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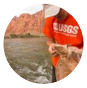

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PHENOLOGY OF THE ADULT ANGEL LICHEN MOTH (*CISTHENE ANGELUS*) IN GRAND CANYON, USA

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ABSTRACT—We investigated the phenology of adult angel lichen moths (*Cisthene angelus*) along a 364-km long segment of the Colorado River in Grand Canyon, Arizona, USA, using a unique data set of 2,437 light-trap samples collected by citizen scientists. We found that adults of *C. angelus* were bivoltine from 2012 to 2014. We quantified plasticity in wing lengths and sex ratios among the two generations and across a 545-m elevation gradient. We found that abundance, but not wing length, increased at lower elevations and that the two generations differed in size and sex distributions. Our results shed light on the life history and morphology of a common, but poorly known, species of moth endemic to the southwestern United States and Mexico.

RESUMEN—Investigamos la fenología de una polilla (*Cisthene angelus*) a lo largo de un segmento de 364 km del río Colorado en el Gran Cañón en Arizona, USA, utilizando un conjunto único de datos de 2,437 trampas de luz recogidos por ciudadanos científicos. Encontramos que *C. angelus* tiene un ciclo de vida bivoltino entre los años 2012 a 2014. Cuantificamos la plasticidad en la longitud del ala y en las proporciones sexuales entre las dos generaciones y a lo largo de un gradiente de elevación de 545 m. Encontramos que la abundancia, pero no la longitud del ala, aumentó con la elevación y que las dos generaciones difirieron en distribuciones de talla y de sexo. Nuestros resultados iluminan la historia de la vida y la morfología de una especie común, pero poco conocida, de polilla endémica del suroeste de los Estados Unidos y México.

Phenology, the study of life-history cycles and seasonal changes in ecosystems, dates back to the earliest scientific observations of the natural world (Post and Inouye, 2008). Over the past few decades, phenological research has emerged as a powerful tool for monitoring the effects of climate change (Easterling et al., 2000; Altermatt, 2010). Aspects of plant and animal life cycles, such as voltinism (number of generations per year), have been correlated with abiotic drivers such as precipitation, fire regimes, snow packs, and changing temperatures (Stefanescu et al., 2003; Blinn and Ruiter, 2009). Thus, observing the impacts of such environmental variables on organism size and life-history stages provides a crucial baseline for understanding and predicting how ecosystems are affected by natural and anthropogenic environmental change.

Organisms with short life cycles, such as most insects, facilitate the study of organismal adaptation and survival in response to variations in environmental conditions. In some species, multiple generations can mature within the span of a single season or year (i.e., multivoltinism: Martín-Vertedor et al., 2010; Teder et al., 2010). Many insect taxa exhibit plasticity in voltinism, whereby the number of generations maturing in a given year can vary according to environmental conditions such as temperature, moisture availability, and photoperiod (Huryn, 1990; Tobin et al., 2008; Bentz et al., 2014). For example, some species of moths are univoltine at higher latitudes, but are bivoltine or multivoltine at lower latitudes where growing seasons are longer (Tobin et al., 2008; Altermatt, 2010). Species exhibiting such plasticity in voltinism are model organisms for observing how environmental conditions and changes in climate affect phenology (Gomi, 1997; Lambin and Yoccoz, 2001).

The focal species of this study is the angel lichen moth, *Cisthene angelus,* a member of the Lithosiini tribe, subtribe Cisthenina, in the family Erebiidae. Within the genus *Cisthene,* 20 species are known north of Mexico, but the majority are more equatorial, with population ranges extending to South America (Knowlton, 1967; Lafontaine and Schmidt, 2010). *Cisthene angelus* range from western Texas to Arizona and to southern Nevada and Utah (Powell and Opler, 2009) and have been documented in northern Mexico as well (Brown, 2004). As adults, *C. angelus* have brightly patterned wings in shades of pink and orange with a distinctive broad, pale orange band on the forewing. The natural feeding habits of *C. angelus,* and *Cisthene* in general, are unknown. However, *C. angelus* has been reared ex ova in the lab on a diet of the alga *Protococcus viridus* (Wagner et al., 2008), and Lithosiini as a tribe are known to feed on lichen and algae as juveniles (Powell and Opler, 2009). The majority of erebiids in temperate climates overwinter as larvae and many genera found in arid climates are known to extend their larval life stage late into summer (Conner, 2008), but it is unknown whether *C. angelus* diapauses in a larval or pupal stage.

In this paper we describe the phenology and morphology of adult *C. angelus* along an elevation gradient in the canyon-bound, riverine environment of the Colorado River in Grand Canyon, northern Arizona, USA. We correlate empirical data on the emergence and morphology of mature *C. angelus* to geographical and temporal variables. Our goal was to describe the phenology of this obscure, yet common, species over broad spatial and temporal scales. Although no prior data exist on the abundance or morphology of *C. angelus* in Grand Canyon, we suspected that populations would exhibit variation in abundance and morphology along the elevation and temperature gradients that exists. Specifically, we predicted that *C. angelus* adults captured at lower elevations would be more numerous and larger than adults captured at higher elevations because of presumed developmental and fitness benefits conferred by warmer temperatures at lower elevations.

Materials and Methods—We conducted sampling for *C. angelus* along a 364-km segment of the Colorado River in Grand Canyon from 2012 to 2014. This river segment begins at the boat ramp at Lees Ferry (River km 0), ~25 km downstream of Glen Canyon Dam near the town of Page in northern Arizona, USA. It ends at the boat ramp at Diamond Creek, on the Hualapai Reservation near the town of Peach Springs, Arizona (Fig. 1a). The total elevation loss from Lees Ferry to Diamond Creek is 545 m. The average river surface slope throughout the study area is 0.0015, although it is punctuated frequently by rapids in which the gradient can exceed 0.01. The majority of these rapids are located in the upstream section of the study area; the Colorado River loses 93% of its initial elevation within the first 250 km (Schmidt and Graf, in litt.).

We coordinated and trained river runners as citizen scientists in a light-trap–based collection protocol (see Acknowledgements and Kennedy et al., 2016). Citizen scientists deployed light traps along the river's edge throughout the study area from April to October in 2012, from January to November in 2013, and from January to December in 2014. Light traps consisted of rectangular plastic containers (17 × 28-cm opening, and 7 cm deep) with a fluorescent light placed on the short edge of the container. Within 1 h after sunset on each night of their river trip, collectors placed light traps within 3 m of the river's edge, poured 250 mL of 95% ethanol into the trap, and turned on the fluorescent light. After 1 h of deployment, collectors turned off the light, transferred the contents into a 250-mL plastic bottle, labeled the sample, and recorded sample location, open and close times, and weather conditions on an associated data sheet (Kennedy et al., 2016). In 2012, citizen scientists collected an additional sample each night along the perimeter of the predam high-water zone, away from the river's edge. Specimens collected from these additional samples were incorporated with morphological measurement and analysis, but for consistency we used only samples collected along the river's edge for comparison and analysis of abundance across all 3 sampling years.

In the laboratory, we identified and counted all contents from the resultant 2,437 light-trap samples. We used a stratified random approach to select 28 samples from sampling year 2012: 14 from spring and 14 from autumn, that were representative of the spatial extent of our study reach for further measurements. For each of the 28 samples, we recorded sex and wing length of *C. angelus* for 100 randomly selected individuals. In instances when samples contained <100 individuals, we recorded all sex and wing lengths. We measured wing length as the longest axis across the forewing using a reticle combined with a stage micrometer in a stereo microscope at 40×. In total, we recorded the wing length and sex of 2,674 *C. angelus* individuals, and also calculated sex ratios for each of the 28 subset samples. Additionally, we developed a length–mass regression for *C. angelus* by measuring the dry weights for up to 20 males and up to 20 females from each of the 28 subset samples. In total, we took weight measurements from 1,102 individuals; several samples contained fewer than 20 individuals of each sex.

We evaluated the importance of environmental and spatial variables to *C. angelus* abundance and morphology data using Akaike's Information Criterion values derived from generalized linear mixed-effects models (Burnham and Anderson, 2002). We constructed models using a negative binomial distribution for abundance data and a Gaussian distribution for all other data, which were normally distributed. We included sample identification number as a random intercept in these models. We compared morphological differences between *C. angelus* generations, adult cohorts, and sexes using one-way analysis of variance and two-sample *t*-tests with $\alpha = 0.05$; we compared light-trap catch rates using one-way analysis of variance. We completed all statistical analyses using R 3.2.1 (R Foundation for Statistical Computing, Vienna, Austria).

Results—Of the 2,437 light-trap samples that were collected along the river's edge from 2012 to 2014, 903 samples contained *C. angelus,* representing 73,481 individuals. Total catch per light-trap sample ranged from 0 to 4,216 individuals of *C. angelus*. Sampling ranged from 13 April to 14 October in 2012, from 10 January to 16 November in 2013, and from 9 January to 10 December in 2014. With the exception of a 15-day sampling lapse in October 2013 due to a temporary shutdown of the United States government that closed Grand Canyon National Park, no more than 2 days elapsed between samples from mid-April to mid-October for all 3 years. Throughout the entire study reach, 99.8% of adults were in flight from 5 April to 19 June and 9 August to 15 November. Across all 3 years, 136 individuals from 3 samples (<0.2%) were collected between the dates of 20 June and 8 August (Fig. 1b).

Within samples that contained *C. angelus,* the average number of moths per sample declined with each sampling year, with 154, 92, and 36 moths per sample in 2012, 2013, and 2014, respectively. Conversely, light-trap sampling effort increased from 2012 to 2014, with 485, 814, and 1,138 samples collected at the river's edge each year, respectively. Amplified sampling

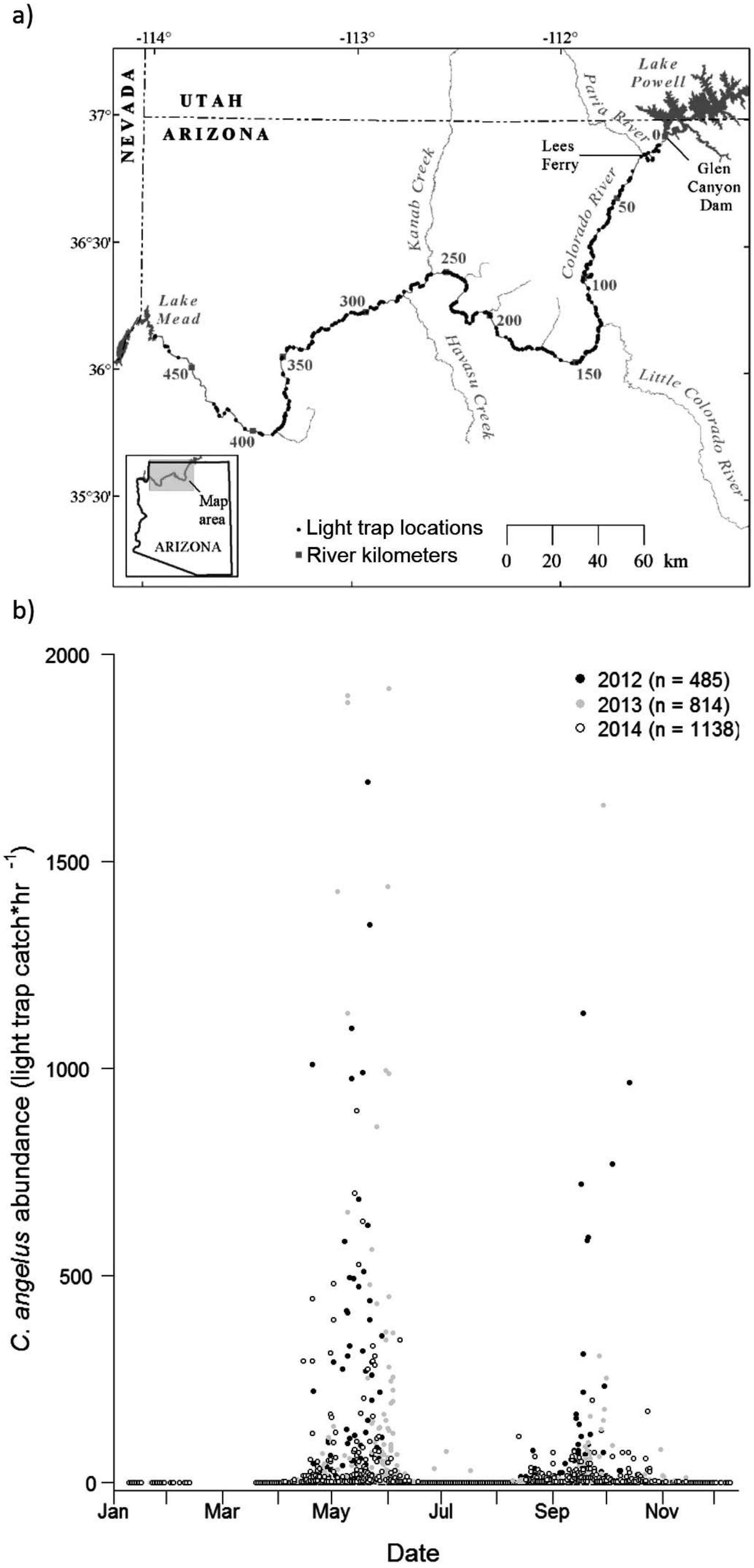

Fig. 1—Light-trap catch rates of *Cisthene angelus* through space and time. a) Distribution of light-trap samples along the Colorado River through Grand Canyon. Elevation at river level decreases along a downstream gradient proceeding from east to west. b) *C. angelus* light-trap catch rates (moths*sample^{-1}*h^{-1}) in 2012, 2013, and 2014. Legend describes number of samples collected per year.

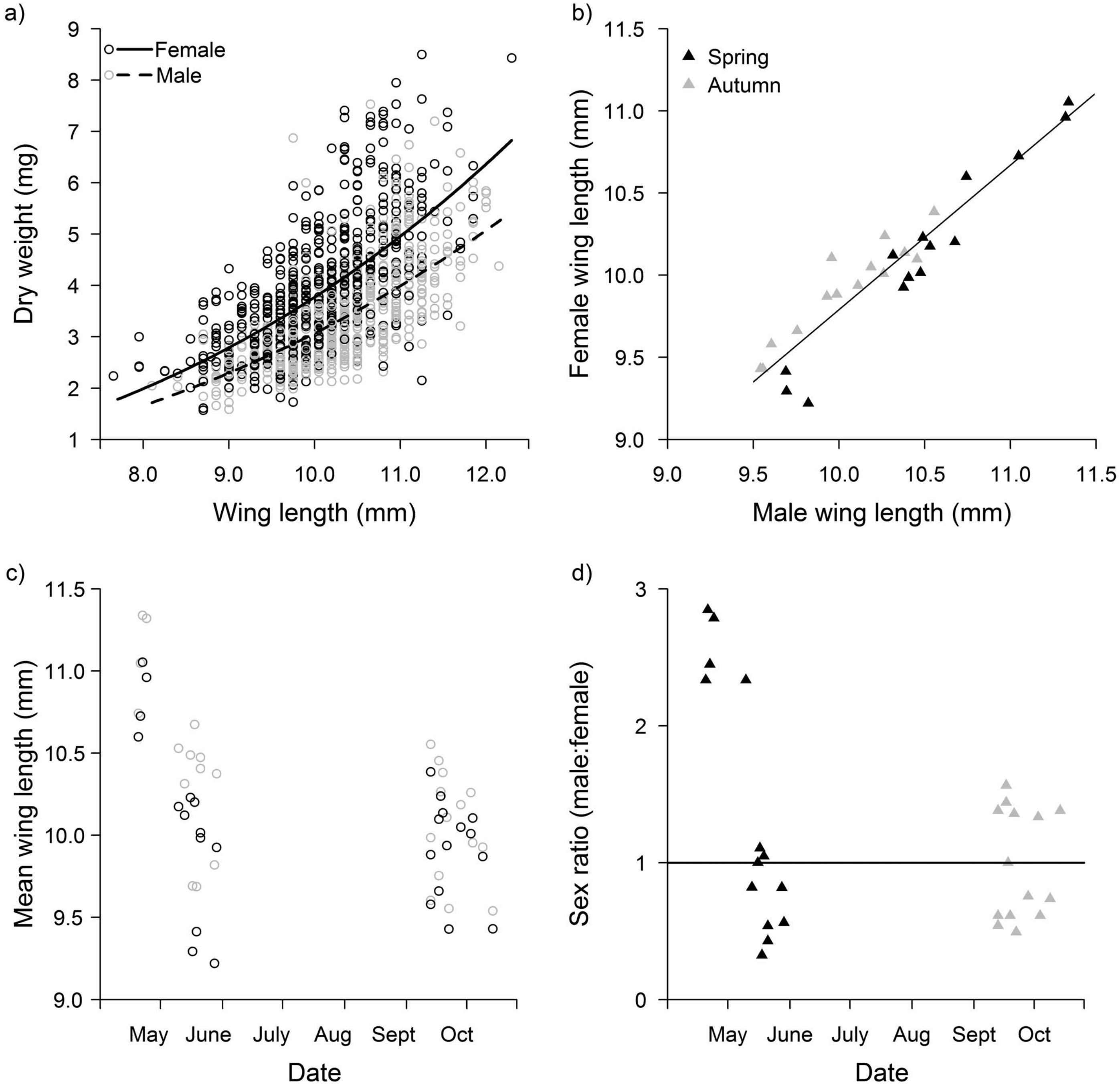

FIG. 2—Morphological measurements and sex ratio comparisons for Angel Lichen moths (*Cisthene angelus*) collected in 2012 from the Grand Canyon in Arizona. Black circles represent females and grey circles represent males. Black triangles represent the spring flight period and grey triangles represent the autumn flight period. a) Length–mass regressions for *Cisthene angelus,* which were best described with exponential functions: female dry weight $= 0.005 \times$ female length$^{2.867}$, $r^2 = 0.44$ and male dry weight $= 0.005 \times$ male length$^{2.755}$, $r^2 = 0.51$. b) The relation between mean male and female wing lengths were best described with a linear function: female length $= 0.99 + 0.88 \times$ male length, $r^2 = 0.88$. c) Mean wing lengths for males and females by month. d) Sex ratios of *Cisthene angelus* from Grand Canyon. The horizontal line represents a 1:1 sex ratio.

effort in 2013 and 2014 increased the number of samples collected outside of *C. angelus'* flight period as compared with the sampling effort in 2012. Consequently, the percentage of samples collected throughout the year that included *C. angelus* decreased from 40.6% in 2012, to 39.1% in 2013, to 34.1% in 2014. Catch rates of *C. angelus*/light-trap sample/h were significantly higher during the spring flight period than during the autumn flight period across all 3 years (Fig. 1b; $F = 22.3$, $P < 0.001$).

Table 1—Summarized model comparison for *Cisthene angelus* abundance and wing length. Specimens ($n = 30{,}349$) collected along Colorado River corridor in Grand Canyon, Arizona, USA, in 2012.

Model	AIC	ΔAIC	Weight
Abundance			
Base model	2,756	20	0
Date (contiguous)	2,760	24	0
Elevation	2,740	4	0.063
River surface slope	2,759	23	0
River width	2,758	22	0
Generation	2,756	20	0
Adult cohort	2,750	14	0
Elevation + Adult cohort	2,736	0 [a]	0.468
Elevation × Adult cohort	2,736	0 [a]	0.468
Wing length			
Base model	5,003	113	0
Sex	4,912	22	0
Sex + Elevation	4,916	26	0
Sex + River km	4,924	34	0
Sex + Generation	4,912	22	0
Sex + Adult cohort	4,907	17	0
Sex × Adult cohort	4,890	0 [a]	0.999

[a] Delta Akaike's Information Criterion (ΔAIC) values representing the strongest models

We conducted analyses of wing length and dry body weight measurements on samples collected in sampling year 2012. Both males and females of the spring generation had greater mean wing length than their counterparts in the autumn generation of that year: mean wing length for the spring generation was 5% and 1% greater than the autumn generation for males and females, respectively ($T = 13.4$ and 3.0, $P < 0.001$ and 0.003, respectively). Wing length was significantly greater for males than females in both the spring and autumn generations (Fig. 2a and 2b; $T = 13.1$ and 2.8, $P < 0.001$ and 0.004, respectively), and these differences were more pronounced in the spring than the autumn generation (mean difference of 0.56 mm compared with 0.14 mm, respectively).

Although males had longer wings than females, for a given wing length females were consistently heavier than males (Fig. 2a). Specifically, females had an average body mass index (dry weight/wing length) that was 17% and 15% greater than males in the spring and autumn generations ($T = 7.1$ and 7.7 respectively, $P < 0.001$ for both). Both males and females of the spring generation were heavier than their counterparts in the autumn generation: males and females were 30.6% and 25.6% heavier in spring than autumn, respectively ($T = 11.5$ and 8.3, $P < 0.001$ for both).

Overall, the largest individuals in the measured 2012 data set were part of the spring generation, which exhibited longer wing lengths than the autumn generation (Fig. 2c; $T = 11.9$, $P < 0.001$). This variation was primarily driven by a cohort of individuals that emerged in April and early May, the first 4 weeks of the spring generation. Mean wing length of this early spring cohort was 9.4% greater than the remainder of the spring generation and 10.2% greater than that of the autumn generation ($T = 25.5$ and 28.5, $P < 0.001$ for both, respectively). Moths emerging after the first 4 weeks of the spring generation's flight period did not have significantly different wing length from those in the autumn generation ($T = 1.9$, $P = 0.052$). Additionally, the cohort of moths that emerged in the first 4 weeks of the spring generation appeared to be protandrous, with a mean sex ratio of 2.5 (males: females; Fig. 2d). In contrast, the mean sex ratios for the remainder of the spring generation and for the autumn generation were 0.78 and 0.92, respectively.

Elevation and adult cohort were the only informative predictors of *C. angelus* abundance among the suite of demographic and environmental variables we considered (Table 1). Including three adult cohorts of *C. angelus* (protandrous spring moths, nonprotandrous spring moths, and autumn moths) improved models of wing length and abundance more than incorporating only two generations (spring and autumn). In contrast, elevation was not an informative predictor of *C. angelus* wing length, nor were any of the other environmental variables considered. Indeed, the only models that improved upon the base (predictor-free) model for wing length were ones that included gender. The best of those models also included adult cohort, either additively or with an interaction term with sex.

Discussion—The two nonoverlapping flight periods we observed in *C. angelus* light-trap catches across 3 separate years demonstrate that *C. angelus* are bivoltine in Grand Canyon (Fig. 1b). Indeed, <0.2% of individuals were collected outside date ranges spanning 77 days in spring (5 April to 19 June) and 69 days in autumn (9 August to 15 November) across all 3 years. Further, the individuals collected outside these date ranges were from three samples that were not spatially aggregated, spanning a range of 147.5 river km with different precipitation regimes and habitats (Caster and Sankey, 2016). This suggests that these samples were stochastic outliers rather than representing facultative brooding, which can occur in insects in response to climatic microhabitat conditions (Tauber et al., 1998; Stefanescu et al., 2003).

In our models, elevation was a good predictor of abundance, but not of wing length. These results partially supported our hypothesis that abundance and wing length would increase at lower elevations, because it is apparent that there were fewer moths at higher, more upstream elevations (Table 1). One potential explanation for abundance increasing down the elevation gradient while wing length did not might be that juvenile stages of *C. angelus* at lower elevations have a higher survival rate than those at higher elevations. The increase in abundance down the elevation gradient might be related to differences in the availability of algae and lichens, which most likely serve as the food source for *C. angelus* in its larval life stage (Wagner et al., 2008). This, in turn, could be closely related to moisture availability and temperature. The lower elevations are located in western Grand Canyon, which has warmer temperatures and receives more winter precipitation and less intense summer thunderstorms than the northeastern, higher elevation region of our study area (Caster and Sankey, 2016).

The morphological characteristics and sex ratios of adults captured in our light traps in 2012 differed significantly among the two temporally distinct generations. Most notable were the moths emerging in the first 4 weeks of the spring generation, which included the largest males and females of the year. Additionally, the males of this early eclosure emerged earlier than most females. The autumn generation lacked an analogous group of large-bodied or protandrous individuals during its emergence in mid-August. Among Lepidoptera, large and protandrous males often have greater mating success than smaller males that eclose at the same time or later than females (Wiklund and Fagerström, 1977; Thornhill and Alcock, 1983). Additionally, large female Lepidoptera are thought to have higher fecundity than small females (Abrams et al., 1996; Tammaru et al., 2002). Thus, the large and protandrous *C. angelus* individuals that eclosed at the onset of the spring generation flight period might have had higher fecundity and greater mating success than the smaller, nonprotandrous moths from the remainder of the spring generation and from the autumn generation.

Gender was the best predictor of wing length across generations. Males consistently had greater wing length than females, especially in the protandrous cohort of early spring (Fig. 2). This pattern of sexual dimorphism is common among Lepidoptera. Sexual selection and mating systems are commonly considered as the two primary drivers of this phenomenon, although specific mechanisms vary by species (Allen et al., 2011). Accounting for three unique cohorts of emergence (protandous, early spring; nonprotandous, late spring; autumn) further improved models of wing length, as compared with models that only accounted for a spring and an autumn generation (Table 1).

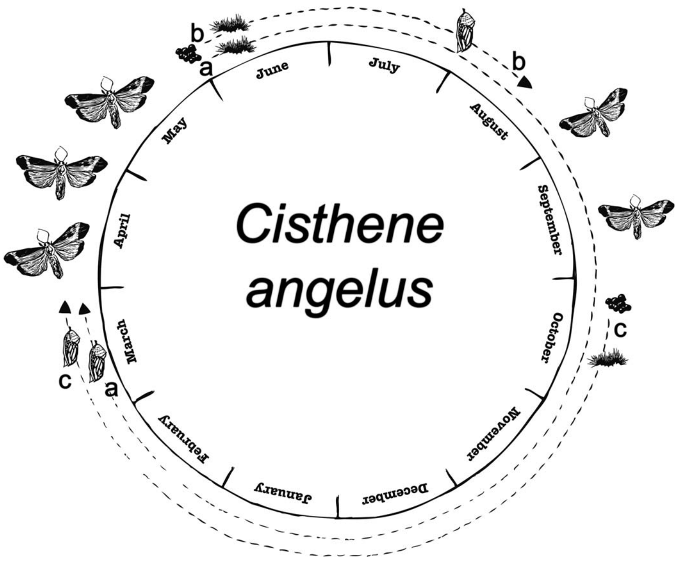

FIG. 3—A hypothesized life cycle for *Cisthene angelus* based on adult phenology, proposing two temporally distinct generations and three potential developmental pathways for maturation: a) development from eggs deposited in spring by the diapausing generation of the year prior; b) development in autumn from eggs deposited in spring by the same year's spring generation; and c) development from eggs deposited in autumn by the same year's autumn generation. Timing and duration of juvenile life stages are unknown for this cryptic caterpillar (Figure adapted from Wiklund et al. 1991).

Although we lack data specific to juvenile life stages, the presence and model support of three distinct cohorts of adults is indicative of three distinct developmental pathways for *C. angelus* (Fig. 3). Based on our adult collections, it seems probable that the spring generation has up to 12 months in its juvenile life stages, whereas the autumn generation has approximately 8 months to complete development. In this context, the largest and uniquely protandrous adults in our data set were likely the same individuals that had the longest available developmental time (Fig. 3). This potential disparity in development time for juvenile life stages could explain the correlation between adult cohort and wing length, but would require the currently infeasible collection of juvenile life stages to be adequately tested. In fact, juvenile life stages of *C. angelus* have never been observed or collected in Grand Canyon, and we have conducted informal surveys of rock and tree lichens for eggs, caterpillars, and pupae in Grand Canyon to no avail. In addition to understanding larval development time as a constraint on adult body size, growth rate itself should be treated as an independent and plastic variable (Wiklund and Forsberg, 1991; Klingenberg and Spence, 1997; Nylin and Gotthard, 1998; Nijhout et al., 2014). Further study on the life history of *C. angelus,* especially the undescribed juvenile stages, would elucidate the role of environmental variables on the morphology and phenological adaptations of this widespread and charismatic species that is endemic to the southwestern United States and Mexico.

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