Multi-year occupancy of the hops blue butterfly (*Celastrina humulus*): habitat patch colonization and extinction

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Abstract The hops azure (*Celastrina humulus*) is a locally-abundant, rare butterfly in Colorado and Montana, that uses wild hops (*Humulus lupulus*) as a host plant. Because of the patchy distribution of wild hops and current land use changes, the butterfly is a species of conservation concern. The hops azure is abundant along the riparian systems of the U.S. Air Force Academy (Academy) because wild hops is readily available and most land-use impacts have not reached much of the Academy. However, the riparian systems of the Academy are experiencing increased flooding from off-base, hard-surface development, making it harder for riparian vegetation, like wild hops, to thrive. To describe the prevalence and persistence of the hops azure, we conducted multi-year occupancy sampling to understand habitat-patch occupancy changes, such as patch extinction and colonization, and to identify factors that impact detectability. Wind speed, the area of wild hops, and the amount of cloud cover and solar exposure influenced probability of hops azure detection. Patch occupancy and extinction are influenced by the area of wild hops, suggesting that as host plant patch sizes get smaller, patch extinction increases and occupancy decreases. Detectability and occupancy were higher than expected, and the probability of patch extinction and colonization were extremely low. Management efforts to expand wild hops growth within the hops azure's range, increase continuity of wild hops expanses, and retain the hydrology that supports wild hops should increase the stability of azure populations.

Keywords *Celastrina humulus* · cloud cover · extinction · habitat patch size · hops · *Humulus lupulus* · occupancy

Introduction

Butterflies are valuable indicators of ecosystem condition because they often show strong host-plant specificity (Thompson and Pellmyr 1991), are sensitive to changes in environmental conditions (Oostermeijer and van Swaay 1998), and their presence can correlate to plant and animal biodiversity (Kremen et al. 1993; Blair 1999). Because of this ecological importance and the charisma of the fauna, butterflies are receiving increased conservation attention (Pollard 1991; New 2012). Not surprisingly, population declines for rare butterflies can have ramifications for ecological systems and biodiversity conservation, thus, assessing population stability is valuable for conservation, effective habitat management, and preservation of ecological processes (New et al. 1995). Quantifying such declines requires information on distribution, habitat preferences, population structure, and the threats to persistence (Bried et al. 2012; Fernández-Chacón et al. 2014). One of the threats to butterfly populations is the conversion or alteration of the habitat upon which they depend (Baur and Erhardt 1995; New et al. 1995). Some species may tolerate or thrive in habitat alterations, abandon habitat patches, or be attracted to sink populations, and understanding these metapopulation dynamics, and the resource availability within patches, can guide conservation and habitat management for butterfly persistence (Thomas and Hanski 1997). Understanding the value of habitat patches and reserves, and butterfly use of habitat patches, is important for conserving these species (Koh and Sodhi 2004).

The drivers for butterfly patch occupancy and persistence are varied. In some cases, habitat patch occupancy and persistence are related to host plant availability and dietary needs, but for many species the patch-specific features that influence butterfly occupancy are unknown (Hill et al. 1996, Thomas and Hanski 2004). It is likely that butterfly habitat-patch use is driven by a combination of environmental and site-specific factors (Kral et al. 2018). Identifying these drivers, and understanding the availability of these drivers, is a critical to understanding butterfly habitat patch use dynamics, which is essential for guiding conservation planning for butterfly species (Thomas and Hanski 2004). For rare butterflies with limited, patchy distribution, habitat patch occupancy can be less stable, increasing the need for managing habitat resources that increase occupancy (Krauss et al. 2004).

Celestrina humulus, or the hops azure (herein called “azure”), is a small (2-3 cm) rare butterfly with a restricted range of 12 counties along the Front Range of Colorado, with possible occurrence in Wyoming and Montana (Fisher 2009). Because the azure’s range overlaps a region experiencing some of the fastest urban development rates in Colorado and the United States, it is vulnerable to extinction. The azure’s limited range, and the rapid development along the Front Range that fragments suitable habitats (Kuby et al. 2007) has increased conservation interest and motivated a need to understand how the butterfly persists in suitable habitat patches (Puntenney and Schorr 2016). Suitable habitat patches contain the butterfly’s larval host plant. The azure has two ecotypes that have specific larval host plant affinities, one associated with wild hops (*Humulus lupulus)*, and the other associated with *Lupinus*. Females lay eggs on male flowers and the larvae, tended by ants that protect them (Kubik and Schorr 2018), grow to maturity on the plant (Scott 1992; Pratt et al. 1994). Wild hops plants grow along floodplains, rocky slopes and gulch bottoms, with vines climbing up to 9 m on surrounding bushes and trees (Hampton et al. 2001).

Recent efforts to estimate azure habitat patch occupancy show that the azure is prevalent in areas where its host plant is available, and that it is more likely to occupy habitat where the host plant is more prevalent (Puntenney and Schorr 2016). This has been valuable for understanding the butterfly's affinity for habitat patches, and these initial estimates of patch occupancy provide a baseline for monitoring populations (MacKenzie et al. 2004). Conducting multiple years of occupancy sampling at the same locations is promising as a method of assessing population or patch use changes for butterflies (Bried and Pellet 2012; Fernández-Chacón et al. 2014). Occupancy modeling also allows assessment of meta-population dynamics more economically than more-intensive sampling techniques (MacKenzie et al. 2005).

Long-term monitoring to assess habitat patch occupancy trends and persistence has not been conducted for the azure. It is unclear how azure patch occupancy dynamics vary with environmental conditions and host plant distribution and abundance, so we conducted a multi-year azure occupancy study to clarify occupancy patterns, understand the persistence of hops azures, and identify drivers and patterns of colonization and extinction of habitat patches. Additionally, we wanted to clarify what factors affect detectability and occupancy probabilities of the azure.

Materials and Methods

Study Area

We conducted our study at the U.S. Air Force Academy (Academy), where populations of azures have been documented in several riparian systems (Puntenney and Schorr 2016). We sampled a 14.1-km section of Monument Creek, which is the largest contiguous riparian system at the Academy. Monument Creek maintains hydrological and geomorphological features of historic riparian systems along the Front Range, and is home to other riparian-adapted rare species (Schorr 2012). The riparian system can be 100 m wide and is densely vegetated with forbs, grasses and shrubs, including willows (*Salix* spp.), snowberry (*Symphoricarpos occidentalis*), wild rose (*Rosa woodsii*), currant (*Ribes* spp.), and wild hops. The adjacent uplands have Ponderosa pine (*Pinus ponderosa*) woodlands with scrub oak (*Quercus gambelii*), choke cherry (*Prunus virginiana*), sage (*Artemisia frigida*), and grasses. Since lupine is not found along the Monument Creek waterway, the primary larval host plant for the azure along Monument Creek is wild hops.

Sampling Design and Data Analysis

We visited randomly-selected, 100-m-long sections of Monument Creek, and, because not all sections of the creek are well vegetated, we sampled the best 50-m section of habitat within each 100-m section (Puntenney and Schorr 2016). In 2014, we visited 83 sites twice, beginning surveys on June 10 and ending when adult butterflies were no longer active on July 11. A survey consisted of two individuals searching the 50-m section for 10 minutes. We (CPP and technician) surveyed each site for 10 minutes on rainless days between 0930 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. 2007; Bried and Pellet 2012). In 2015, sampling methods were similar, except we (RMM and technician) sampled the same 83 plots three times, with one person searching for butterflies for 20 minutes and spending an additional 10 minutes looking for ant mounds (Kubik and Schorr 2018). We defined “ant mounds” for the purpose of this study as observable collections of soil and other organic debris on the surface of the ground. Two of the sites surveyed in 2015 were excluded from the occupancy analysis because they were not surveyed in 2014.

We collected environmental and site-specific data to account for habitat and meteorological heterogeneity that could affect occupancy and detection. We recorded the maximum shrub width (m), dominant shrub species, percent canopy cover, and dominant canopy species for each 100-m site (Pocewicz et al. 2009). We recorded the maximum wind speed (mph), temperature (°C), percent cloud cover using a spherical densiometer (Forestry Suppliers, Jackson, MS), and percent humidity using a Kestrel 3000 Pocket Weather Meter (Nielsen-Kellerman, Boothwyn, PA) during each survey because conditions during sampling can influence butterfly detectability (Krauss et al. 2004; Wikström et al. 2007). We recorded whether wild hops plants were present at the survey site, and we estimated the total area of hops (m^2), the size of the largest hops patch (m^2), the percent solar exposure at the largest hops patch, the total number of hops patches in the survey area, and the percentage of time the sun was not covered by clouds (Pocewicz et al. 2009; Fernández-Chacón et al. 2014). When the hops azure was detected at a site, we recorded the number of butterflies seen, whether butterflies landed and 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, multi-season occupancy model in Program MARK (Gary White, Colorado State University, Fort Collins, CO). Models of occupancy (ψ) and detection probabilities (p) were compared 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 modeling approach, we modeled probability of detection first, and then used the most-parsimonious models of detection probability to build models of occupancy, patch extinction (ε) and patch colonization (γ). Probability estimates were model-averaged over the set of most-parsimonious models and profile likelihood estimates were used to better estimate parameter variability (Burnham and Anderson 2002).

Results

Hop plants were prevalent along Monument Creek with vines found at 98% of survey plots in 2014 and 92% in 2015. Azures were seen at nearly all sites that had >80 m^2 of wild hops. The largest number of butterflies (25) was seen at an area with over 250 m^2 of wild hops. During the 166 surveys (83 sites visited twice) in 2014, 158 hops azures were seen at 44 of the 83 sites (53%). During the 255 surveys (85 sites visited three times) in 2015, 330 hops azures were seen at 56 of the 85 sites (66%).

While holding ψ, ε, and γ constant, 30 models were run to determine what covariates best explained p. The most-parsimonious model ($w = 0.35$) used covariates of hops area and cloud cover for Year 1 and solar exposure, cloud cover, hops area, and wind speed for Year 2. The next best model ($w = 0.19$) differed by excluding cloud cover from modeling p Year 2. All other models of p were less parsimonious ($w < 0.11$). We used the two most-parsimonious parameterizations of p when modeling the covariates of interest (ψ, ε, and γ). The most-parsimonious model ($w = 0.34$) used covariates of hops area to model ψ, hops area-squared to model ε, and γ was held constant over time (Table 1). The next best model ($w = 0.23$) used the same covariate for ψ and γ, but used hops area to explain ε. There were three models with moderate support ($w = 0.10$) using various parameterizations of hops area and number of hops patches for ψ, ε, and γ (Table 1). No other models had $w > 0.07$.

Detection probability was influenced by the prevalence of wild hops at a site and environmental covariates during the day of surveying (Figure 1). In 2014, cloud cover decreased detection probability during the surveys ($\beta = -0.015$, 95% CI = -0.029, -0.001), but was less important in 2015 ($\beta = 0.006$, 95% CI = -0.004, 0.016). In 2015, solar exposure had a mildly positive impact on detectability ($\beta = 0.008$, 95% CI =

-0.002, 0.018) and wind speed had a negative impact on detectability (β = -0.139, 95% CI = -0.303, 0.026). As the area of wild hops increased the probability of detection increased in 2014 (β = 0.017, 95% CI = 0.003, 0.023), but only mildly increased detection probability in 2015 (β = 0.0004, 95% CI = 0.0000, 0.0007). Model-averaged estimates of detection probability over the two sampling occasions in 2014 were p_1 = 0.45 (SE = 0.05, 95% CI = 0.35, 0.56) and p_2 = 0.40 (SE = 0.05, 95% CI = 0.30, 0.51). In 2015, model-averaged estimates of detection probability over the three sampling occasions typically were higher than in 2014, with p_1 = 0.53 (SE = 0.05, 95% CI = 0.42, 0.63), p_2 = 0.36 (SE = 0.16, 95% CI = 0.12, 0.69) and p_3 = 0.55 (SE = 0.05, 95% CI = 0.45, 0.64).

Hops area increased ψ (β = 0.16, 95% CI = -0.09, 0.41), and ψ increased from year 1 (ψ = 0.64, SE = 0.08, 95% profile likelihood CI = 0.50, 0.84) to year 2 (ψ = 0.72, SE = 0.06, 95% profile likelihood CI = 0.60, 0.84) (Figure 2). Patch extinction was minimally decreased as hops patch size increased ($\beta < -0.11\text{x}10^{-5}$, 95% CI = $-0.34\text{x}10^{-5}$, $0.11\text{x}10^{-5}$). Model-averaged estimates of ε were low (ε = 0.06, SE = 0.07, 95% CI = 0.01, 0.40) and γ was unreliable with incredible variability estimates ($\gamma < 0.0001$, SE = 0.004, 95% profile likelihood CI = 0.000, 0.008).

Discussion

The use of multi-season occupancy models to understand butterfly patch colonization and extinction is growing (van Strien et al. 2011; Dinsmore et al. 2019), and these techniques allow formal inclusion of detection probability in estimation of patch occupancy, extinction, and colonization. With azure probabilities of detection p <1 (p range: 035 - 0.55), inclusion of detectability is vital for accurate assessments of azure occupancy and patch dynamics. Azures are small, have white underwings, live in dense vegetation, and are easily missed because, unless in flight, they can be mistaken for sunlight reflection or gaps in the vegetation. Naïve estimates of azure occupancy (53% in 2014, 66% in 2015) that neglect the probability of missing butterflies would have underestimated patch occupancy (ψ_{2014} = 0.64, ψ_{2015} = 0.72) and would not provide estimates of variability.

Although rare, the azure is locally abundant in habitats where hops is prevalent (Puntenney and Schorr 2016), and match similar patterns of host-plant dependence seen in other butterflies (Krauss et al. 2004; Bauerfeind et al. 2009; Sanford et al. 2011; Fernández-Chacón et al. 2014). However, considering that the distribution of wild hops in Colorado is patchy and less contiguous than in other areas (Smith et al. 2006) azure populations likely are similarly disjunct. Along Monument Creek, where wild hops plants are readily available, azures are relatively common, and azure patch occupancy is high. The dense riparian vegetation along Monument Creek provides an abundance of structure for hops vines to climb, and in some areas, the vines grow so densely as to make passage difficult and have grown tall enough to overgrow small alder (*Alnus tenuifolia*) trees (5 m). This degree of riparian vegetation growth is not ubiquitous throughout the Front Range of Colorado, and habitats that support wild hops are decreasing as urban sprawl overtakes many of the riparian systems (Baron et al., 2004; Kuby et al. 2007). Monument Creek and its surrounding tributaries have been insulated from development because the Academy limits on-base development, but as urban development encroaches from the east, riparian systems are increasingly being degraded (Schorr 2012). Because hops are particularly sensitive to availability of water and humidity (Fandiño et al. 2015), disruptions to hydrology that feed riparian areas can impact permanence of the plant and subsequently, the organisms it supports (Hampton et al. 2001). Continued channelization and dropping of the water table along the Monument Creek watershed will limit water availability for riparian-associated species. Combined with climate change projections for Colorado that suggest decreasing water availability (Smith et al. 2006; Ray et al. 2008), it is likely the precipitation-fed Monument Creek, and the riparian areas it supports, will diminish; thus, reducing habitat for the azure and increasing habitat fragmentation. Efforts to connect riparian habitat would decrease threats to azure populations, and such efforts can be partnered with similar efforts to conserve riparian habitat along the Front Range (USFWS 2018). Should hydrologic patterns deteriorate the riparian habitat that supports wild hops, azure populations may begin to resemble other rare butterfly populations that have been jeopardized by habitat fragmentation (Hanski et al. 1995; Bauerfeind et al. 2009).

Low estimates of patch colonization suggest there were few occasions when unoccupied patches became occupied by azures. It is unlikely that unoccupied sites in 2014 had enough hops growth in 2015 to show increases in patch colonization. Similarly, patch extinction estimates were low, suggesting that there were very few previously-occupied patches that became unoccupied, and as hops area became larger there was a lower probability that azures would cease to use the area. Hops distribution along Monument Creek has expanded and contracted over the past 20 years, and it is likely that azure distribution has as well; however, hops has always been available along the Monument Creek and its tributaries during that time (pers. obs. RAS). Because azures are reliant on hops that likely fluctuate in abundance and cover with drought (Garssen et al. 2014), they too may show patch occupancy dynamics that fluctuate with drought. Fortunately, our study was conducted during years when precipitation was not limiting, and hops plants were comparably available in each year, but, as climate change increases the frequency of drought conditions in Colorado (Ray et al. 2008), it is likely azure populations will become more isolated and azure population dynamics more unpredictable (van Bergen et al 2020). Studies of rare butterfly patch occupancy dynamics have demonstrated the detrimental effects climate change may play on rare populations (Johansson et al. 2019).

Many lycaenid butterflies, including azures (Kubik and Schorr 2018), have mutualistic relationships with ants, called myrmecophilies, where ants provide protection of larvae in exchange for an energetic or protein reward (Pierce et al. 2002). These myrmecophilies have survivorship benefits for butterfly larvae, especially for rare species (Thomas et al. 2020). We incorporated observations of ant mounds in the azure survey protocol as a proxy for ant presence to determine if butterfly occupancy was closely tied to the presence of ants. A majority (87%) of survey locations had ant mounds, and because ants were so prevalent, models including ant presence did not carry much explanatory power. Later studies found that mound-building *Formica spp*. to be one of the ant species that tend azure larvae (Kubik and Schorr 2018). Future azure surveys should document the location of ant nests, the species that built the nest, and the relative size of the colony because species-specific myrmecophilies may influence azure presence. Some species of Lycaenid butterflies can be vulnerable to environmental changes that impact their primary host plant and the ants that tend their larvae (Ueda et al. 2016), and further studies should investigate these and other ecological relationships for the azure.

This is the first study of habitat patch occupancy dynamics for azures, and, albeit a short temporal window of a specific region, provides insights into the importance of host plant availability and an initial management strategy for expanding habitat for this rare Lycaenid. Expanding hops along riparian systems of the Front Range can be a conservation measure for azures, an erosion control mechanism, and, in a region where beer production is prized, a broadly-popular method of increasing awareness of the importance of riparian systems for water resource values (DeLyser and Kasper 1994, Poff et al. 1997). These estimates of occupancy dynamics and the factors influencing occupancy provide a baseline for spatial and temporal comparison. Although only a snapshot of azure ecology, this study provides insight for the development of management strategies, habitat mitigation, and species conservation. In particular, occupancy can be influenced by numerous factors, including habitat structure, nectar availability, diversity and abundance of host plant resources, host plant phenology and growth, and host plant quality, which this study did not address. Attempts to quantify the vertical expanse of wild hops, as well as area, may be valuable covariates for azure detectability because of butterflies' affinities for the plant and the likelihood the vertical structure of hops provides protection from the wind. Additionally, our study focused on adult occupancy and did not attempt to locate larvae. Estimating larval habitat occupancy, and identifying the drivers for larval success, such as abundance and availability of hops male flowers, will be critical for understanding immature resource needs. Some butterflies are associated with specific host plant species for reproduction, but feed on a wider range of flowering plant species in their adult stage (Hardy et al. 2007). Documenting the presence of other flowering plant species, like dogbane (*Apocynum cannabinum*), which is used as a nectar resource (RAS obs.), may be valuable covariates for improving estimates of occupancy. Continued efforts to improve sampling design can increase azure detectability and increase estimate precision. In particular, avoiding days with excessive wind or cloud cover, when lycaenid butterflies are less likely to be in flight (Douwes 1976; Puntenney and Schorr 2016), and making an effort to move through the dense vegetation to induce azure flight can increase detectability.

Early projections of sampling effort (85 sites sampled 3 times) to produce $SE_{\psi} \sim 0.05$ approximated the level of precision ($SE_{\psi} = 0.06 – 0.08$) seen in this study of 83 sites visited 3 times (Puntenney and Schorr 2016). However, using this protocol for long-term monitoring throughout azure range may be challenging because other areas likely do not have the ubiquity of wild hops, and efforts to increase sample sites, visits, or detectability may be required to observe similar variance estimates. Further attempts to estimate azure occupancy at other locations can clarify the level of effort needed, will provide baseline data on azure populations, and can help direct conservation resources for maintaining azure populations.

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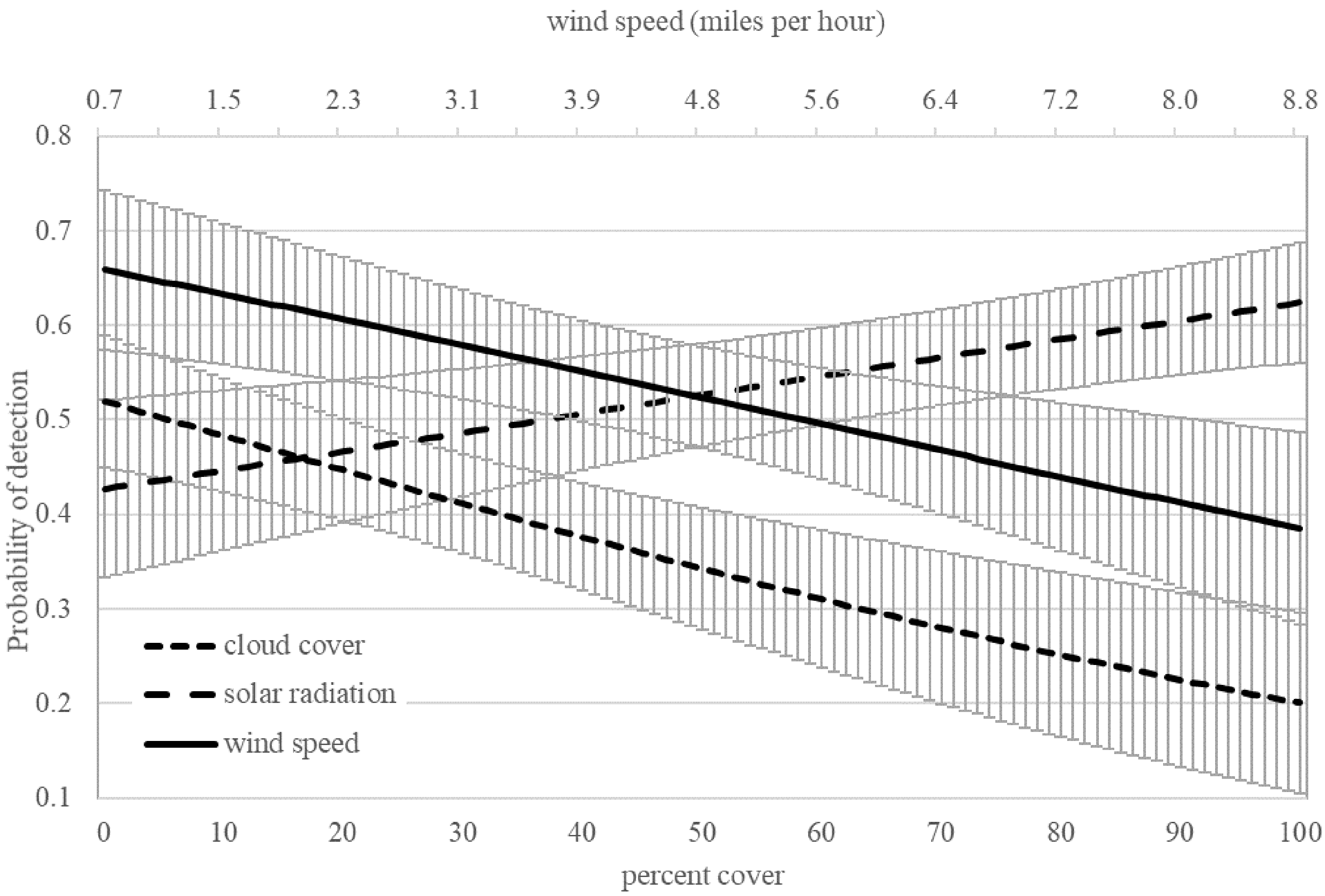
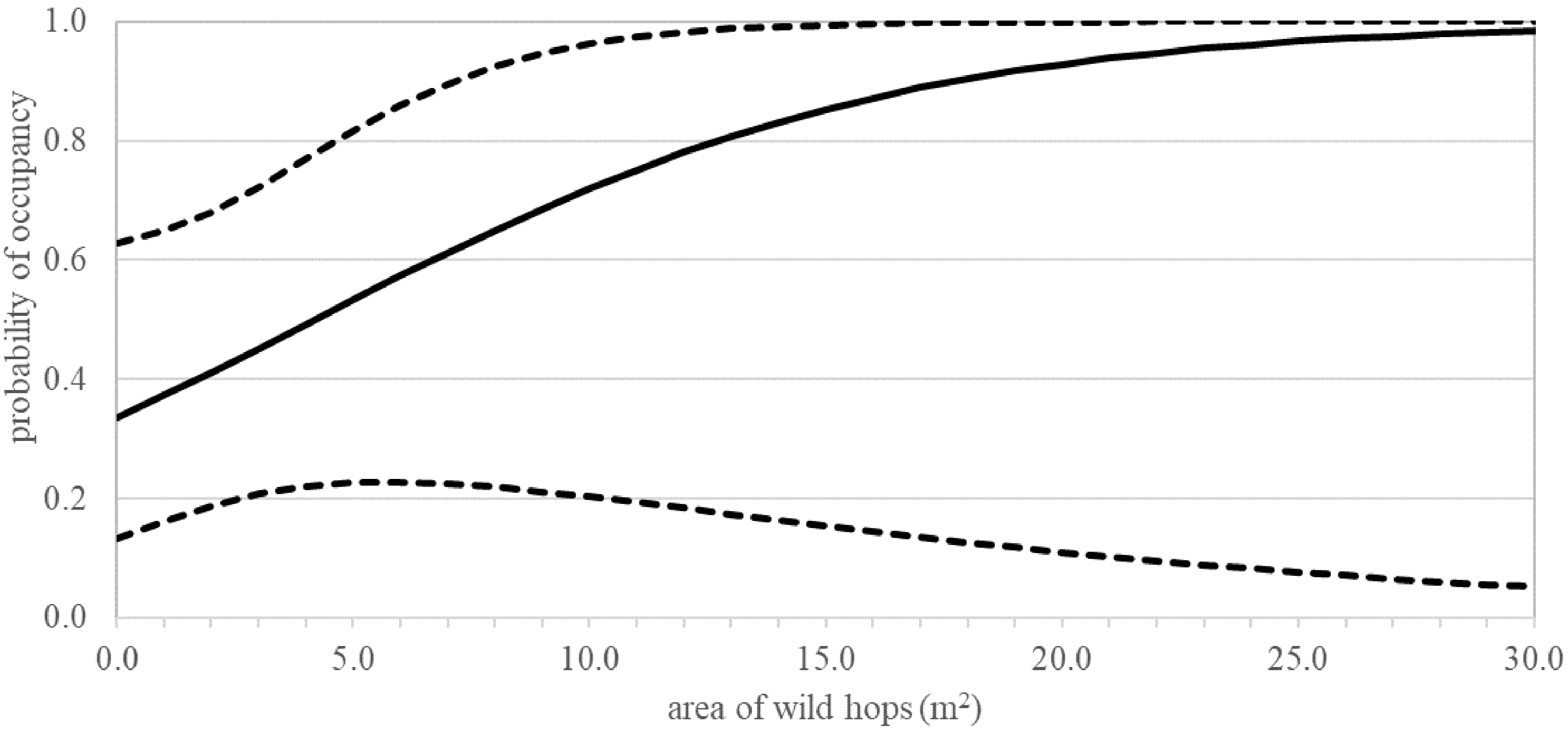
Figure 1. Probability of detection as a function of wind speed (mph; 2015), cloud cover (%; 2014), and solar exposure where butterfly was seen (%; 2015) along Monument Creek, U.S. Air Force Academy, Colorado Springs, Colorado, 2014-2015.

Figure 2. Probability of hops azure (*Celastrina humulus*) occupancy with area of hops (m^2) along Monument Creek, U.S. Air Force Academy, Colorado Springs, Colorado, 2014-2015.

Table 1. Most-parsimonious models of hops azure (*Celastrina humulus*) probability of habitat patch occupancy, colonizaiton, and extinction along Monument Creek, U. S. Air Force Academy, Colorado Springs, Colorado, 2014 - 2015. For all models, detection probability was modeled as a function of hops area and cloud cover in Year 1, and as a function of solar exposure, cloud cover, hops area, and wind speed in Year 2. AIC*c* is Akaike's Information Criterion, ΔAIC*c* is the difference in the model and the most-parsimonious model, *w* is the AIC*c* weight of the model, K is the number of parameters. *ψ* is the probability of occupancy, ε is the probability of patch extinction, and γ is the probability of patch colonization.

Model name	AIC*c*	Δ AIC*c*	*w*	K
ψ (2015 hops area), ε(2015 hops area squared) γ(constant over time periods)	442.62	0.00	0.34	13
ψ (2015 hops area), ε(2015 hops area) γ(constant over time periods)	443.35	0.74	0.24	13
ψ (2015 hops area), ε(2015 hops area squared) γ(2015 hops area)	445.00	2.39	0.10	14
ψ (2015 hops area), ε(constant over time periods) γ(constant over time periods)	445.07	2.45	0.10	12
ψ (2015 number of hops patches), ε(2015 hops area squared) γ(constant over time periods)	445.08	2.46	0.10	13
ψ (2015 hops area), ε(2015 hops area) γ(2015 hops area)	445.74	3.13	0.07	14


wind speed (miles per hour)
0.7
1.5
2.3
3.1
3.9
4.8
5.6
6.4
7.2
8.0
8.8
Probability of detection
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
cloud cover
solar radiation
wind speed
0
10
20
30
40
50
60
70
80
90
100
percent cover


1.0
0.8
0.6
0.4
0.2
0.0
probability of occupancy
0.0
5.0
10.0
15.0
20.0
25.0
30.0
area of wild hops (m²)