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ORIGINAL PAPER

Patch occupancy and habitat of the hops azure (*Celastrina humulus*), a rare North American endemic butterfly: insights for monitoring and conservation

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Abstract The hops azure (*Celastrina humulus* Scott & D. Wright 1998) is a rare butterfly found along the Front Range of Colorado. Data on the prevalence of the butterfly and its preferred habitats are lacking. To describe the habitat of *C. humulus* at the southern part of its range, explore what factors impact *C. humulus* detectability, and estimate *C. humulus* habitat use along a riparian area known to support it, we conducted an occupancy analysis along the largest riparian system at the U.S. Air Force Academy (USAFA) in Colorado, USA. We used environmental and site-specific covariates to model the probability of detection and the probability of occupancy. Probability of detecting *C. humulus* was influenced by the amount of cloud cover during sampling, while the probability of occupancy was influenced by the total area of the host plant (wild hops) at the site. Probability of detection was higher during the first visit (69 %) than the second visit (64 %), and the probability of occupancy was higher (77 %) than assumed (30 %). Despite the host plant being patchily distributed throughout the butterfly's range, the riparian areas at USAFA had a high prevalence of both wild hops and *C. humulus*. We use the project findings to develop future sampling efforts for the butterfly along tributaries at other locales within the butterfly's range.

Keywords *Celastrina humulus* · Cloud cover · Habitat patch size · Hops · *Humulus lupulus* · Occupancy

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Introduction

Historically, invertebrates have not been the focus of landscape management but, as evidence grows that invertebrates are valuable indicators of ecosystem health, they have received more attention (Niemelä 1997; Anderson and Majer 2004; Maleque et al. 2009), and rare species have been recognized as conservation priorities (New 2012). Butterflies are particularly useful for assessing management and conservation actions because some species have strong host-plant specificity (Thompson and Pellmyr 1991), are sensitive to environmental conditions (Oostermeijer and van Swaay 1998), and correlate to plant and animal biodiversity (Kremen et al. 1993; Blair 1999). Although there has been a lack of attention directed at invertebrate conservation research (Clark and May 2002), butterflies are one of the charismatic invertebrate groups being addressed (Pollard 1991; New et al. 1995).

Despite the attention they receive, many rare butterfly species still lack distribution and population structure information (Bried et al. 2012). *Celastrina humulus*, possibly Colorado's only endemic butterfly (Fisher 2009), is a small (2, 3 cm wingspan) butterfly found only in 12 counties along Colorado's Front Range (Scott and Wright 1998; Fisher 2009). It is a species of conservation concern because of its limited range, patchy distribution, and the rapid urban and suburban development that jeopardizes habitat and disrupts population connectivity along the Front Range (Kuby et al. 2007). NatureServe considers it a globally- and state-imperiled species vulnerable to extinction (www.explorer.natureserve.org). Preliminary data on habitat affiliations and distribution of *C. humulus* exist, but rigorous data on population status are lacking, especially in the southern part of its range (Scott and Wright 1998). The *C. humulus* range overlaps a portion of the range of a similar butterfly, the spring blue (*C. ladon* Cramer 1780), but *C. humulus* can be distinguished by having smaller, less-abundant black spots on the white undersides of the wing, and adults typically emerges a month later than *C. ladon*. Adult *C. ladon* are seen during spring months (April–May) while *C. humulus* emerge in early summer at the beginning of June (Fisher 2009). Several plants like waxflower (*Jamesia americana*) and lupine (*Lupinus argenteus*) are used by *C. humulus*, but its primary host plant is wild hops (*Humulus lupulus*) (Scott 1992). In Colorado, wild hops grow along floodplains, rocky slopes and gulch bottoms, with vines climbing up to 9 m on surrounding bushes and trees (Scott and Wright 1998; Hampton et al. 2001). Female *C. humulus* lay eggs on male hop flowers, where the larvae hatch and grow to maturity on the plant (Scott 1992; Pratt et al. 1994).

Understanding the distribution, habitat preferences, and population biology of rare butterflies, like *C. humulus*, allows development of management practices to conserve butterfly populations (New et al. 1995; Fernández-Chacón et al. 2014). Assessments of *C. humulus* abundance would provide baseline data for monitoring populations through time. Count-index methods are the most popular technique for estimating abundance, but this technique unrealistically assumes that the probability of detection is equal to 1 and that the observed individuals represent a proportion of the true population size consistently across the landscape (Anderson 2001; but see Bried and Pellet 2012). Several methods of monitoring populations that assume the probability of detection is less than 1, including mark-recapture and distance sampling, can be difficult to apply to butterfly populations. Mark-recapture studies of abundance are hampered by cost, sample size, impacts to animals' behavior, low recapture rates, uncertainty of meta-population structures, and the stress and damage that can be imposed on individuals (MacKenzie et al. 2005; Haddad et al. 2008). Distance sampling can be costly and can fail to produce reliable estimates when few animals are detected. Additionally, the constant movement of butterflies in flight can make it difficult to meet the model's assumptions (Isaac et al. 2011; Bried and Pellet 2012).

Occupancy modeling holds promise as an alternative method of assessing population change for butterflies (Bried and Pellet 2012; Fernández-Chacón et al. 2014). Occupancy modeling estimates the probability of a site being occupied by a species and accounts for probabilities of detection less than 1 (MacKenzie et al. 2002). The assumptions of occupancy modeling are that a surveyed site is occupied by the species of interest for the duration of the study, the species is not falsely detected, but can be present and undetected, and species detection at a site is independent of detection at other sample sites (MacKenzie et al. 2002). Probability of occupancy assumes a close relationship with the abundance of a species so it may be used as proxy to estimate the population status of rare species. The more abundant a species is in an area, the greater the probability a section of the area is occupied by an individual of the species. Occupancy modeling can assess meta-population dynamics, which can be helpful for long term studies of fragmented butterfly populations (MacKenzie et al. 2005).

To address the lack of published data on *C. humulus* distribution and habitat use, we conducted an occupancy modeling study to describe habitat patch-use, estimate the probabilities of occupancy and detection in known habitat, understand the environmental and site-specific variables that influence the probabilities of occupancy and detection, and provide preliminary data for designing future patch-use studies.

Materials and methods

Study area

We conducted our study at the U.S. Air Force Academy (USAFA) in Colorado Springs, Colorado, USA. We sampled the 14.1-km extent of Monument Creek that flows through USAFA property because it is a large contiguous riparian system known to support *C. humulus*, and natural resource managers at the USAFA have prioritized conservation of the ecological and geomorphological attributes conducive to rare and endangered species habitat. The riparian system along Monument Creek is densely vegetated with forbs, grasses and shrubs, including willows (*Salix* spp.), snowberry (*Symphoricarpos occidentalis*), wild rose (*Rosa woodsii*), and currant (*Ribes* spp.). The adjacent uplands have Ponderosa pine (*Pinus ponderosa*) woodlands with scrub oak (*Quercus gambelii*), choke cherry (*Prunus virginiana*), sage (*Artemisia frigida*), and grasses.

Sampling design and data analysis

We used personal observations, *C. humulus* survey reports, and published literature on occupancy study design (MacKenzie and Royle 2005; Guillera-Arroita et al. 2010) to develop study design parameters. We hypothesized the probability of detecting (p) *C. humulus* in habitat patches would be high ($p = 0.8$), but the probability of *C. humulus* occupying patches (ψ) along Monument Creek would be low ($\psi = 0.3$). To attain reasonably precise (SE $= 0.05$) occupancy estimates, we hypothesized we would need to visit approximately 85 sites three times during the sampling period (MacKenzie and Royle 2005; Bailey et al. 2007). We randomly selected 85 100-m-long sections of

Monument Creek (Fig. 1). We visited each 100-m section and sampled a 50-m sub-section within that area with the most promising habitat (most densely vegetated) for *C. humulus*. Distances between randomly-selected 100-m sections ranged from 0 to >200 m. We began surveys on June 10, 2014 and continued until adult butterflies were no longer available (July 11, 2014). A survey consisted of two people searching the 50-m sub-section for 10 min on rainless days between 930 and 1600 h when temperatures exceeded 13 °C with no more than 40 % cloud cover, or when temperatures exceeded 19 °C irrespective of cloud cover (Pollard 1977; Wikström et al. 2009; Bried and Pellet 2012).

At each of the 50-m subsections, we collected environmental and site-specific data to account for habitat and meteorological heterogeneity that could affect probabilities of occupancy and detection (Krauss et al. 2004). We recorded the maximum shrub width (m), dominant shrub species, percent canopy cover, and dominant canopy species for each site to understand if shrub and tree cover along Monument Creek helped explain butterfly occupancy (Pocewicz et al. 2009). We recorded percent cloud cover and the maximum wind speed (mph), temperature (°C), and percent humidity using a Kestrel 3000 Pocket Weather Meter (Nielsen-Kellerman, Boothwyn, PA, USA) during each survey (Krauss et al. 2004; Wikström et al. 2009). We recorded whether wild hop plants were present, and we estimated the total area of hops (m^2), the size of the largest hop patch (m^2), the percent solar exposure at the largest hop patch, the total number of hop patches in the surveyed sub-section, and the percentage of time the sun was not covered by clouds (Pocewicz et al. 2009; Fernández-Chacón et al. 2014). When *C. humulus* was detected at a site, we recorded the number of butterflies seen, whether butterflies landed, what plant species they landed on, and if they attempted to oviposit (Longcore et al. 2010). When possible, we recorded the sex of the butterflies (Scott and Wright 1998).

We analyzed data using a single-species, single-season occupancy model in Program MARK (Gary White, Colorado State University, Fort Collins, CO, USA). Models of occupancy and detection probabilities were compared

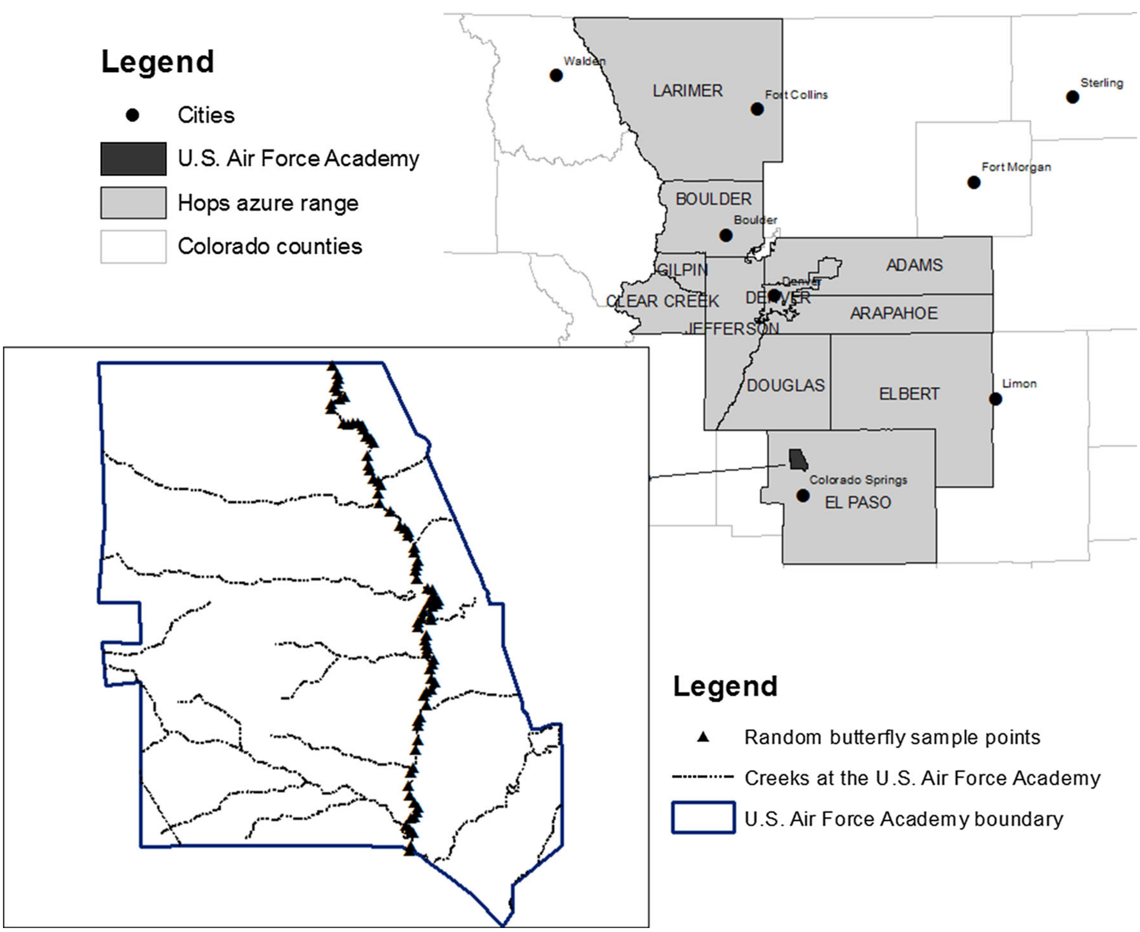

Fig. 1 Distribution of *Celastrina humulus* in Colorado, study area at the U.S. Air Force Academy, and sampling plots along Monument Creek, U.S. Air Force Academy, Colorado

using Akaike's Information Criterion with small sample size bias correction (AIC_c) and the probability of a model being the most-parsimonious model, AIC_c weight (w) (Burnham and Anderson 2002). As a model-development protocol, first we modeled estimates of probability of detection using those covariates we believed would impact detection. Then, using the models of detection probability with the most support (highest w) we modeled occupancy using covariates that might impact *C. humulus*' probability of using a habitat patch.

One advantage of using this analysis framework is that it does not rely on one model as the basis for all probability estimates (Burnham and Anderson 2002). Because it is difficult to know which model matches reality, this methodology allows the use of multiple models as the basis of estimating detection and occupancy probabilities. This is accomplished by weighting estimates from models that explained more of the variability in the data, and prioritizing estimates from models that carry more w than others (model-averaging). We model-averaged estimates of detection and occupancy over the set of most-parsimonious models (Burnham and Anderson 2002).

To illustrate the relationship between predictor variables on *C. humulus* abundance we developed general linear models using the Poisson distribution for count data and tested for variable significance using Program R (version 3.1.2, The R Foundation for Statistical Computing).

Results

We visited 83 sites twice before the end of *C. humulus* flight (July 11, 2014). Although 85 sites were chosen, two were not visited more than once and were removed from analysis. Detection of butterflies was not consistent across the habitat. During the 166 surveys (83 sites visited twice), 158 butterflies were seen at 53 % (44 of 83) of sites. Hop plants were prevalent along Monument Creek with vines found in 98 % of the survey areas. The size of hop patches varied from a few m^2 to patches with vines spreading more than 400 m^2.

The most-parsimonious model ($w = 0.37$) used the covariate of percent cloud cover to explain the probability of detection and the covariate of total area of hops to model the probability of occupancy (Table 1). The next best model ($w = 0.18$) used the same covariate of total area of hops to model the probability of occupancy, but used wind speed and percent cloud cover to explain the probability of detection (Table 1). Wind speed and percent cloud cover explained the probability of detection for the third-best model ($w = 0.12$), but, the probability of occupancy was modeled using total area of hops and the presence of Ponderosa pine (*Pinus ponderosa*) in the overstory (Table 1). The next best model ($w = 0.12$) explained the probability of detection using percent cloud cover and the cubed function of temperature and again modeled the probability of occupancy using total hops area. No other models had an AIC_c weight greater than 0.08.

The probability of detection was different for each survey occasion with the first visit having a greater probability of detection ($p = 0.69$, 95 % CI = 0.56, 0.80) than the second visit ($p = 0.63$, 95 % CI = 0.51, 0.75). The probability of occupancy ($\psi = 0.77$, SE = 0.10, 95 % CI = 0.52, 0.91) was higher than the hypothesized 0.30. As cloud cover increased the probability of detection decreased during the surveys ($\beta = -0.02$, 95 % CI = −0.03, 0.00) (Fig. 2). The probability of occupancy increased as the total area of hops increased at a site ($\beta = 0.03$, 95 % CI = 0.01, 0.05) (Fig. 3).

As the total area of hops increased at a site, the number of butterfly detections increased. The largest number of *C. humulus* seen (25) was at a survey site with over 250 m^2 of wild hops, and *C. humulus* were seen at nearly all sites that had >80 m^2 of wild hops (Fig. 4). The number of *C. humulus* seen at a site could be modeled using the linear regression $y = 0.108 + 0.005x$, where y is the number of butterflies seen and x is area of hops (m^2) at a site (adjusted $R^2 = 0.32$, degrees of freedom = 81, F-statistic = 38.9). The influence of area of hops helped explain the number of butterflies seen (Z-value = 12.4, $p < 0.001$). Thus, as hops area increased by 1000 m^2 there is an expected increase of five butterflies (Fig. 4).

Discussion

Wild hops and *C. humulus* are more prevalent along Monument Creek than previously assumed. Wild hops was found at a vast majority of plots along Monument Creek, and the lower 95 % confidence limit on the mean probability of *C. humulus* occupancy (0.52) is higher than our hypothesized value ($\psi = 0.30$). Although not widely distributed, experts speculate that *C. humulus* is locally abundant in appropriate habitats (Paul Opler, C. P. Gillette Museum of Arthropod Diversity, pers. comm.). No estimates of *C. humulus* abundance exist; however, unpublished distributional surveys and annual indices of *C. humulus* abundance are available from other locations (Chu and Sportiello 2008). Unfortunately, these data have not accounted for the probability of detection and are unreliable for establishing long-term population trends (MacKenzie et al. 2002). If we assume we did not count the same butterflies repeatedly during the first occupancy sampling effort, the minimum population size along Monument Creek may be near 100 individuals. Occupancy studies have been used to estimate population size of low-

Table 1 Most-parsimonious models of occupancy and detection probability for the hops blue butterfly (*Celastrina humulus*) along Monument Creek at the U.S. Air Force Academy, El Paso County, Colorado

Model	AIC_c	ΔAIC_c	*w*	Parameters
p (cloud cover) ψ (hops area)	177.97	0.00	0.37	4
p (wind speed, cloud cover) ψ (hops area)	179.35	1.38	0.18	5
p (cloud cover) ψ (Ponderosa pine, hops area)	180.15	2.18	0.12	5
p (temperature^3, cloud cover) ψ (hops area)	180.23	2.26	0.12	5
p (constant) ψ (hops area)	180.96	2.99	0.08	3
p (temperature^3, wind speed, cloud cover) ψ (hops area)	181.62	3.65	0.06	6
p (wind speed) ψ (hops area)	183.05	5.08	0.03	4
p (temperature^3, wind speed, cloud cover) ψ (Ponderosa pine, hops area)	183.89	5.92	0.02	7
p (cloud cover) ψ (largest patch of hops)	184.57	6.60	0.01	4

AIC_c, Akaike's Information Criterion for small sample size; ΔAIC_c, difference in AIC_c between select model and top model; *w*, AIC_c weight; Hops area, total area of wild hops (*Humulus lupulus*); temperature^3, the cubic function of ambient temperature

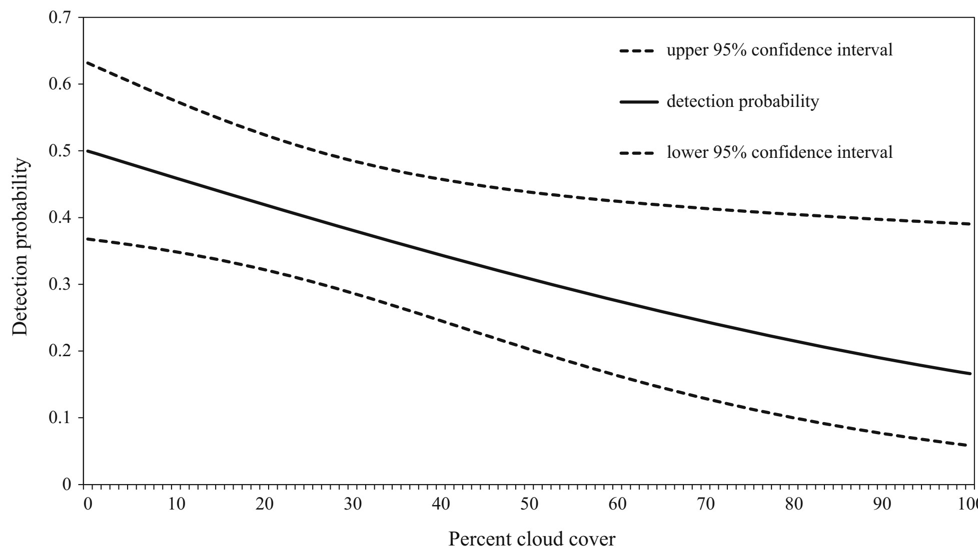

Fig. 2 Probability of detection for *Celastrina humulus* as a function of percent cloud cover at Monument Creek, U.S. Air Force Academy, Colorado Springs, Colorado

density species (Royle and Nichols 2003), yet have underestimated abundance of other Lycaenid butterflies (Bried and Pellet 2012). Although estimates of abundance historically have been the standard for monitoring the status of rare populations, other parameters, such as population change (λ) or probability of occupancy, can be valuable metrics of population condition (Sandercock and Beissinger 2002; MacKenzie et al. 2005). Given the difficulty of estimating *C. humulus* abundance accurately, annual occupancy estimates may clarify the stability or ephemerality of *C. humulus* populations along the Front Range.

Similar to other butterfly species, presence of the host plant does not determine butterfly occupancy, but increasing host-plant patch size increases the likelihood of occupancy (Krauss et al. 2004; Hardy et al. 2007; Pocewicz et al. 2009; Sanford et al. 2011; Fernández-Chacón et al. 2014). Conservation of *C. humulus* populations will be dependent upon conservation of large, relatively-contiguous patches of wild hops. Wild hops grow along riparian corridors, among willow (*Salix* spp.) patches, along exposed rock outcrops, and across upper floodplain terraces (Hampton et al. 2001; Smith et al. 2006), in fragmented, dense patches that can undergo rapid expansion and extinction events (Smith et al. 2006). The authors (RAS) have witnessed dramatic expansion and contraction of the area of hop patches along Monument Creek over the past 15 years. Currently, the riparian habitat along Monument Creek is a contiguous corridor of willow and other shrubs with substantial expanses of wild hops. The continuity of dense riparian vegetation and hop growth at USAFA is an anomaly along the Front Range, as urbanization has

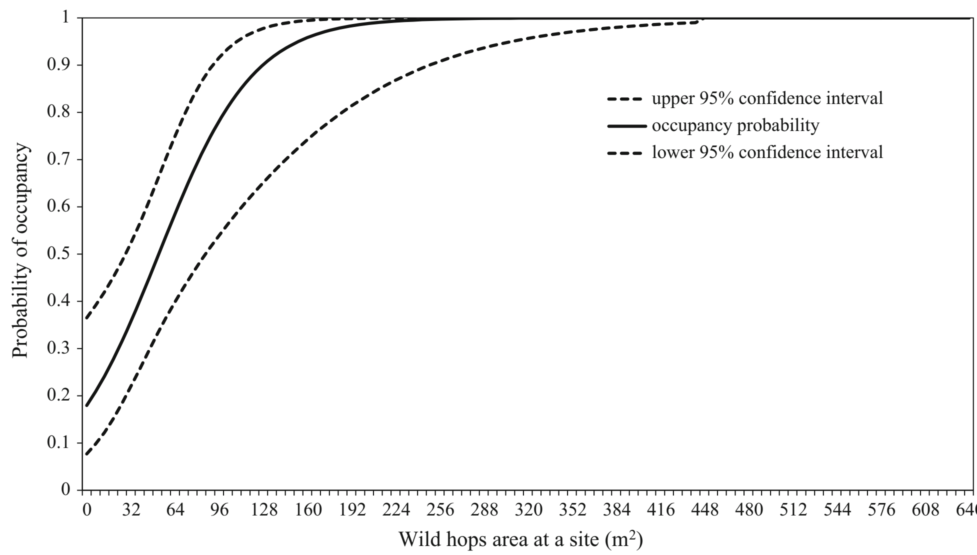

Fig. 3 Probability of occupancy for *Celastrina humulus* as a function of area of wild hops (*Humulus lupulus*) (m^2) at Monument Creek, U.S. Air Force Academy, Colorado Springs, Colorado

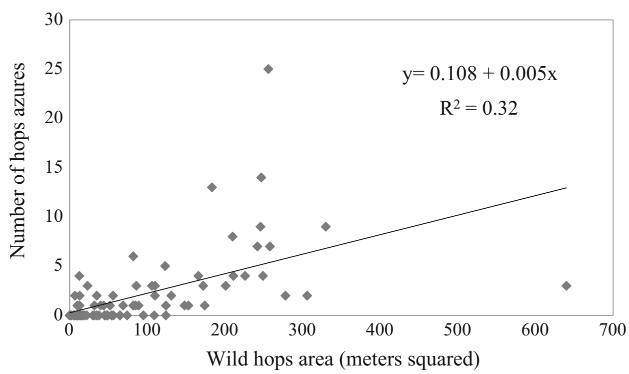

Fig. 4 Predictive model for number of *Celastrina humulus* seen (y) as a function of area of wild hops at a plot (x) at a survey plot at the U.S. Air Force Academy, Colorado Springs, Colorado

fragmented riparian habitats and limited wild hop availability (Smith et al. 2006; Kuby et al. 2007). Conservation may be challenged by the encroachment of urban and suburban development into riparian habitats. Other riparian-obligate species along the Front Range are impacted by urban-influenced habitat alterations (Schorr 2012), and it is likely that the same habitat impacts may jeopardize *C. humulus* populations. Efforts to conserve existing patches of wild hops, and manage the hydrology that allows hops and other riparian vegetation to expand, should improve habitat quality for *C. humulus*.

The impact of cloud cover on *C. humulus* detectability is not surprising because solar exposure and temperature can determine adult butterfly activity (Pivnick and McNeil 1987; Wikström et al. 2009). The body temperature of a butterfly drives activity rates, and butterflies can moderate body temperature with behaviors like basking or shade seeking (Pivnick and McNeil 1987). The importance of cloud cover on *C. humulus* detectability may be sex-specific. Cloud cover negatively impacted detectability in our study, which may be linked to female activity because females may be more temperature sensitive than males (Pivnick and McNeil 1987). A majority of our *C. humulus* detections were of females because they tend to fly lower and at slower speeds than males (Fisher 2009), so future occupancy studies may need to focus on female detectability and occupancy because of the challenges in observing the faster males.

Occupancy estimates depend on the assumption that the system is closed and the occupancy status does not change during the course of the study (MacKenzie et al. 2002). Our study may have violated the closed system and constant occupancy assumptions of occupancy modeling. The assumption that plots have a constant probability of being occupied during the duration of surveys was jeopardized by the adult *C. humulus* flight time ending prior to the completion of the second sampling visit and by our inability to get to all sites twice within the short, 1-month-long flight period of adult *C. humulus*. The second sampling event for most sites occurred in early-July and coincided with the end of the adult life stage, when there were fewer adults flying (Longcore et al. 2010). Future occupancy studies should complete sampling by the first week of July to guarantee access to flying adults. The closure assumption may have been violated by the mobility of *C. humulus* and the distance between sampling sites. Although the flight distances of *C. humulus* are not well-described, the majority of maximum movement distances for other Lycaenids are less than 100 m (Knutson et al. 1999; Maes et al. 2004). It is likely that *C. humulus* individuals flew among adjacent sampling areas during the study (Otto et al. 2013). When emigration and immigration at a site are random the occupancy estimate can be interpreted as probability of use rather than probability of occupancy and still provides valuable and relevant habitat information (Bailey et al. 2007). Additional studies need to clarify the movement distances of azures to better adapt occupancy study sampling designs and understand dispersal capacity among isolated patches of appropriate habitat.

The precision of our probability of occupancy estimates (SE = 0.10) is less than desirable for confidently comparing changes in the future. Using probability of occupancy and probability of detection estimates from this pilot study, we can generate sampling efforts that increase precision (SE = 0.05) in future studies (MacKenzie and Royle 2005). To estimate the probability of occupancy with SE = 0.05, assuming probability of occupancy of 0.77 and probability of detection of 0.69, future researchers should sample a comparable number of sites (83) three times. If we assume *C. humulus* adults are in flight for 1 month starting in early June, then approximately 31 sites would need to be sampled per week. This level of sampling is manageable for two surveyors, but inclement weather (e.g., high winds, rain, hail) and unpredictable adult phenology can reduce the number of viable sampling days. Because of inclement weather, only 67 % of the allotted field season days in 2014 were appropriate for sampling *C. humulus*. It is wise to assume the same proportion of good-weather sampling days in future studies because weather along the Front Range can be unpredictable. Additionally, we may have started sampling late (June 10), so we recommend mid-May to late-May reconnaissance visits to better determine the beginning of adult emergence.

Although we believe the site-specific covariates of probability of occupancy and probability of detection were valuable predictors, we realize some environmental factors precluded their usefulness. For example, wind speed is a good predictor of being able to detect butterflies (Krauss et al. 2004), but we did not sample sites on excessively windy days to confirm the impact on detection probability. Additionally, we found that some days were inconsistently windy or calm and it may be important to record wind speed at the precise time of *C. humulus* detection to assess the threshold for the probability of detection in wind. It would be valuable to include covariates of adult attractants, such as muddy banks where adults sip, flowering plants that are *C. humulus* nectar resources, such as waxflower (*Jamesia americana*), and alternate host plants such as lupine (*Lupinus argenteus*) (Scott and Wright 1998). These alternate host plants are not prevalent along Monument Creek, but waxflower is found at higher elevations on the USAFA.

Long-term monitoring will provide valuable information about the metapopulation dynamics of *C. humulus* along Monument Creek. In particular, repeat visits to the sampling areas will allow modeling of extinction and colonization rates (MacKenzie et al. 2005). Identification of factors impacting colonization and extinction rates will help inform management of riparian habitat suitable for wild hops and *C. humulus* at USAFA and throughout the butterfly's range. The presence of *C. humulus* may be a useful indicator of riparian habitat quality along the Front Range of Colorado because it is strongly tied to a riparian plant species and could indicate where other rare riparian species, such as Preble's meadow jumping mouse (*Zapus hudsonius preblei*) can be found.

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