bennett and Dawson 1976; Huey 1982). Along with biotic features of the environment (e.g., predators, competitors), the spatial and temporal distribution of environmental temperatures determines how well an ectotherm can exploit the environment for effective thermoregulation (Huey and Slatkin 1976; Sears and Angilletta 2015) and the amount of time that can be spent at physiologically optimal $T_b$’s (thermal opportunity; Sinervo and Adolph 1994). A reduction in thermal opportunity can have a strong effect on energy acquisition and assimilation rates in ectotherms, thus affecting the NAE available for competing functions (Sinervo and Adolph 1994; Beaufre 1995b, 2002; Niewiarowski 2001; Sears 2005).

In terrestrial ectotherms, food intake rates are usually maximized at physiologically optimal $T_b$’s (Huey and Slatkin 1976; Porter and Tracy 1983). Similarly, ingestion rates typically increase allometrically with increased daily activity time as a result of filling of the gut and the processes of digestion, absorption, and excretion, which cause a physiological bottleneck by modulating gut space (Grant and Portar 1992; Adolph and Porter 1993). Therefore, at its optimal $T_b$, an animal foraging for twice as long would not enjoy twice the energy gain because refilling of the gut requires processing and passage of previously ingested food. Among lizards, efficient digestion and absorption may occur only over a relatively narrow range of temperatures (Huey and Stevenson 1979; Huey 1982; Angilletta 2001, 2006). Therefore, factors that restrict the time that an animal can maintain preferred $T_b$ (i.e., thermal opportunity) can reduce energy acquisition rates, energy assimilation rates, or both.

Eastern collared lizards (Crotaphytus collaris) in the Ozark Highlands are an ideal model system to investigate the interactions among habitat alteration, time-energy constraints, and extirpations in an at-risk species. First, Ozark glades (xeric limestone/dolomite prairies; Baskin and Baskin 2000) have been exposed to more than a century of anthropogenic fire suppression, resulting in extensive woody plant encroachment of these structurally open habitats (Neuwald and Templeton 2013). Second, C. collaris populations have declined considerably in recent years throughout the Ozarks ecoregion (Templeton et al. 2001; Grimsley 2012; Brewster 2019), prompting conservation listing in Arkansas and Missouri. Last, C. collaris populations in encroached glades have reduced age-specific growth and reproductive rates compared with populations in habitats with lower woody vegetation density (intact glades; Brewster et al. 2018). Annual fecundity of C. collaris in encroached glades was estimated to be ~50% lower than that in intact glades. Thus, the observed shifts in life history traits of C. collaris in encroached glades likely play an important role in extirpations of this species throughout the Ozarks.

Previous research in the Ozarks suggests that woody vegetation encroachment may reduce thermal opportunity in C. collaris, potentially resulting in time-energy constraints (Brewster 2019). Recent data suggest that digestive processing in C. collaris is strongly affected by temperature, with colder $T_b$’s resulting in substantial decrements in the rate of energy assimilation (Brewster et al. 2020). Thus, it is possible that reduced environmental heat loads available to C. collaris in habitats with greater woody vegetation density (encroached glades) ultimately result in reduced rates of energy assimilation (fig. 1).

Here, we seek to examine the mechanistic processes that link habitat structural alteration with local extirpation using data on C. collaris in the Ozark Mountains. We tested for differences in the biophysical environment (thermal environment) and the resource environment (prey availability) that could lead to time-energy constraints (Grant 1990) in C. collaris (fig. 1). We then examined population-level differences in time-energy budgets that could explain a decline in the NAE available for growth and reproduction (fig. 1), which likely represents a key factor leading to extirpations of this species in the Ozarks. Specifically, we compared individual movement rates, surface-active $T_b$’s, daily activity time, and meal frequency between populations in encroached and intact glades (fig. 1). We then combined data from our results with data on the thermal sensitivity of digestive performance in C. collaris (Brewster et al. 2020) and modeled the effect of time-energy constraints on the NAE available for growth and reproduction of individuals in intact and encroached habitats.

**Methods**

**Study Sites**

We sampled Crotaphytus collaris populations from six sites and designated each glade site as either intact, with low levels of woody vegetation density and shade cover ($n = 3$), or encroached, with high levels of woody vegetation density and shade cover ($n = 3$; for summary data describing glade types, see Brewster et al. 2018). All glade sites occurred within an 80-km radius along the White and Buffalo Rivers, in the Ozark–St. Francis National Forest in northen Arkansas. Sampling for most statistical comparisons (early May to mid-July) was done across the reproductive
season (vitellogenesis begins on emergence in late April to early May; copulations from early May to early July; oviposition from late May to mid-July) of *C. collaris* in northern Arkansas (Trauth 1978; Brewster et al. 2018).

**Biophysical Comparisons**

**Prey Availability.** If dense woody vegetation in encroached glades results in reduced prey availability, this could lead to time-energy constraints in *C. collaris* (fig. 1). We used linear observational transects to estimate arthropod densities per square meter sampled. All estimates included only numbers of arthropods within seven suborders known to represent 95% of *C. collaris* diet: Orthoptera, Coleoptera, Lepidoptera, Hymenoptera, Araneida, Hemiptera, and Diptera (McAllister 1985). Sampling was conducted by walking along ten 20-m transects per site and counting the number of arthropods observed from the ground to waist height and within 0.5 m on either side of the transect. Sampling was standardized by time of day (between 11:00 and 15:00), on sunny days, and only when *C. collaris* were active. We conducted linear transect sampling in May, June, and July (10 replicates/month/site) for three consecutive summers (2014–2016). Data analyses of prey densities between glade types were conducted using a mixed model (nlme package in R; Fox and Weisberg 2002), with glade type (intact vs. encroached) and month (May, June, or July) as fixed effects and glade site (six total sites repeatedly sampled) as random effects.

**Operative Environmental Temperature.** A reduction in thermal opportunity in encroached glades as a result of an increase in dense woody vegetation could also lead to time-energy constrains in *C. collaris* (fig. 1). We used two metrics to compare thermal environments between encroached and intact glades: (1) the percentage of operative environmental temperature (*T*<sub>3</sub>; Bakken 1992) within the range of voluntary active *T*<sub>n</sub>’s of *C. collaris* and (2) a thermal quality index (*d*<sub>c</sub>; Hertz et al. 1993). A recent study suggested that *C. collaris* uses postural adjustments as a means to behaviorally thermoregulate, and this behavior can have a major influence on the predicted available activity time and *d*<sub>c</sub> in this species (Brewster and Beaupre 2019). Thus, we used the same *T*<sub>3</sub> modeling procedures as Brewster and Beaupre (2019; OTM<sub>ideal</sub>) that accounts for postural adjustments by *C. collaris* to estimate *d*<sub>c</sub> and the frequency distribution of *T*<sub>3</sub> in this study. In brief, we used three different types of operative temperature models (OTMs) modified from a 12-cm length (2.5 cm diameter) of hollow copper pipe, painted to match the reflective properties of *C. collaris*: (1) a stilted OTM that mimics the biophysical properties of *C. collaris* in an elevated posture, (2) an unmodified OTM that mimics the biophysical properties of *C. collaris* in an intermediate posture, and (3) a compressed OTM that mimics the biophysical properties of *C. collaris* in a prostrate posture. All three OTM types were validated against live *C. collaris* individuals in the corresponding posture in the field (see fig. 48 in Brewster and Beaupre 2019). For each glade site, we used a total of 75 OTMs to estimate the *T*<sub>n</sub> distribution of 25 randomly selected microsites. At each microsite we placed three OTMs (one of each type; stilted, unmodified, or compressed) side by side, oriented in the same direction. We suspended a single iButton temperature data logger (Maxim Integrated Products) in the center of each OTM using a piece of aluminum screening and set the loggers to record temperature every 20 min (OTM time constant ~3.5 min). We logged thermal environment estimates simultaneously between one encroached and one intact glade for a minimum of 5 days and alternated among glade sites across the activity season. Each glade-to-glade comparison included three sunny days in May, June, and July (9 days total for each glade-glade comparison).

To compare thermal environments between encroached and intact glades we estimated the percentage of microhabitats (*n* = 25 for each site) within the voluntary active *T*<sub>n</sub> range (*T*<sub>ACT</sub>) of *C. collaris*. We used the central 99% of all *T*<sub>n</sub>’s recorded on surface-active *C. collaris* in our study populations to estimate *T*<sub>ACT</sub> (31.2°C–42.6°C). Using the posture-specific modeling procedure described above (OTM<sub>ideal</sub>; Brewster and Beaupre 2019), we estimated the percentage of microhabitats at a given time point within *T*<sub>ACT</sub>. Percentages were calculated every 20 min from 7:00 to 21:00, and comparisons were made across days (*n* = 3 per glade site) for May, June, and July (9 days total per glade site).

We also compared thermal environments by estimating the thermal quality index (*d*<sub>c</sub>) between glade types. The thermal quality index provides the average absolute deviation between *T*<sub>n</sub> and the set-point *T*<sub>s</sub> range (*T*<sub>SET</sub>; Hertz et al. 1993). We used the central 60% of all *T*<sub>n</sub>’s selected by *C. collaris* in a laboratory gradient (34.8°C–38.1°C; Firth et al. 1989) as our metric for *T*<sub>SET</sub> (Brewster and Beaupre 2019). Using OTM<sub>ideal</sub>, we estimated the average absolute deviation between *T*<sub>n</sub> and *T*<sub>SET</sub> at a given time point. Average absolute deviations were calculated every 20 min from 7:00 to 21:00, and comparisons were made across days (*n* = 3 per glade site) for May, June, and July (9 days total per glade site). We used a linear mixed model (nlme in R) to compare *d*<sub>c</sub> by glade type. We designated glade type and season as fixed effects and glade site (sampled repeatedly) as a random effect. We made no formal statistical comparisons of percentage of *T*<sub>n</sub> within *T*<sub>ACT</sub> between glade types. Instead, we use this comparison to more effectively visualize the thermal environment in each glade type.
Time-Energy Budget Comparisons

Movement Rates. If *C. collaris* in encroached glades have greater movement rates from increased thermoregulatory effort (i.e., shuttling among basking sites; Huey and Slatkin 1976; Withers and Campbell 1985; Basson et al. 2017), this could result in greater proportions of energy allocated to activity, leaving less energy available for growth and reproduction (fig. 1, b3; Brewster et al. 2013). To determine whether *C. collaris* in encroached glades allocate more energy to locomotion, we estimated movement rates of individuals. Because of time constraints (all field sampling in this study was conducted by one of the coauthors) we were able to estimate movement rates only on a subsample of individuals from one encroached and one intact glade. We opportunistically chose five males and three females from both glades to estimate movement rates. Subjects were observed through binoculars from a distance of 30–70 m (so as to not impact behavior), for 10-min time blocks, and only on days and at times when multiple individuals were surface active. All subjects had been previously captured within the past 1–4 days and had been temporarily marked on their dorsum with a white paint pen (i.e., a single letter) to allow visual identification of the individual by the observer. We sampled movement rates of individuals over a 10-day period in May 2015, with a total of five observations (50 min) per subject. We estimated the total distance moved (when animals moved greater than 10 m at a time, we used a laser range finder; Nikon model AL-11, estimated to the nearest 1 m) per 10-min time block. Data analysis of movement rates were conducted using mixed models (nlme package in R; Fox and Weisberg 2002). We designated glade type and sex as fixed effects and subject ID (individuals sampled repeatedly) as a random effect.

Surface-Active *T*a. If *C. collaris* in encroached glades experience reduced surface-active *T*a, this could suggest that individuals suffer reduced physiological performance, leading to reduced processing rates (fig. 1, b5; Huey 1982; Congdon 1989; Beaupre et al. 1993a; Brewster et al. 2020) and/or reduced harvesting rates (fig. 1, b3; Huey and Stevenson 1979; Avery et al. 1982; Smith and Ballinger 2001). To determine whether *C. collaris* in encroached glades experience lower *T*a’s during surface activity, we used *T*a data collected from 2013 to 2017. Animals were captured with a pole and lasso from late April through late July, and cloacal *T*a’s were recorded using a quick-read digital thermometer (model HH1800, Omega Engineering). We used *T*a data only from animals known to be surface active for a minimum of two thermal time constants (time for the temperature of an object to change by ~63% of the differential between the initial temperature and the ambient temperature; *C. collaris* time constant ~6.5 min; Grigg et al. 1979), to ensure they were near equilibrium *T*a and where *T*a was recorded within 2 min after capture. Comparisons of *T*a’s between glade types were made using a mixed model (nlme package in R; Fox and Weisberg 2002). We designated glade type, sex, and month as fixed effects and subject ID (individuals were sampled repeatedly and at variable time points) as a random effect.

Time Surface Active. If *C. collaris* in encroached glades spend less time surface active, this could leave them with less time at *T*a’s where digestion is optimal (Dunham et al. 1989), resulting in reduced processing rates (fig. 1, c3). Similarly, reduced activity time could leave less time available for foraging (Grant and Dunham 1988; Adolph and Porter 1993), resulting in reduced harvesting rates (fig. 1, c3). To compare total daily surface activity times between glade types, we made focal observations on *C. collaris* surface activity. A pilot study in 2014 suggested that surface activity (percentage of animals in the population on the surface) was stable (>50% of animals) during midday (11:00 to 21:00), assuming typical climatic conditions during the activity season. We estimated total activity hours per day by recording the onset of surface activity in the morning and the end of surface activity in the evening. We conducted observational transects on 10–20-min intervals starting at local sunrise until the onset of activity was observed and then conducted hourly observational transects through the midday. Within 2 h of local sunset, we again returned to 10–20-min intervals between observational transects until lizards were no longer observed to be surface active. Activity time estimates (total number of hours animals were observed surface active) were made on 3 days for each glade site, in May, June, and July (9 days total per glade site) in 2015–2016. Estimates were made only on days with typical climatic conditions for a given month. We used a mixed linear model (nlme package in R; Fox and Weisberg 2002) for statistical analyses of hours active between glade types. We designated glade type and month as fixed effects and glade site (repeatedly sampled) as a random effect.

Frequency of Recent Meal. If *C. collaris* in encroached glades spend more time with an empty stomach as a result of low absolute prey availability (fig. 1, d4) and/or reduced capture performance (fig. 1, b3), this could result in reduced harvesting rates (fig. 1, d4). To test for differences between glade types in the frequency of a recent meal, we used palpation data collected on *C. collaris* captured from 2013 to 2017. On capture, we physically palpated the abdomen of individuals to feel for the presence of a recent meal. In our experience, females in late gravidity (those with shelled oviductal eggs) typically had an empty stomach, suggesting that they
stopped foraging until after oviposition. Thus, we excluded females from our palpation data set if they contained large, soft follicles or oviductal eggs (reasonably distinct in shape and texture from food items). To analyze presence/absence data, we used a general linear mixed model (glmer in R; Bates et al. 2015), fit with the binomial (logit) function. We designated glade type and sex as fixed effects and subject ID (individuals sampled repeatedly) as a random effect.

**NAE Model**

We used the results from our statistical comparisons to model their effects on the NAE available for growth and reproduction of *C. collaris* in our study populations. The goal of the NAE model was to predict the annual NAE and the corresponding number of eggs produced by *C. collaris* female individuals in intact and encroached glades, given the specific conditions identified in our statistical comparisons (operational environments, *T* <sub>i</sub>’s, activity times, movement rates, and meal frequencies). Detailed methods and parameterization of the NAE model are provided in the section “Net Assimilated Energy (NAE) Model Parameterization” of the supplemental PDF, available online. In brief, the NAE model uses data on variation in time (hours active and inactive per day) and *T* <sub>i</sub>’s of individuals in encroached and intact glades to predict their effects (time at *T* <sub>i</sub>) on digestive processing rates. We used general principles provided by Congdon et al. (1982) to estimate the various components of *C. collaris* energy budgets, assuming that

\[
\text{NAE} = \text{ME} - \text{M},
\]

where NAE is net assimilated energy, ME is metabolizable energy (energy consumed minus energy lost in feces minus energy lost in uric acid; \( C = F - U \)), and M is metabolic maintenance cost (kJ/day for all).

To estimate *T* <sub>i</sub>’s of *C. collaris* during inactivity periods, we assumed that while inactive, the mean and variance in *T* <sub>i</sub>’s of animals would approximate the mean and variance of under-rock refugia (based on biophysical principles; Porter and Gates 1969). We calculated the hourly mean and variance of *n* = 7 deep crevice microsites used by *C. collaris* at each of the six glades during May, June, and July (see “Operative Environmental Temperature”). We wrapped a single iButton temperature data logger (Maxim Integrated Products) with aluminum foil and attached a length (~1.5 m) of surveyor marking tape to the unit. We used a 1-m dowel (2 cm diameter) to guide the iButton unit into the refugia (~15–30 cm deep), leaving the remaining length of surveyor tape on the surface for ease of retrieval. iButtons logged temperature at 20-min intervals over the same time periods as the surface *T* <sub>i</sub> estimates at a given site. Refugia sites were chosen opportunistically, on the basis of previous observations of individuals using these sites. We did not make any formal statistical analyses on refugia temperatures. Instead, we used estimates of refugia temperatures to provide a 24-h *T* <sub>b</sub> profile of *C. collaris* in our populations and to parameterize the NAE model. We did not deploy temperature loggers in April and August; thus, for these months our model used mean hourly operative temperatures for May and July, respectively. During activity time each month we assumed lizards effectively thermoregulated to their mean field body temperature for a given month. During inactivity, hourly lizard body temperature was taken as the average hourly refuge temperature. To parameterize the NAE model we combined temperature-specific digestive processing data from Brewster et al. (2020), lizard bioenergetic data in the literature, and estimates from our statistical comparisons in this study. We provide a glossary of acronyms, terms, equations, estimates, and citations used in the NAE model in table S1 (tables S1, S2 are available online).

We computed model estimates using a script written in R version 3.6.2 (R Core Team 2019). We obtained estimates of annual NAE and predicted egg production of 1-year-old (1YO; 15 g) and 2-year-old (2YO; 25 g) female *C. collaris* individuals from intact and encroached sites by iterating the model 1,000 times. Two primary variables were allowed to vary randomly within the bounded values for each model iteration: consumption on an empty stomach (*C<sub>GS</sub>*), and metabolic scope (*M<sub>SCOPE</sub>*). We chose to vary these two estimates because these variables were assumed to strongly influence our model predictions and because of the substantial observed variation (*C<sub>GS</sub>* and activity season length; Brewster 2019) or unknown variation (*M<sub>SCOPE</sub>* in *C. collaris* for these estimates. We conducted model sensitivity analyses by rerunning models each fixing these parameters at specific values and examining variation in model-predicted egg production and annual NAE (fig. S1; figs. S1, S2 are available online). In all analyses, assumptions of normality and homogeneity of slopes were met. Data underlying statistical comparisons have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.wpzgmsbnd; Brewster et al. 2021).

**Results**

**Biophysical Comparisons**

**Prey Availability and Environmental Temperature.** Arthropod densities were significantly greater in encroached than in intact glades (*n* = 398 sample transects; *F*<sub>1,8</sub> = 12.2, *P* = .018) and declined each month across the activity season (May–July; *F*<sub>3,87</sub> = 3.8, *P* < .001; fig. 2). The percentage of microsites within *T* <sub>ACTS</sub> increased each month (*n* = 27 daily comparisons) and were greater in intact glades...
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Figure 2: Arthropod densities (number observed per 20-m transect) observed in intact (black circles) and encroached (gray circles) glades. Shown are the mean and 95% confidence interval by month (May–July covers the reproductive season of eastern collared lizards [Crotaphytus collaris] in northern Arkansas). Arthropod densities include only arthropods within seven suborders known to represent 95% of the C. collaris diet (see “Methods”). P = .018.

(average daily mean = 47.31% ± 3.75% SE) than in encroached glades (28.15% ± 3.75% SE; fig. 3A–3C). Similarly, d, (thermal quality index) declined over the activity season (n = 27 daily comparisons; $F_{2,14} = 19.6, P < .0001$) and was significantly lower in intact sites (average daily mean = 4.43°C ± 0.51°C SE) than in encroached sites (6.51°C ± 0.51°C SE; $F_{2,14} = 24.9, P = .0075$; fig. 3D). We found no significant glade type × month interactions affecting prey availability or $d_\nu$.

Movement Rates and Surface-Active $T_\nu$. Total distances moved did not differ significantly between glade types (n = 102 observations; $F_{1,13} = 0.64, P = .436$) or sex ($F_{1,13} = 2.50, P = .138$). Males moved an average of 0.629 m/min in intact sites (SE = 0.182) and 0.471 m/min in encroached sites (SE = 0.189). Females moved an average of 0.367 m/min (SE = 0.089) in intact sites and an average of 0.209 m/min (SE = 0.102) in encroached sites. We found no significant sex × glade type interaction affecting distances moved. Surface-active $T_\nu$'s increased significantly over the activity season (May–July; n = 364 $T_\nu$ replicates; $F_{2,168} = 16.21, P < .0001$) but were not different between glade types ($F_{1,168} = 2.82, P = .094$; fig. 4A). We found no significant month × glade type interactions affecting surface-active $T_\nu$'s.

Time Surface Active and Frequency of Recent Meal. The number of hours per day Crotaphytus collaris was observed to be surface active increased throughout the activity season (n = 27 daily comparisons; $F_{2,14} = 45.77, P < .0001$) and was statistically greater in intact sites (across season mean = 12.2 h) than in encroached sites (across season mean = 9.1 h; $F_{1,14} = 108.14, P < .0005$; fig. 4B). We found no significant month × glade type interactions affecting surface-activity times. The frequency of a recent meal was not significantly different between glade types (n = 172 observations; intact = 90.1%, encroached = 85.4%; $\chi^2 = 0.914, df = 1, P = .339$). We observed no significant glade type × sex interaction affecting meal frequency.

NAE Model

To parameterize time budgets in the NAE model, we used the mean of hours surface active and inactive for each month across the season (April–August) for individuals in intact sites (active season average = 12:12, active to inactive) and encroached sites (active season average = 9:15, active to inactive; fig. 4B). To parameterize active $T_\nu$ in the NAE model, we used the mean of surface-active $T_\nu$'s for each month during activity time periods (fig. 4A). Because we did not deploy temperature loggers in April and August, we used data for May and July for these months, respectively. To parameterize inactive $T_\nu$'s, we used mean hourly overnight refugia temperatures for each month (fig. 5). Figure 5 provides the 24-h $T_\nu$ profiles of C. collaris in intact and encroached glades in the middle of the activity season (June).

Based on our model, C. collaris in encroached glades would experience a 50.1% (1YO, 15-g female) or a 51.9% (2YO, 25-g female) decline in annual NAE compared with intact sites (fig. 6; table S2). The NAE model predicted 2.91 ± 1.08 (mean ± SD) eggs for 1YO females in encroached glades and 8.90 ± 1.49 eggs for 1YO females in intact glades (fig. 6; table S2). Similarly, our model predicted 10.30 ± 1.73 eggs for 2YO females in encroached glades and 20.50 ± 2.42 eggs for 2YO females in intact glades (fig. 6; table S2).

Discussion

The goal of our study was to examine the effects that habitat alterations can have on the time-energy budgets and life history traits of an at-risk species using data on Crotaphytus collaris in the Ozark Mountains. Our first set of comparisons examined differences in operational environments (environmental temperatures or prey availability; fig. 1) that could lead to constraints on the time-energy budgets of C. collaris in encroached habitats. Arthropod densities were
statistically greater in encroached glades than in intact glades (fig. 2). Thus, our data suggest that *C. collaris* in encroached glades are not limited by prey availability. Alternatively, encroached glades had lower percent $T_e$ within the active $T_e$ range ($T_{ACT}$; fig. 2A–C) and significantly lower thermal quality indices ($d_e$) than intact glades (fig. 3D). Taken together, our $T_e$ comparisons support the notion that *C. collaris* in encroached glades experience a greater constraint on time-energy budgets associated with reduced thermal opportunity.

Our second line of questions examined differences in time-energy characteristics that might explain a link between differences in operational environments and a shift in life history traits. First, we found no significant difference in surface-active $T_e$'s between glade types (fig. 4A). Thus, we concluded that if *C. collaris* in encroached glades experienced a decline in physiological performance during surface activity (i.e., digestion or prey capture rates), it was not because of reduced surface-active $T_e$'s (fig. 1). Our data indicated that *C. collaris* in encroached habitats were surface active for 3.1 fewer hours per day than those in intact glades. Our findings on observed surface-activity time between glade types (fig. 4B) align with our $T_e$ assessment of available hours for activity (fig. 3A–3C). Thus, we conclude that *C. collaris* in encroached glades do experience a reduction...
in thermal opportunity, which results in reduced daily activity time.

Movement rates of *C. collaris* in encroached glades did not differ significantly from those of lizards in intact glades. Our data do not support the explanatory hypothesis that increased movement rates of *C. collaris* in encroached glades lead to a reduction in NAE allocated to reproduction and growth. Finally, we tested for a difference in the presence of a recent meal in *C. collaris* from intact and encroached glades and found no significant difference. Our results suggested that *C. collaris* in both glade types experience an empty stomach relatively infrequently (9.9%–14.6% of the time for intact and encroached, respectively; see "Results"), which is consistent with our findings that prey densities are not lower in encroached glades (and are actually greater; fig. 2) and that animals experience similar active *T*_a’s (fig. 4A) between glade types. Therefore, if *C. collaris* in encroached glades do experience lower consumption rates, it is not because of reduced prey availability or reduced *T*_a-associated capture performance.

In all of our statistical comparisons, the only variables that differed in a way that could explain time-energy constraints of *C. collaris* in encroached glades were the availability of suitable *T*_a (fig. 3) and the time animals were surface active (fig. 4B). Reduced activity time budgets represented the most probable source of constraint in time-energy budgets experienced by *C. collaris* in encroached glades. We focused our modeling efforts on the potential effects of reduced activity times on NAE.

Lizards in encroached glades spent less time surface active (~3 h/day; fig. 4B), which indicates that they spent 3 h per day longer in their under-rock refugia (fig. 5). Assuming that *C. collaris* *T*_a’s approximate refugia *T*_a’s when they are inactive (based on fundamental biophysical principles; Porter and Gates 1969), then *C. collaris* in encroached glades spend 3 h longer per day at *T*_a’s substantially lower (refugia *T*_a’s = 15°C–25°C) than their active *T*_a’s (34°C–39°C; fig. 5). Digestive performance in *C. collaris* is substantially reduced at *T*_b’s ≤ 8°C and below, primarily due to increased gut passage times and reduced feeding rates (Brewster et al. 2020). Thus, we designed the NAE model to focus on the effects that variation in time at *T*_b may have on NAE available for growth and reproduction (table S1).

Results from the NAE model (table S2) suggested that female *C. collaris* in encroached glades experienced a substantial deficit in their available NAE by approximately 51% (fig. 6). By converting age-specific growth rates and total number of eggs produced by female *C. collaris* in intact and encroached glades (Brewster et al. 2018) into annual NAE (table S2), we provided a comparison of the observed annual NAE to the predicted annual NAE (fig. 6). Model predicted annual NAE for both age classes and between glade types are

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**Figure 4:** Body temperature (*T*_b; A) and daily surface activity (B). Shown are the mean and 95% confidence interval of surface-active *T*_b (\( P = .0947 \)) and number of hours observed to be surface active (\( P < .0005 \)) between eastern collared lizards (*Crotaphytus collaris*) in intact (black circles) and encroached (gray circles) glades.
similar to the observed annual NAE estimated from actual lizards (see horizontal lines in fig. 6). Next, we converted the NAE available for reproduction (by subtracting NAE estimated from observed annual growth in mass) into the predicted number of eggs (fig. 6). Model predictions suggested that females in encroached glades would produce far fewer eggs annually than in intact glades (mean = 46% across both age classes and all input variables; fig. 6). Model predictions of a 46% decline in the annual number of eggs produced are remarkably similar to the observed declines in annual fecundity (49%) of populations in encroached glades (Brewster et al. 2018). Furthermore, within age class predictions from the NAE model bounded the observed number of eggs produced by females in intact and encroached glades (fig. 6). Thus, the NAE model appears to provide a reasonable approximation of the actual observed differences in NAE allocated to reproduction of C. collaris in intact and encroached sites, all as a function of variation in time at $T_b$. In short, the NAE model implies that constraints on daily (24-h) digestive processing rates, as a function of time at $T_m$, may explain the majority of variation in growth and reproduction between C. collaris in intact and encroached glades in northern Arkansas.

Previous authors have suggested that energy assimilation will increase asymptotically with thermal opportunity in surface-active ectotherms, thus resulting in diminishing returns in energy assimilation (Grant and Porter 1992; Adolph and Porter 1993). There are only a few studies that have
addressed the diminishing returns pattern, but there are empirical data to support this assumption (Sinervo and Adolph 1994; Levy et al. 2017). We did not specifically test for this pattern in our study, but we did incorporate this function (from Levy et al. 2017) in subsequent versions of our model to test the sensitivity of its predictions to this assumption (see the supplemental PDF). Applying the diminishing returns function to our model had a minimal effect on our predictions (fig. S2) and resulted in no change to our general inferences. We note that our model is based on assimilation/passage rate data from Brewster et al. (2020) and assumed that lizards will continue to eat (replace ingested meals) as long as they have processed the previous meal. The function empirically derived in Levy et al. (2017) was from an experiment that allowed lizards to eat only for a 2-h time block once per day, regardless of the status of the recent meal. Since energy assimilation rates are highly dependent on consumption rates, constraining consumption in energy budget models could result in overestimation of the strength of the diminishing returns pattern. Nonetheless, we recognize the implications of such an effect when modeling the relationship between activity time and energy assimilation but conclude that this pattern likely has limited importance in explaining current variation in life history patterns in our study system. Future studies should explicitly test for the effect of increased opportunity for daily consumption on the relationship between thermal opportunity and energy assimilation.

In a seminal study, Congdon (1989) described four categories of proximate constraints on the energetics of reptiles: “(1) absolute resource availability; (2) harvest rate limitations; (3) process rate limitations; and (4) limitation on harvest or processing resources imposed by risk of predation” (p. 356). Our results appear to refute the first (prey availability data), second, and fourth (movement rates, gut palpation, and surface-active $T_b$ data) proximate

![Figure 6: Predicted annual net assimilated energy (NAE; kJ/year; A) and annual number of eggs produced (B) assuming 15-g (1-year-old [1YO]) and 25-g (2-year-old [2YO]) female eastern collared lizards (Crotaphytus collaris) inhabiting an intact (black rectangles) or an encroached (gray rectangles) glade. Black lines = mean observed 2YO (solid black line) and 1YO (dashed black line) annual NAE and number of eggs produced by female C. collaris in intact glades; gray lines = mean observed 2YO (solid gray line) and 1YO (dashed gray line) annual NAE and number of eggs produced by female C. collaris in encroached glades (Brewster et al. 2018). Predicted NAE and number of eggs were calculated on the basis of time at $T_b$ (fig. 5) effects on digestive processing rates using digestive performance data from Brewster et al. (2020). See table S1 for a summary of the equations and estimates used to calculate model predictions. See table S2 for a summary of calculations and results of the NAE model. Boxplots depict the median, interquartile range, range, and outliers based on 1,000 model iterations.](image-url)
constraints. Alternatively, our results appear to follow closely the mechanistic explanation described in the third constraint—a reduction in time at $T_\text{a}$, leading to a decline in processing rates. Adolph and Porter (1993) provided several predictions to explain the link between the thermal opportunity and life history traits, many of which are supported by our results. Variation in the time lizards were surface active was explained by variation in the thermal environment. Daily energy assimilation increased with activity time, and population fecundity increased with surface-activity time. In fact, our results appear to follow nearly all of the primary predictions posited by Adolph and Porter (1993) except for one—the prediction of a negative relationship between fecundity and survivorship, which we did not test for in this study.

Sinervo et al. (2010) showed the utility of modeling constraints in activity time as a result of climate change to predict extinction rates in multiple lizard taxa over regional and global spatial scales. Our findings appear to provide a mechanistic explanation to support some of the assumptions made in the extinction model provided by Sinervo et al. (2010). For example, the Sinervo et al. model assumed that when lizard populations experienced a large deficit in thermal opportunity, that population would become extinct based primarily on energetic requirements. Our study showed how constraints on thermal opportunity can lead to reduced NAE rates, reduced growth and reproduction, and ultimately to extirpations.

Several studies have used information on the thermal environment and activity time budgets to explain shifts in life histories in ectotherms (e.g., Grant and Dunham 1990; Angilletta 2001; Niewiarowski 2001; Hodkinson 2005; Buckley 2008; Kingsolver et al. 2011). Thus, the identification of a mechanistic link between thermal environments and life history traits of an ectotherm is not specifically novel. What is novel is the application of these principles to identify constraints imposed by habitat degradation (Brewster et al. 2018) rather than differences associated with climate change (Buckley 2008; Sinervo et al. 2010; Kingsolver et al. 2011; Levy et al. 2017), latitude (Angilletta 2001; Niewiarowski 2001), or elevation (Grant and Dunham 1990; Hodkinson 2005). Additionally, predictions from mechanistic models that address environmental change are difficult to test with empirical data, whereas the study presented here was specifically designed to do so. The initial motivation for investigating time-energy constraints in our study system was to understand potential mechanisms leading to current extirpations of *C. collaris* in the Ozarks (Brewster 2019). Thus, this study not only provides a novel viewpoint to understanding local extinction but has also provided valuable information that is being used to inform land management and population conservation decisions in northern Arkansas (Brewster 2019). Indeed, habitat restoration efforts to reduce vegetation encroachment and improve thermal opportunity for *C. collaris* are underway at all of the encroached glades in this study.

We note that our study cannot rule out other potential factors contributing to observed shifts in life histories. Explanatory mechanisms in ecology are typically complex (Quinn and Dunham 1983; Dunham and Beaupre 1998). For example, our study cannot rule out that some type of genotypic difference between *C. collaris* in intact and encroached glades is contributing to shifts in life histories. Similarly, there could be some other important differences not accounted for in our study (i.e., immunologically induced maintenance costs [Agugliaro et al. 2020], predator effects on activity [Congdon 1989; Downes 2001], or predator-induced shifts of food preferences [Hawlena and Pérez-Mellado 2009]) that contribute to constraints on time-energy budgets. However, given the large estimated differences in available NAE based on the time at $T_\text{a}$ model as well as the similarity of model predictions to empirical estimates of growth and reproduction of *C. collaris* in northern Arkansas, it appears that time at $T_\text{a}$ effects play a primary role in observed life history trait differences between intact and encroached glades.

**Conclusions**

Habitat degradation and climate change continue to push more species toward extinction. One important component to understanding, predicting, and ameliorating local extinction is to identify the effects of environmental change on thermal opportunity and time-energy budgets in terrestrial ectotherms. Our study highlights the strong effect that habitat degradation can have on population persistence and shows the utility of analyzing time-energy constraints to identify factors that link habitat alteration to extirpations in terrestrial ectotherms. We encourage investigators to consider the importance of time-energy constraints in understanding patterns associated with at-risk ectothermic species and, when appropriate, to use a mechanism-specific approach to investigate the effects of environmental change.

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Statement of Authorship
All authors contributed critically to the experimental design, analyses, and writing of the manuscript and gave final approval for publication. C.L.B. was responsible for data collection, the original draft (PhD dissertation), and funding acquisition. S.J.B. and J.O. were responsible for model conceptualization and design. M.G. was responsible for model analyses and coding simulation.

Data and Code Availability
R code for analyses is available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.wpzgmsbnd; Brewster et al. 2021).

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"In the bats one sees the culmination of volant adaptation on the part of the Mammalia and the entire order has reached a state of perfection excelled only by the birds and pterodactylos." From "Volant Adaptations in Vertebrates" by Richard S. Lull (The American Naturalist, 1906, 40:537–566).