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Habitat-specific capture timing of deer mice (Peromyscus maniculatus) suggests that predators structure temporal activity of prey

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Risk, Rodents, and Activity Timing: Habitat-Specific Capture Timing of Deer Mice (*Peromyscus maniculatus)* Suggests That Predators Structure Temporal Activity of Prey

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Abstract

Timing is an essential component of the choices that animals make: the likelihood of successful resource capture (and predator avoidance) depends not just on what an animal chooses to do, but when it chooses to do it. Despite the importance of activity timing, our ability to understand the forces that constrain activity timing has been limited because this aspect of animal behavior is shaped by several factors (e.g., interspecific competitors, predators, physical conditions), and it is difficult to examine activity timing in a setting where only a single factor is operating. Using an island system that makes it possible to focus on the effect of predation risk in the absence of interspecific competition, we examine how the onset of activity of the deer mouse (*Peromyscus maniculatus*) varies between habitats with unique predation risks (i.e., minimal shrub cover versus abundant shrub cover sites). Using capture time to assess the timing of mouse activity, we found that mice in habitats with minimal shrub cover were captured 1.7 hours earlier than mice in habitats with abundant shrub cover. This difference in timing between habitats was likely a direct response to differences in predation risk between the two habitats: there were no differences in thermal conditions between the two habitats, and the difference in activity timing disappeared during a night when overcast skies reduced island-wide predation risk. Our results demonstrate that predation risk, independent of interspecific competition, can generate significant changes in animal activity timing. Our work suggests that habitat structure that provides safety (i.e., refuge habitats) play a direct role in the timing of prey activity and that habitat modification that alters refuge availability (e.g., shrub dominance) may alter the timing of animal activity.

Key words: animal condition, islands, predation risk, refuge, temperature loggers, trap timing}

INTRODUCTION

The daily timing of animal activity reflects the need for individuals to balance daily energy requirements via foraging (Kotler et al. 2002) or participating in other fitness-enhancing activities (e.g., territory defense), while simultaneously limiting the risk of either predation or exposure to adverse climatic conditions (Halle and Stenseth 2000 and references therein; Kronfeld-Schor and Dayan 2003). For example, examinations of activity timing inform prey survival and fitness (Halle 2000a), and estimates of activity timing can help explain important components of animal behavior (e.g., behavioral syndromes, Sih et al. 2004) as well as aspects of population and community ecology (e.g., predator-interactions and niche partitioning, Kotler et al. 1993; 2002; Halle 2000a; transmission and prevalence of zoonotic disease, Dizney and Dearing 2016). Small mammals, in particular, are well-suited for exploring the factors shaping animal activity patterns (Halle & Stenseth 2000). Predation risk has important effects on small mammal behavior in general (Brown& Kotler 2004; Monterroso et al. 2013) and is hypothesized to be a primary driver of small mammal activity patterns (Halle and Stenseth 2000 and references therein). However, activity timing can also be affected by interspecific competition (Hughes et al. 1994; Halle 2000b; Ziv & Smallwood 2000; Gliwicz & Dąbrowski 2008), abiotic conditions (e.g., Sears et al. 2006; Váczi et al. 2006; Pita et a. 2011), or characteristics of individual foragers (e.g., age, body size, Halle 2000b; Sears et al. 2006) making it challenging to evaluate the unique role that predation risk may play in shaping the timing of activity. Moreover, although the nature of predation risk is also highly dependent upon habitat structure (e.g., dense habitats may be places where rodents more easily escape detection or predation from mammalian predators and owls, Jacob & Brown 2000; Brown & Kotler 2004; Verdolin 2006) it is unclear whether differences in risk generated by habitat structure result in differences in the timing of small-mammal activity.

Islands are excellent natural systems to evaluate hypotheses regarding how predation risk shapes small mammal activity patterns, as predators clearly shape the behavior of island rodents (Orrock 2010; Orrock & Fletcher 2014; Thomsen & Green 2016) just as they shape the behavior of mainland rodents (Brown & Kotler 2004; Verdolin 2006; Kotler et al. 2010). Importantly, islands may have small-mammal communities with few or no interspecific competitors, making it possible to more clearly focus on the unique role of predation risk in shaping activity patterns. Islands are typically characterized by a reduced number of predator species, facilitating an evaluation of the role that particular predators might play in shaping small mammal behavior (Blumstein et al. 2000; 2004). Finally, island systems also contain habitats that differ in structure and predation risk (Orrock & Fletcher 2014), making it possible to examine hypotheses about how rodent activity timing is affected by particular predators in particular habitats. For example, we might expect that small mammals residing in habitat with dense vegetative cover may be active later at night in an effort to avoid strong overlap with peak activity windows of diurnal or crepuscular snakes (e.g., Diller & Wallace 1996; Ealy et al. 2004) that preferentially hunt underneath shrub cover (Kotler et al. 1993; Bouskila 1995; Bleicher et al. 2016). Small mammals residing in more open habitats may shift onset of activity sooner in the evening to minimize overlap with the activity times of nocturnal mammalian predators (e.g., foxes, skunks) or owls that move or hunt more commonly in open habitats (e.g., Laughrin 1977; Longland & Price 1991; Farías et al. 2012).

In this study, we use a recently developed trap-timing method (Orrock & Connolly 2016) to examine how capture timing of deer mice (Peromyscus maniculatus) on Santa Rosa Island differs among habitats that differ greatly in shrub cover, and thus in their overall predation risk. Peromyscus maniculatus is the only rodent species on the island and it serves as a prey item for a diverse community of predators: several species of owls, two mammals (island fox [Urocyon littoralis], western spotted skunk [Spilogale gracilis]), and one reptile (gopher snake [Pituophis catenifer pumilis]; Orrock et al. 2011). Previous studies have shown that the owls and mammalian predators affect island deer mouse behavior (Orrock 2010; Orrock & Fletcher 2014; Thomsen &

Green 2016), and we hypothesize that deer mice will be active earlier at sites with minimal shrub cover (i.e., more open sites) because by allocating activity to a time when these nocturnal predators are less active, rodents may reduce the risk of foraging in a location that is otherwise risky. Within dense vegetation (i.e., abundant shrub cover sites), we hypothesize that predation risk posed by snakes may result in deer mouse activity later at night because foraging later will reduce the risk of encountering these diurnal and crepuscular predators. Additionally, because our method of assessing activity time links timing with particular individuals (Orrock & Connolly 2016), we also evaluate the role of body size in affecting activity timing in different habitats.

METHODS

STUDY SYSTEM

Study sites on Santa Rosa Island (Lat: 33.99°; Long: -120.06°; Island Area: ~21,527 ha) were located in high- or low-density chaparral or coastal sage scrub vegetation communities. Briefly, chaparral on Santa Rosa Island is typified by the co-occurrence of island scrub oak (*Quercus pacifica*) patches interspersed between largely contiguous stands of prostrate chamise (*Adenostoma fasciculata* var. *prostrata* and *Adenostoma fasciculata* var. *fasciculata*). Coastal sage scrub habitat typically consisted of co-occurrence of California sagebrush (*Artemisia californica*) with intermittent occurrence of coyote brush (*Baccharis pilularis*) and scrub lupine (Junak et al. 2007). Shrub density varies within natural vegetation communities on Santa Rosa Island, most likely influenced by the island's historical use as pasture land (Junak et al. 2007). Santa Rosa Island is located 42 km from mainland and 5 km from the nearest other major island (San Miguel Island). Study sites on Santa Rosa Island were located 0.3 - 2.0 km from the ocean.

QUANTIFYING RODENT ACTIVITY

Deer mouse trapping and activity timing took place over five consecutive nights at 10 independent sites (2 sites per night) on Santa Rosa Island from 18-23 July 2016. Our trapping session occurred during a full moon (proportion moon illuminated during our study: 0.95-1.0). Starting at 15:30 each day, 16 Sherman live traps (23.5 cm [long] x 8.0 cm [wide] x 9.0 cm [tall]) were deployed in two 50-m, roughly perpendicular transects within two different sites (32 total traps per night). Live traps along one randomly selected transect at each site were equipped following Orrock and Connolly (2016) to measure mouse capture timing (see description below), live traps located along the second transect at each site were not equipped to measure capture timing.

Site selection included one site with abundant shrub cover and one site with minimal shrub cover site each night (72 ± 4% cover and 37 ± 6% cover, respectively; Appendix S1). Each site was located >300 m from the nearest other site to eliminate the possibility of recaptures. There were eight traps in each transect (spaced ~6 meters apart). Care was taken to position transects within physiognomically similar habitats with a substantial buffer (>30 m) from different habitat timing. structure. Transects were positioned at new sites each night in order to sample the largest number of individual mice. All traps were baited with rolled oats.

At each site, mouse capture timing was estimated for each trap located along one randomly-selected transect (16 activity timing traps per night, 8 timing traps per site) using the method described in Orrock and Connolly (2016). Briefly, in order to estimate capture timing two temperature data loggers (i.e., Thermochron iButtons®, Maxim-Integrated, San Jose, CA, USA) were deployed in an aluminum metal mesh bag and positioned so that one logger was located on either side of the trap's back door (i.e., one temperature logger was positioned inside the trap and a paired logger located just outside the trap). Mouse capture time was estimated by the time at which the temperature of the two loggers diverged (since endothermic mice heat the trap interior upon capture; Orrock and Connolly 2016).

At seven of the 10 sites, a second transect of traps, i.e., traps that were not setup to evaluate mouse capture time, allowed us to test if temperature logger deployment within the trap altered small mammal capture probability (Willis et al. 2009); supplementary analysis suggests there is no difference in capture probability between traps containing Thermochron iButton® temperature loggers (55 ± 11%, percent traps occupied ± SE) and those without temperature loggers (39 ± 10%; t = 1.07, d.f. = 11.8, *P* = 0.306, Appendix S2).

Traps were left overnight and then checked the following morning between 05:45-08:30. Captured mice were weighed and morphometric traits were noted. Mice were then released at the site of capture and temperature loggers were collected from each trap for data collection and estimation of trap entry time. Each trapping night and morning we noted important environmental conditions known to influence small mammal perception of predation risk (i.e., moon illumination, cloud cover).

Because foxes are important predators on island deer mice (Crooks and Van Vuren 1995; Orrock 2010, Orrock and Fletcher 2014), we estimated habitat-specific activity of island foxes around each transect immediately following the completion of each trapping session. We counted the number of individual scat piles located within 3-m on either side of the main transect (6-m x 50-m search area). Searching consisted of walking down the transect line and the parallel borders of the plot for approximately 15 minutes. Plots were checked for fox scat only after the trapping session had concluded; differences in detectability between the two habitat types are unlikely given the conspicuous nature of island fox fecal piles (e.g., feces can be present in latrines used by multiple foxes; Laughrin 1977) and the intensive nature of our search (20 m^2/minute).

DATA ANALYSIS

Our response variable was the duration of time in hours between sunset (range 20:05-20:07 hours) and the time of rodent capture; consequently, the capture time data were analyzed in time- to-event format. We used Cox's proportional hazard analysis to evaluate how differences in shrub cover related to the trap timing of island deer mice (we note that using different approaches, e.g., analysis of variance, lead to identical conclusions). Shrub cover was treated as categorical variables with two levels, abundant shrub cover versus minimal shrub cover. Given overcast conditions can fundamentally change island deer mouse foraging behavior (e.g., Orrock and Fletcher 2014) and the unbalanced nature of the design, we subset data prior to survival analysis into two groups: clear nights (i.e., no cloud cover overnight) or overcast nights (i.e., persistent cloud cover overnight). We note, however, results do not differ if both overnight conditions and shrub cover are included in the same model (Appendix S3, Table S1, Figure S2). All data analysis was conducted in the program R (R Core Team 2016), using package "survival" for the Cox's proportional hazard analysis (Therneau 2015) and "ggplot2" to generate density distribution figures (Wickham 2009).

RESULTS

We evaluated the capture timing of 39 individual P. maniculatus captured over the 5 night study period: 19 mice (10 females, 9 males) captured on minimal shrub transects and 20 mice (12 females, 8 males) captured on transects with abundant shrub cover. All captured mice were adults; only one male was reproductively active. The mass of individual P. maniculatus was greater in the abundant shrub habitat (20.6 ± 0.7 g) than the mice in the minimal shrub habitat (18.5 ± 0.7 g; F1,36 = 4.24, P = 0.047); this comparison excludes the single reproductively active male captured (24.0 g) given the disproportionate influence active reproductive status has on individual weight. No P. maniculatus were recaptured, i.e., every trap timing event represents the capture timing of a different individual. At least one trap remained unoccupied on each transect each night, suggesting that our estimates of activity time were not biased by the availability of open traps. The proportion of traps occupied each night did not differ between the two habitat types (abundant shrub cover: 0.50 ± 0.10 vs. minimal shrub cover: 0.60 ± 0.15; t = 0.55, d.f. = 7.1, P = 0.601). Average overnight temperatures and minimum temperatures (calculated between 19:00-06:00 hours) did not differ between for shrub-rich habitat (overnight temperature [±SE]: 14.9 ± 0.4°C, minimum temperature: 13.7 ± 0.4°C) and minimal-shrub habitats (overnight temperature: 15.5 ± 0.3°C, minimum temperature: 14.3 ± 0.2°C; overnight temperature comparison: t = 1.18, d.f. = 7.3, P = 0.272, minimum temperature comparison: t = 1.11, d.f. = 6.2, P = 0.308). Ambient temperatures at the time of capture on abundant and minimal shrub cover transects and on clear and overcast nights are reported in Appendix 4 (Fig. S3). The number of fox scat piles differed between the abundant shrub cover (0 scat piles, N = 5) and minimal shrub cover (3.0 ± 1.6 scat piles, N = 5) habitats; few foxes were also observed in these abundant shrub habitats compared to minimal shrub habitat (B.M. Connolly, personal observation).

We caught 27 *P. maniculatus* on clear nights (20-23 July 2016): 14 mice on abundant shrub cover transects and 13 mice on minimal shrub cover transects. On clear nights, we observed a significant difference in capture timing between the two habitats (β_i [SE] = 1.44 [0.47], z = 3.08, *p* = 0.002; Fig. 1A): individuals were captured 1.7 hours earlier on transects with minimal shrub cover (1.31 ± 0.23 hours, mean duration until capture after sunset ± SE) than on transects with abundant shrub cover (2.98 ± 0.37 hours). For *P. maniculatus* captured on clear nights, rodent mass did not interact with shrub cover habitat type to influence capture timing ($F_{1,22}$ =0.294, p= 0.593).

A single night was overcast during our study (19 July 2016). On this overcast night we caught 12 *P. maniculatus:* 6 mice on the abundant shrub cover transect and 6 mice on the minimal shrub cover transect. In contrast to our results for clear nights, there was no difference in the timing of capture between habitat types on the overcast night β_i [SE] = 0.83 [0.72], z= 1.14, p= 0.253) and the range of capture times spanned the entire night (Fig. 1B). Similar to results for individuals captured on clear nights, the interaction between individual *P. maniculatus* mass and shrub habitat type did not influence capture timing on this overcast night (($F_{1,8}$ *p* = 0.978).

DISCUSSION

Predators structure choices that prey make regarding habitat use and also alter the temporal pattern of predation risk (Brown and Kotler 2004; Verdolin 2006; Gorini et al. 2012), however less is known about how predators alter the timing of prey activity (but see Monterroso et al. 2013). Our results demonstrate that the timing of prey capture was strongly related to variation in habitat structure in a manner that is consistent with habitat-specific variation in overall risk. Moreover, capture time patterns within each habitat suggest that timing maximizes avoidance of predators that preferentially hunt in that particular habitat. Captures in more open, minimal shrub cover habitat occurred at times that would likely minimize encounter with owls and foxes, whereas later mouse activity in abundant shrub cover habitats may minimizes interactions with crepuscular gopher snakes. We observed these differences in prey activity timing in the absence of other factors known to affect activity timing (e.g., interspecific competition, thermal stress), as interspecific competitors are absent in this system and there were no detectable differences in thermal conditions between habitats that would generate physiological stress. Moreover, overcast conditions during one night of our study provide strong support for the role of predation risk in structuring the difference in timing we observed: on the night when overcast conditions reduced predation risk across the entire island, differences in activity timing between the two habitats disappeared (Fig. 1B). Mice often exhibit an increase in anti-predator behavior during nights with greater moon illumination because visual predators are more successful on such nights (Clark 1983; Kotler et al. 1988); overcast conditions eliminate or greatly reduce nocturnal illumination, leading to shifts in habitat use behavior of Channel Islands mice (e.g., Orrock and Fletcher 2014). In addition to demonstrating how prey activity may be shaped by habitatspecific variation in predation risk, our work suggests that changes in predation risk (e.g., via addition or removal of predator species, via modification of habitat structure) may have unappreciated effects on the timing of prey activity.

Differences in the nature of predation risk between habitats can directly inform patterns of deer mouse capture timing. We found evidence of temporal mismatch in P. maniculatus foraging within minimal- and abundant-shrub habitats and reported activity profiles for predators that preferentially hunt in these habitats, suggesting that mice time their activities to minimize the relative likelihood of encountering a predator. In open habitats and on clear nights, P. maniculatus captures began shortly after sunset (earliest capture: 20:37) and captures accumulated rapidly; eleven out of thirteen mice (85%) were caught before astronomical twilight (i.e., the onset of true dark; Fig. 1A). By being active earlier, P. maniculatus in shrub-poor habitats may minimize risk from predators that are effective in open habitats (i.e., island foxes, spotted skunks, barn owls), as these predators typically display peak activity after this time period. Crooks and Van Vuren (1995) report the greatest cumulative levels of diel activity for skunks and foxes from 20:00 to 24:00; a more recent report (Hudgens and Garcelon 2011) indicates island fox activity peaks starting one hour after civil twilight (21:33-21:36 hours during our study, Fig. 1A). No reports describe barn own (*Tyto alba*) diel activity on the California Channel Islands, but controlled behavioral studies suggest that barn owl activity begins soon after the onset of dark (Ekert 1969). Similarly, little is known about the summer activity timing patterns of the island gopher snake (*Pituophis catenifer pumilis*), but summer monitoring of two other *Pituophis* spp. suggests members of this genus are seldom active after darkness and aboveground activity decreases rapidly after 20:00 (Diller and Wallace 1996; Ealy et al. 2004). Snakes can be important predators on rodents, particularly during summer (Jones et al. 2001), and *P. maniculatus* capture timing within habitats dominated by abundant shrub cover (mean capture time: 23:02, Fig. 1A) suggests *P. maniculatus* may avoid gopher snakes by foraging later at night because colder night temperatures may limit snake activity. Importantly, additional evidence supports the primacy of predation risk as a factor structuring prey activity timing. Overcast conditions reduce nocturnal predation risk on deer mice island-wide (Orrock and Fletcher 2014) and, consistent with expectations, our study shows that habitat-specific patterns of *P. maniculatus* capture timing apparent on clear nights (Fig. 1A) are not apparent during overcast conditions (Fig. 1B). Overall, our work suggests that small mammal activity timing may be better understood by carefully considering how patterns of diel predation risk differ not only over small spatial scales (e.g., under shrub cover versus open, Kotler et al. 2010), but also between habitats with different dominant predators.

Observations of mouse activity during overcast conditions were limited to a single night. We cannot control for other factors possibly influencing behavior during that trapping session (e.g., rate of diurnal resource renewal, difference in insect prey availability or activity), but given that 1) our results are consistent with other independent and long-term evaluations of island mouse behavior during overcast conditions (Orrock and Fletcher 2014), 2) mice were less active on clear nights (3.4 captures per transect) than on the overcast nights (6.0 captures per transect), and 3) mouse capture timing responded similarly in two independent sites on the same overcast night (Fig. 1B) we consider reduced nocturnal predation risk one of the most likely drivers of this changes in small mammal behavior.

Predator and prey activity patterns, however, are not fixed. Prey activity patterns balance the necessity of foraging against the effectiveness of different predators across the diel and lunar cycles, the importance of a prey species in a predator's diet, and predator abundance within a habitat (Halle 1993). Predators can shift activity to maximize hunting efficiency and encounter rates with preferred prey species (e.g., microtine rodents, Halle 1993). Consequently, predator and prey activity patterns are likely to be in dynamic equilibrium, balancing the temporal availability of resources with the organism's aptitude for acquiring those resources. More data summarizing the concurrent activity time profiles for predators (i.e., foxes, skunks, and snakes) and prey (i.e., island deer mice) will help resolve the importance of activity timing in predator-prey relationships in these island habitats. Further, activity time sampling during other seasons or lunar phase on Santa Rosa Island or sampling on different neighboring islands with simpler predator communities will also help determine the extent to which resource acquisition or predator avoidance contribute to prey activity timing.

We also found that individual characteristics (i.e., body mass) correspond to differences in capture times between minimal and abundant shrub habitats; mice in minimal shrub habitats weighed less than mice captured in abundant shrub habitats. Individual animal condition may help structure time allocation and early foraging and lower body mass may indicate that the minimal shrub habitat is poorer quality than the abundant shrub habitat. Alternatively, mice in more open, riskier habitats may maintain lower body mass because of a constant trade-off between resource acquisition and safety, i.e., regulating body mass at lower values implies they may encounter certain predators less or find it easier to escape predators (e.g., Kotler et al. 1988). Our work demonstrates that, in the absence of interspecific competition, both prey size class distributions and predator community composition are important sources of variation in field studies evaluating small mammal behavior. Importantly, we did not detect an interaction between rodent mass and shrub habitat type, suggesting these factors may contribute independently to small mammal activity in this system. However, resolving and quantifying the independent contributions of habitat-specific predation risk and individual condition to small mammal activity timing will require further evaluation. Trap-timing studies could examine differences in space use and population size between habitat types by pairing activity timing studies with habitat use information provided by motion-sensing wildlife cameras deployed simultaneously at trapping sites. This joint approach could provide simultaneous estimates of predator density and community structure, predator activity patterns, and overall habitat use by predators and prey on a limited spatial scale (i.e., camera data) linked with prey activity timing measures and individual characteristics across a broader spatial scale (i.e., trap timing).

Our results suggest a strong link between habitat structure and the onset of small mammal activity. Natural disturbance or human-induced rapid environmental change (HIREC, Sih 2013) will likely generate scenarios that: 1) test the plasticity of individual animal behaviors (e.g., activity timing) to adapt to systems with novel structures and, similarly, 2) may alter predator-prey dynamics by influencing the effectiveness of static anti-predator behaviors. For example, nocturnal small mammal species differ in the degree to which their activity timing shifts as a function of seasonality or habitat (Diete et al. 2017), i.e., activity patterns are more conserved across habitats and seasons in some species than others. Natural communities are undergoing a constant process of simplification and fragmentation (e.g., Estes et al. 2011; Haddad et al. 2015), suggesting that the ability of animals to shift their behavior to better match their novel environment will directly influence their participation in community interactions (e.g., susceptibility as prey, consumption of vegetation). Given the tight connection we, and others (e.g., Diete et al. 2017), demonstrate between animal activity patterns and habitat structure, our work reiterates that a major, but under-examined, consequence of habitat alteration is the potential to generate mismatches between animal behavior and their habitats.

FUTURE DIRECTIONS

Behavioral plasticity is likely to be an important component in species' weathering habitat changes (Sih 2013) and behavioral mismatches within novel habitats may generate long-term population dynamics of endemic animal populations (and their predators) mediated in part through altered predation risk. Our work demonstrate that predation risk is a significant determinant of capture timing in small mammals, and our work highlights how these differences can be detected in field settings with free-living animals. However, the differences in timing that we document may also be driven by 1) differences in resource availability or resource renewal rates, 2) genotypic differences in mouse habitat selection and activity time, or 3) behavioral plasticity. Future studies that quantify diurnal resource deposition (e.g., via seed traps, pitfall traps) while simultaneously using common-garden or reciprocal-transplant designs to evaluate small mammal timing in different habitats will be essential for understanding the strongest drivers (e.g., temporal and spatial variation in resource availability or predation risk) of timing in natural populations. An additional, and untested, possibility is that there is a linkage between activity timing and natal habitat preference induction (Mabry and Stamps 2008). For example, mice born in open habitats might prefer those habitats and also exhibit patterns of timing that are optimal for that habitat.

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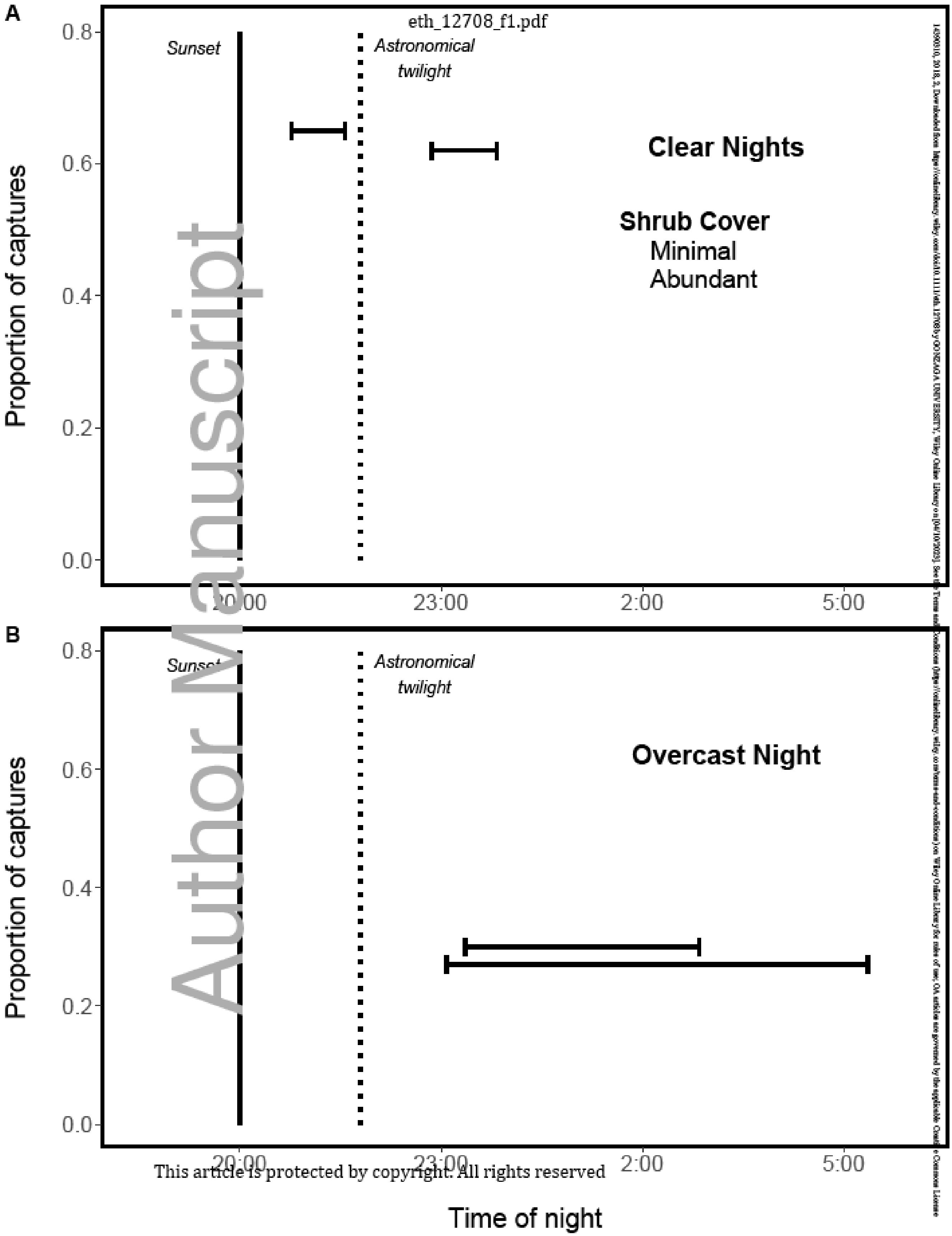
FIGURE CAPTIONS

Figure 1. **(A)** Deer mouse (*Peromyscus maniculatus*) capture time distributions on transects with minimal (light grey) or abundant (dark grey) shrub cover on clear nights for 20-23 July 2016 (N = 26 captures); (**B**) deer mouse capture time distributions on transects with minimal or abundant shrub cover on a single overcast night [19 July 2016; N = 12 captures]. Vertical lines denote transitions towards full dark: sunset (20:06 ± 2 minutes, solid line), and astronomical twilight (21:46 ± 2 minutes, dotted line) during our trapping session. Inset circular dots located above each capture time distribution represent mean capture time post sunset on transects with minimal (light grey) or abundant (dark grey) shrub cover with corresponding bars representing the 25% to 75% quartile range.


A
Proportion of captures
0.0
0.2
0.4
0.6
0.8
Sunset
Astronomical twilight
Clear Nights
Shrub Cover
Minimal
Abundant
20:00
23:00
2:00
5:00
B
Proportion of captures
0.0
0.2
0.4
0.6
0.8
Sunset
Astronomical twilight
Overcast Night
20:00
23:00
2:00
5:00
Time of night