Diversity, distributions, and activity of bats in the San Juan Islands

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Abstract

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The loss and fragmentation of natural habitats are some of the greatest threats to terrestrial biodiversity. Much of the practice of conservation science is rooted in Island Biogeography Theory (IBT). IBT postulates that species richness on islands is driven by a dynamic equilibrium between the effects of area on extinction rates and the effects of isolation on colonization rates. However, studies of plants and animals on oceanic islands and man-made habitat islands suggest that IBT needs to be broadened to consider additional habitat characteristics beyond area and isolation. Additionally, species-specific differences in ecology,

life-history, morphology, and mobility are all implicated to mediate how species respond to habitat fragmentation.

In Chapter one, I investigated how island area, isolation, and habitat quality influence species richness in a naturally fragmented landscape - The San Juan Archipelago. I also examined whether ecological traits or morphological traits associated with mobility mediate species-specific distribution and activity patterns on the islands. I found that species richness increased on larger islands, but was not affected by habitat quality or isolation at this scale. I also found that species with more specialized diets were less prevalent among the islands. I did not find that any morphological traits related to mobility influenced species distribution patterns.

In Chapter two, I analyzed activity patterns of bats on the San Juan islands. I found that the combined activity of all bat species was higher on larger islands and was not reduced on more isolated islands. My results suggest that islands with a greater abundance of potential roosting habitat (i.e., snag density) also have higher bat activity. I found that activity of larger bats tended to increase on islands with higher snag densities, but snag density had no influence on *Myotis* spp. activity. At the site scale, I found that *Myotis* spp. activity was positively related to canopy cover, whereas large bat activity tended to increase in more open habitats. Overall bat activity was also significantly higher adjacent to fresh water resources.

Considering the results of Chapters one and two together, large islands are necessary to maintain higher bat species richness, but small isolated islands also provide habitat for bats. Importantly, availability of fresh water resources is also important for bat activity in the region.

In Chapter three, I investigated how environmental characteristics in turn influence bat morphology. Specifically, I examined the intraspecific morphological variation in the Pallid Bat (*Antrozous pallidus*) and tested whether temperature, seasonality, or resource availability drive

size variation differences in this wide-ranging Western bat species. I found that primary productivity and, to a lesser extent, temperature (via heat conservation) explain Pallid bat size variation across its distribution. My results also indicate that larger bats possess morphological traits associated with greater bite force production. The results of this study suggest that variation in resource availability may be a key factor underlying spatial patterns in size, morphology and, possibly, feeding performance in bats.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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I am sure that I am forgetting more people that helped me along the way, and I am so sorry for this. I also have other animals to be grateful to for their support. My cat Odin and my dog Django have kept me sane these past years, and Django was also a great field assistant at times. Of course, I am also so grateful to all of the bats, which I thank for being the adorable, amazing, fascinating little animals that inspired this all.

DEDICATION

To my parents, who have always believed in me and that I could accomplish anything; without their support I could not be writing this.

EPIGRAPH

“ If at first the idea is not absurd, then there is no hope for it.” -Albert Einstein

Chapter 1. ISLAND AREA AND DIETARY BREADTH PREDICT DIVERSITY AND DISTRIBUTIONS OF BATS IN A PACIFIC NORTHWEST ARCHIPELAGO

1.1 ABSTRACT

Aim We investigated the effects of island area, isolation, and habitat quality on the diversity of bat species across temperate near-shore islands, and evaluated whether differences in morphological and ecological traits among species influence their prevalence across islands.

Location Twenty-one islands in the San Juan Archipelago and adjacent northwest coast of Washington State, USA. The size of surveyed islands ranged from 0.01 to 436.95 km^2, and their distance to the coast of Washington was between 0.35 and 35.58 km.

Methods We conducted presence-not-detected surveys for bats using mist net and acoustic surveys. We calculated total species richness using Chao 2 and first order Jackknife estimators. We fit linear regressions testing the effects of $\log_{10}$ island area, island isolation distance, canopy cover, snag density, and Old Growth Stand Index on bat species richness. We also tested whether ecological (dietary niche breadth, foraging guild) or morphological (body mass, forearm length, wing loading) traits affect species prevalence across the islands.

Results Across 21 of the San Juan islands and the North Washington coast, we detected a total of nine bat species using combined mist net and acoustic survey data. We found that island size strongly influenced patterns of species richness; larger islands have a greater number of bat species. However, neither island isolation nor any measure of habitat availability were significant predictors of species richness at the scale of this study. Additionally, we found that dietary niche breadth, as opposed to any morphological trait, best predicted the prevalence of species across the islands.

Main conclusions Our study provides insight into how geographic and ecological factors affect the diversity of insular bat communities. Furthermore, our results suggest that species with more specialized diets may be more vulnerable to habitat fragmentation. This adds to growing knowledge about the role of species' traits as mediators of their responses to large-scale landscape structure.

1.2 INTRODUCTION

Understanding the factors that underlie species' diversity and distributions is essential for conservation and management (Hughes et al. 2008, Puechmaille et al. 2011, Miller-Butterworth et al. 2014). Island Biogeography Theory (IBT) is one of the most well-known ecological theories explaining patterns of species richness among islands (MacArthur and Wilson 1967), and is widely applied to island-like systems (Matthews et al. 2015, Rabelo et al. 2017). IBT states that the equilibrium number of species is determined by the balance of immigration and extinction rates, which are driven by island isolation and area, respectively. Over the past fifty years, studies of many insular taxa (i.e., inhabiting islands or habitat patches) have found that species richness is explained by either island size, isolation, or both (Diamond 1975, Lomolino 1994, Frick et al. 2007a, Wang et al. 2009, Spengler et al. 2011, Franzen et al. 2012). However, despite broad support for the species-area relationship (SAR), there is still debate about the mechanism generating this pattern. In classical IBT, area is thought to directly affect species richness because larger islands support larger populations, which are in turn less vulnerable to stochastic extinction (MacArthur and Wilson 1967). Additionally, the 'target effect' hypothesis proposes that larger islands have more species because they are larger targets for colonizing individuals (MacArthur and Wilson 1967, Gilpin and Az 1976, Lomolino 1990). Alternatively, area may indirectly influence species richness via its effects on habitat, for example if greater area is associated with greater habitat diversity or availability, which in turn would facilitate species coexistence through niche partitioning (MacArthur and Wilson 1967, Kohn and Walsh 1994, Marini et al. 2010). However, distinguishing the contributions of area and habitat to species richness is often confounded by their intercorrelation (Kohn and Walsh 1994, Kallimanis et al. 2008a). Several authors have further suggested that the mechanisms underlying the habitat and area relationships are not mutually exclusive (Triantis et al. 2003, 2009, Marini et al. 2010), and that their relative influence depends on the traits of the taxa under consideration (Ricklefs and Lovette 1999, Yu et al. 2012).

Traits that influence a species' ability to colonize and persist on islands or habitat patches are key mediators of how their richness is affected by area, habitat, and isolation (Wright 1981, Lomolino 1994, Bommarco et al. 2010, Marini et al. 2010, Franzen et al. 2012). There is growing evidence that traits related to mobility and niche breadth may underlie how species respond to island characteristics and how they are affected by habitat fragmentation (Henle et al. 2004, Prugh et al. 2008, Wang et al. 2009, Marini et al. 2010, MacDonald et al. 2018). Species with high dispersal capabilities are predicted to be less affected by island area and isolation because of their capacity to move more efficiently between islands or habitats (Wright 1981, Lomolino 1984). For example, birds and bats are often expected to be less sensitive to the effects of habitat fragmentation (Lomolino 1984, Koh et al. 2002, Yu et al. 2012). Similarly, species that can exploit a broader range of resources (e.g., diet or habitat generalists) are predicted to meet their resource needs in a wider variety of habitats (Swihart et al. 2006, Bommarco et al. 2010).

Among volant animals, traits related to both mobility and diet breadth seem to mediate how species are impacted by habitat loss and fragmentation (Bommarco et al. 2010, Ockinger et al. 2010, Bueno et al. 2018). Recent studies in birds (Matthews et al. 2014, Dondina et al. 2017) and lepidopterans (Ockinger et al. 2010, Franzen et al. 2012) suggest that highly mobile, generalist species can better withstand the negative effects of habitat loss when compared to specialists with limited dispersal ability. In this study, we use bats –the only mammals capable of flight– as a model to understand the relative effects of area, isolation, and habitat in shaping the diversity and distributions of highly mobile species in a near-shore archipelago. With over 1,300 species, bats are critical contributors to ecosystem functioning, and nearly a quarter of all species are threatened or endangered (Kunz et al. 2011). Therefore, clarifying how species' traits influence how bats respond to habitat fragmentation is valuable for setting conservation priorities. For some bat species, isolation of only 10-15 km reduces colonization of near shore oceanic islands from the mainland (Frick et al. 2007a). Moreover, near shore islands provide a natural experiment for investigating the effects of area, isolation, and habitat on bat species richness because they lack the confounding influence of surrounding matrix habitat quality (Prugh et al. 2008, Duchamp and Swihart 2008, Chazdon et al. 2011, Mendenhall et al. 2014b). These islands can also serve as baselines for future investigations of the effects of anthropogenic habitat fragmentation (e.g., habitat islands; Mendenhall et al., 2014).

Our first objective was to test whether Pacific Northwest bats follow the equilibrium patterns predicted by the IBT. Specifically, we predicted that species richness is positively related to island area. Additionally, we tested whether habitat quality and dispersal limitations affect species richness of Pacific Northwest bats in a near shore archipelago. We predicted that species richness would be positively related to availability and diversity of habitats and ecological resources within the islands, and that island isolation would reduce species richness. Our second objective was to evaluate whether differences in morphological or ecological traits among species influence their prevalence among the islands, as a proxy for their sensitivity to fragmentation. We predicted that species with more specialized diet and foraging behavior, and wing morphology that would confer lower dispersal abilities, would have more restricted distributions among the islands.

1.3 METHODS

1.3.1 *Study area*

The San Juan Archipelago is located in Northwestern Washington State, USA, and is comprised of over 400 rocks and islands (Miller et al. 1935). The San Juan islands are characterized by a moderate maritime climate, with summer average temperatures ranging between 15 and 24 °C (Tucker and King 2012). The rain shadow caused by neighboring coastal mountains reduces precipitation on the islands, which generally receive less than 75 cm of rain annually. Approximately 55% of the land area in San Juan County is forested and dominated by Doulas-Fir and Western Red Cedar. The remaining vegetation on the islands is comprised of agricultural, grassland, and riparian ecosystems (Tucker and King 2012).

1.3.2 *Data collection*

Between 2014-2017, we carried out presence/absence surveys of bat communities along the North Washington coast and a subset of the San Juan Islands (n = 21) representing a gradient of size and isolation (Fig.1.1, Table 1.1). We used a combination of standard bat surveying techniques (mist netting and ultrasonic acoustic surveys). In order to account for species detection biases that are inherent to these different methods, we combined survey techniques across study sites (Flaquer et al. 2007).

1.3.3 *Acoustic surveys*

We carried out acoustic surveys using Songmeter SM2+BAT 192 kHz full-spectrum bat detectors (Wildlife Acoustics Inc., Concord, MA). We recorded in full spectrum formant, and mounted omnidirectional microphones (SMX-U1) on poles 3.7 m off the ground and at least 3 m from any 'clutter' (e.g., trees or buildings) in order to minimize acoustic reflections and maximize the probability of recording diagnostic "search phase" echolocation calls (Russo et al. 2018).

We scaled the number of recording sites per island proportionally with island size (range: 1-11, Table S1.1). We deployed bat detectors at multiple sites across 19 of the 21 islands in our sample, representing all the habitat types present on each island (Fig. 1.1). The habitats of the recording sites included forest gaps and edges, hiking trails, lakes, ponds, grassy knolls and fields, and coastlines. At each site, we passively recorded bat activity for 2-6 nights, and programed detectors to automatically record bat activity from 30 minutes prior to sunset until 30 minutes after sunrise each night. In order to account for seasonal and/or nightly variation in bat activity during the course of the study, we conducted at least two surveys at each site, with at least one in May-July and one in July-September, and surveyed most sites in multiple years (Table S1.1).

1.3.4 *Mist net surveys*

We conducted mist net surveys to verify the identification and occurrence of species on the majority of islands (*n* = 15). We scaled the number of mist net survey sites on larger islands proportionally to their size (Range: 2-14), and resurveyed most sites 1-3 times between May - September over the course of 2-3 years (Table S1.1). At each mist netting site, we deployed mist nets (2-18 m in length and 2.6-7.8 m height) over ponds, and along trails, forest gaps, and creeks. We checked mist nets every 5-10 minutes starting at dusk, and left them open for two to five hours each night.

We captured and handled bats in accordance with the American Society of Mammalogists' guidelines, and UW IACUC Protocol #4307-01. Upon capture, we initially placed each bat in a clean cotton bag. We identified each bat using existing taxonomic keys (Nagorsen 2002), although we did not attempt to distinguish *Myotis evotis* and *M. keenii* because morphological traits are not reliable to distinguish them, and recent genetic evidence suggests they represent one interbreeding species (Lausen et al. 2019). Additionally, to confirm accurate identification of *M. lucifugus* and *M. yumanensis*, for which morphological identification may be unreliable (Weller et al. 2007, Rodhouse et al. 2008, Luszcz et al. 2016), we recorded full spectrum echolocation calls upon release using an Echometer Touch (Wildlife Acoustics Inc., Concord, MA). We used these recordings to distinguish these species based on the minimum frequency of their echolocation calls, following Luszcz *et al.,* (2016). We also sexed individuals, and distinguished between juveniles and adults by examining the degree of ossification in the metacarpal-phalangeal joint of the wing (Anthony 1988). We released juvenile bats and fitted adult bats with a uniquely numbered, lipped 2.4 or 2.9 mm aluminum forearm band (Porzana, Ltd, Icklesham, East Sussex, UK) to identify recaptures. Finally, we collected a 2-3 mm wing biopsy from adult bats using a punch biopsy curette (Miltex Inc, York, PA) prior to releasing them.

In order to further confirm field identification *M. lucifugus* or *M. yumanensis,* we used wing biopsy samples for molecular species identification. We used Qiagen$^{\text{TM}}$ DNEasy tissue extraction kits to extract DNA, then amplified an approximately 300-base-pair (bp) fragment of the mitochondrial control region, hypervariable II domain (HVII) using the primers and PCR conditions described in Burns (2014). We sent the resulting PCR products to MCLAB (San Francisco, CA) for PCR clean up and bi-directional Sanger sequencing using primers L16517 and KAHVII (Burns and Al 2014). We then edited and generated consensus sequences using Geneious 9.0.4 (Biomatters Inc., Newark, NJ, USA) and aligned sequences using the MUSCLE alignment (Edgar et al. 2018) in MEGA 7 (Kumar et al. 2018). We compared our sequences to a local library of previous identified sequences (Bonwitt et al. 2018) to confirm field identifications.

1.3.5 *Species traits*

We compiled data on ecological and morphological traits from our own captured animals and from the literature (Table 1.2). We focused on three morphometric/morphological traits commonly used in bat studies: body mass, wing loading, and forearm length. As measures of body size, we calculated mean forearm length (mm) and body mass (g) from our capture data for all species except *Lasiurus cinereus* (never captured in our study), for which we included data from Nagorsen (2002). We took wing loading (N/m^2) values from Norberg & Rayner (1987). We included two ecological traits previously implicated in influencing sensitivity to fragmentation and extinction risk in bats: foraging guild (Meyer and Kalko 2008) and dietary niche breadth (Boyles and Storm 2007). We assigned each species to one of four foraging guilds (open aerial, edge aerial, gleaning, or trawling) following the classifications in Denzinger & Schnitzler (2013) and published sources (Fellers and Pierson 2002, López-González et al. 2016, Segura-trujillo et al. 2018). Finally, we took dietary data previously collected in the Pacific Northwest for all of the species in our study (Ober and Hayes 2008) to estimate dietary niche breadth. Using the mean percent volume of food items identified in guano samples, we calculated niche breadth using Levin's index (Levins 1968):

$$B = \frac{1}{\Sigma {p_i}^2}$$

where B = Levin's measure of niche breadth and p_i = the proportion of prey category i in the diet.

1.3.6 *Island characterization*

For each island, we calculated the area (km^2), isolation (m), and several measures of habitat availability and diversity using ArcGIS 10.6 (ESRI, Redlands CA; Table 1.1). We defined isolation as the shortest over-water path from each island to the nearest coastline of mainland Washington State. At the landscape level, Pacific Northwest bat distributions are significantly associated with forest availability and structure (Erickson and West 2003, Rodhouse et al. 2015). Therefore, for each island, we extracted proxy measures of roosting and foraging habitat availability, and diversity of forest structure using a 30-m resolution gridded forest structure dataset (LEMMA 2014). Snags (e.g., dying or dead trees) provide important roosting habitat for bats in Western North America (Arnett and Hayes 2009, Lacki et al. 2012), so as a measure of roosting habitat availability, we calculated the mean density of snags ≥ 25 cm diameter at breast height and ≥ 2 m height. As a proxy for habitat availability, we calculated the mean percent canopy cover of all live trees. We calculated the mean regionalized old-growth structure index (OGSI) as a measure of habitat diversity. OGSI is a composite measure of the abundance of large live trees, snags, and the diversity of tree sizes; higher OGSI values represent forest structure associated with old-growth forests in the Pacific Northwest (Davis et al. 2015).

Finally, we calculated correlation coefficients between each of the habitat variables and island area to determine whether they were significantly correlated with island size.

1.3.7 *Species identification Using Acoustics*

We initially processed and filtered full spectrum acoustic files using Kaleidoscope Pro 4.2.0 (Wildlife Acoustics Inc., Concord, MA). In order filter out noise files from bat echolocation calls, we only retained files that contained at least three calls with frequencies between 8-120 kHz and 2-50 ms in duration. These characteristics match call sequences for Pacific Northwest bat species (Reichert et al. 2018). We also used Kaleidoscope Pro's North American Bat Classifier 4.2.0 to assign preliminary species identifications. We then converted all echolocation call files to 8-division zero-crossing format (division ratio 8) within Kaleidoscope Pro.

To confirm species identifications, we also identified echolocation call files manually in AnalookW 4.1 (C. Corben, Columbia, Missouri). We used the diagnostic pulse parameters described in Lausen et al. (2014) to confirm Kaleidoscope Classifier species assignments. We subsequently discarded any call files with conflicting species assignments between automated and manual identification. Furthermore, we used a conservative approach to confirm species presence via acoustic identification alone. If a species had not been captured using mist net surveys on an island, we required a minimum of three separate call files with consistent species assignment to confirm species presence.

1.3.8 *Species richness models*

We conducted all statistical analyses in R v3.4.3 (R Core Team 2017). We initially visualized island survey completeness through species accumulation curves using the ‘speccacum’ function in the package *Vegan* (Oksanen et al. 2012). Since some island inventories had not yet reached an asymptote (Gotelli and Colwell 2001), we computed sample-size based rarefaction and extrapolation of species richness with 100 bootstrap replicates using the ‘iNext’ function in the *iNext* package (Hsieh et al. 2016). We then calculated total species richness using *Chao 2* and first-order jackknife estimators using the ‘specpool’ function in the *Vegan* package (Oksanen et al. 2012). As a measure of sampling completeness, we calculated the percentage between the observed and *Chao 2* extrapolated number of species per island.

To identify which island parameters best explain patterns of species richness, we developed two candidate sets of models, using either observed or extrapolated species richness as the response variable. We then fit linear regressions including the main effects of area (km^2), isolation (km), canopy cover (%), Old Growth Stand Index (OGSI), or snag density (trees/ha) as explanatory variables. To enable comparisons of effect sizes, we standardized each explanatory variable by first centering values relative to the mean, then scaled them to their standard deviation. Finally, we used Akaike’s Information Criterion corrected for small sample size (AIC_c), ΔAIC_c, and relative Akaike weights (*w*) to select top ranking models (Burnham and Anderson 2002).

1.3.9 *Species prevalence models*

Species prevalence is commonly used as a proxy measure for vulnerability to habitat fragmentation (Meyer et al. 2008, Wang et al. 2009, 2015, Bueno et al. 2018). Therefore, we calculated the proportion of surveyed islands that each species occupied as a measure of their sensitivity to habitat fragmentation. We then fit linear regressions including the main effects of each of the five species traits: diet breadth, foraging guild, body mass (g), forearm length (mm), and wing loading (N/m^2). To enable comparisons of effect sizes, we standardized each explanatory variable by first centering values relative to the mean, then scaled them to their standard deviation. Finally, we used Akaike's Information Criterion corrected for small sample size (AIC_c), ΔAIC_c, and relative Akaike weights (w) to select top ranking models (Burnham and Anderson 2002).

1.4 RESULTS

Across 21 of the San Juan islands and the North Washington Coast, we detected a total of nine bat species using a combination of mist net and acoustic surveys (Table 1.1). We carried out 108 mist net survey nights at 71 sites across 15 islands, and captured a total of 699 individuals representing eight species. The total number of individuals captured per island ranged from 3 to 128 (mean ± SD = 44 ± 32, Table S1.1). We also conducted acoustic surveys at 121 sites across 21 islands, and recorded 602 'detector-nights.' This generated a total of 2,020 bat call files that met our criteria to confirm species presence (see *methods*), and allowed us to record the presence of seven species. The number of identifiable bat call files recorded on each island ranged from 3 to 261 (mean ± SD = 92 ± 79, Table S1.1).

1.4.1 *Species richness*

Between our combined mist net and acoustic survey dataset, the number of species detected per island ranged from 2 to 9 (mean ± SD = 6.18 ± 2.21; Table 1.1). Extrapolated *Chao 2* species richness ranged from 2 to 9.49 (mean ± SD = 6.24 ± 2.24) and completeness of our island surveys ranged from 84% to 100% (mean ± SD = 98.81 ± 3.59%) relative to the estimated number of species. Species accumulation curves all reached an asymptote when species richness was extrapolated to twice the reference sample size (Fig. 1.2). Interestingly, both observed and extrapolated species richness were higher among the largest islands than on the mainland coast of Washington (Table 1.1).

We performed linear regressions to test for the effects of island size, isolation, and habitat availability on species richness. Results were nearly identical whether observed or estimated species richness was used. Therefore, here we focus on the results using estimated species richness. Species richness estimators (*Chao* 2 and first-order jackknife) were highly correlated ($r^2 = 0.97$, $P < 0.001$), thus we present results using the *Chao 2* estimated species richness. Island size ($\log_{10}$ transformed) emerged as the only significant predictor of species richness ($r^2_{adj} = 0.66$, $F_{1,19} = 39.81$, $P < 0.001$; Fig. 1.3a) and was clearly the top-ranking model ($\Delta AIC_c = 0$, $w = 1$, Table 1.3). In contrast, neither island isolation nor any of the indices of habitat availability (canopy cover, snag abundance, and Old Growth Stand Index) received considerable AIC_c model support (Table 1.3). Although there was a slight decline in species richness with increasing distance from the mainland, isolation also had no significant effect ($r^2_{adj} = -0.03$, $F_{1,19} = 0.23$, $P = 0.64$), nor received considerable AIC_c model support (Table 1.3). None of the habitat variables were significant predictors of species richness ($P > 0.05$), nor were they significantly correlated with island area ($P > 0.05$).

1.4.2 *Species prevalence*

Prevalence of the nine species detected among the islands ranged from 27% to 91% (mean ± SD = 67 ± 8%). Diet breadth emerged as the only significant and positive predictor of species prevalence across islands ($r^2_{adj} = 0.52$, $F_{1,7} = 9.51$, $P = 0.017$; Fig. 1.3). This result was highly supported based on *AICc* values ($\Delta AIC_c = 0$, $w = 0.93$, Table 1.4). Despite a strong effect of diet breadth on species prevalence, we found no evidence that discrete foraging guilds differed in their prevalence among the islands ($r^2_{adj} = 0.29$, $F_{3,5} = 0.70$, $P = 0.59$). Similarly, we found minimal support for models including any of the explanatory variables associated with mobility (body mass, forearm length, or wing loading; Table 1.2), and none of these were significant predictors of species prevalence ($P > 0.05$, Table 1.4).

1.5 DISCUSSION

As predicted by Island Biogeography Theory (IBT), we found a positive relationship between bat species richness and island size. A positive species-area relationship (SAR) in the temperate, near-shore archipelago focal to this study is consistent with patterns found in other animals that inhabit natural and anthropogenic archipelagos (Koh et al. 2002, Frick et al. 2007a, Jonsson et al. 2011, Mendenhall et al. 2014b). Although habitat diversity has been hypothesized to explain SARs, our results do not support this rationale for temperate bats. Neither measure of habitat availability (canopy cover or snag density) nor habitat diversity (Old Growth Stand Index) significantly influenced species richness in our study (Table 1.3). Although several studies have found that species richness can be predicted from habitat quality or diversity (Ricklefs and Lovette 1999, Frick et al. 2007a, Kallimanis et al. 2008b, Marini et al. 2010), others have found little or no evidence for this relationship (Newmark 1986, Ricklefs and Lovette 1999, Koh et al. 2002, Panitsa et al. 2006). A potential explanation for this discrepancy is that particular habitat variables may not be crucial to the taxa under investigation (Triantis et al. 2003). For example, Newmark (1986) found that vegetation cover diversity failed to predict species richness of North American mammals and suggested that vegetation cover may not accurately reflect habitat diversity as perceived by the species. Although it is possible that our choice of habitat characterization influenced our results, forest availability and structure are known to be critical foraging and roosting resources for temperate bats (Erickson and West 2003, Zielinski et al. 2007, Arnett and Hayes 2009, Rodhouse et al. 2015). Interestingly, our results are consistent with the findings of Ricklefs & Lovette (1999), who also found that island area, as opposed to habitat diversity, best predicted species richness of bats among the Lesser Antilles. These findings suggest that bats may be less sensitive to habitat diversity if they have highly flexible habitat use (Ricklefs & Lovette, 1999). Many temperate bat species are able to modify their foraging strategies behaviorally in order to exploit a variety of habitats (Brigham 1991, Faure and Barclay 1994, Ratcliffe and Dawson 2003), which could explain the patterns found here for bats in the San Juan archipelago.

The observed positive species-area relationship may be attributed to the effects of island size on immigration, extinction, or a combination of both. Consistent with classical IBT, bat species richness may be higher on larger islands because populations are larger and thus less vulnerable to stochastic extinction (MacArthur and Wilson 1967). Alternatively, our results may also be explained by the 'target effect' hypothesis (MacArthur and Wilson 1967, Gilpin and Az 1976); it is possible that bats colonize larger islands more frequently because they represent a larger target habitat. Although the target effect is often overlooked, there is evidence that colonization rates of birds (Russell et al. 2006) and terrestrial mammals (e.g., wolves; Lomolino, 1990) increase with island size. Lomolino (1990) suggested the target effect may be more pronounced in systems involving taxa with high dispersal ability. Since isolation did not have a significant influence on species richness in our system, dispersal ability does not seem to be a limiting factor at the scale of our study.

Although we cannot distinguish whether area is influencing immigration or extinction rates, it is likely that both may play a role to differing degrees among species. For example, the Hoary bat (*Lasiurus cinereus*) is migratory, capable of flying hundreds of kilometers on a seasonal basis (Weller et al. 2016). Considering the scale of movements in this species, it seems plausible that larger islands may represent larger targets for colonizing individuals. In contrast, the rest of the bat species found in the study area are not considered migratory. If they establish resident populations, their distributions more likely to be influenced by area effects on population persistence. Although there is a dearth of information about the overwintering ecology of most Pacific Northwest bat species (Weller et al. 2018), there is evidence that at least some species establish resident populations on near shore islands (Burles et al. 2014). Moreover, our recapture data suggests individuals of at least some species return to the same islands year after year (e.g., 7 *Myotis californicus* individuals were recaptured at the same sites across four islands over the course of 3 years; R.M. Kelly, personal observation).

Identifying traits that influence how species respond to habitat loss and fragmentation is useful for informing conservation priorities (Swihart et al. 2003, 2006, Henle et al. 2004, Duchamp and Swihart 2008). For example, habitat specialization can be used to predict extinction risk among neotropical birds in forest fragments (Lees and Peres 2008). In our study, we used species prevalence as a proxy of sensitivity to habitat fragmentation (Swihart et al. 2006, Wang et al. 2009, 2015, Farneda et al. 2015). Simulations and empirical data support the notion that patch occupancy rates are a good indicator of population viability in fragmented landscapes (Vos et al. 2001, Swihart et al. 2006). Dietary niche breadth emerged as the only species trait associated with sensitivity to natural habitat fragmentation across the nine temperate bat species in our study (Table 1.4). These results suggest that bat species with more specialized diets are most sensitive to fragmentation. Dietary niche breadth is also negatively related to fragmentation sensitivity in other temperate vertebrates (Swihart et al. 2006) and to extinction risk among temperate insectivorous bats (Boyles and Storm 2007). However, traits associated with fragmentation sensitivity also vary among taxa and geographic regions. For example, among Neotropical bats, wing morphology and edge sensitivity, as opposed to dietary specialization, emerge as important predictors of fragmentation sensitivity (Meyer et al. 2008, Farneda et al. 2015). Although wing morphology is also related to extinction risk in temperate bats (Safi and Kerth 2004), we found no evidence that wing morphology influenced sensitivity to habitat fragmentation in our study. All nine species in our study belong to the family Vespertillionidae, which are less variable in terms of wing morphology and diet than species within most Neotropical bat communities (Farneda et al. 2015). The importance of particular species traits as habitat sensitivity predictors may depend on how variable the traits are within the source community, as well as how they are estimated. For example, although there is more dietary diversity among species within Neotropical bat communities, Meyers *et al.* (2008) and Farneda *et al.* (2015) categorized dietary specialization into one of three discrete categories. Thus, a lack of a dietary signal to habitat fragmentation in these studies could be due to the limited resolution of dietary classifications.

In our study, we found that island area best explains patterns of species richness among Pacific Northwest bats, and that bat species with more specialized diets may be more vulnerable to natural habitat fragmentation. In contrast, we did not find any evidence that habitat diversity explains the species-area relationship, or that morphometric proxies of vagility predict sensitivity to habitat fragmentation. Our results are consistent with the findings of Rickleffs & Lovette (1999), who suggested that bats may not be as sensitive to habitat diversity relative to other taxa (e.g., butterflies and lizards). However, regional differences in island characteristics indicate that habitat diversity may play a role in species diversity in other bat communities (Frick et al. 2007a). Although habitat diversity did not emerge as a predictor of species richness at the island scale, this does not rule out its importance for species-specific distributions and abundances among fragmented landscapes. Habitat fragmentation disproportionately affects species with particular combinations of traits (Newbold et al. 2012). Although dispersal ability does not appear to be limiting in this system, we show that dietary specialization is linked with fragmentation sensitivity among temperate bats. This adds to growing evidence that ecological traits mediate how species respond to landscape structure (Swihart et al. 2006, Duchamp and Swihart 2008, Ockinger et al. 2010).

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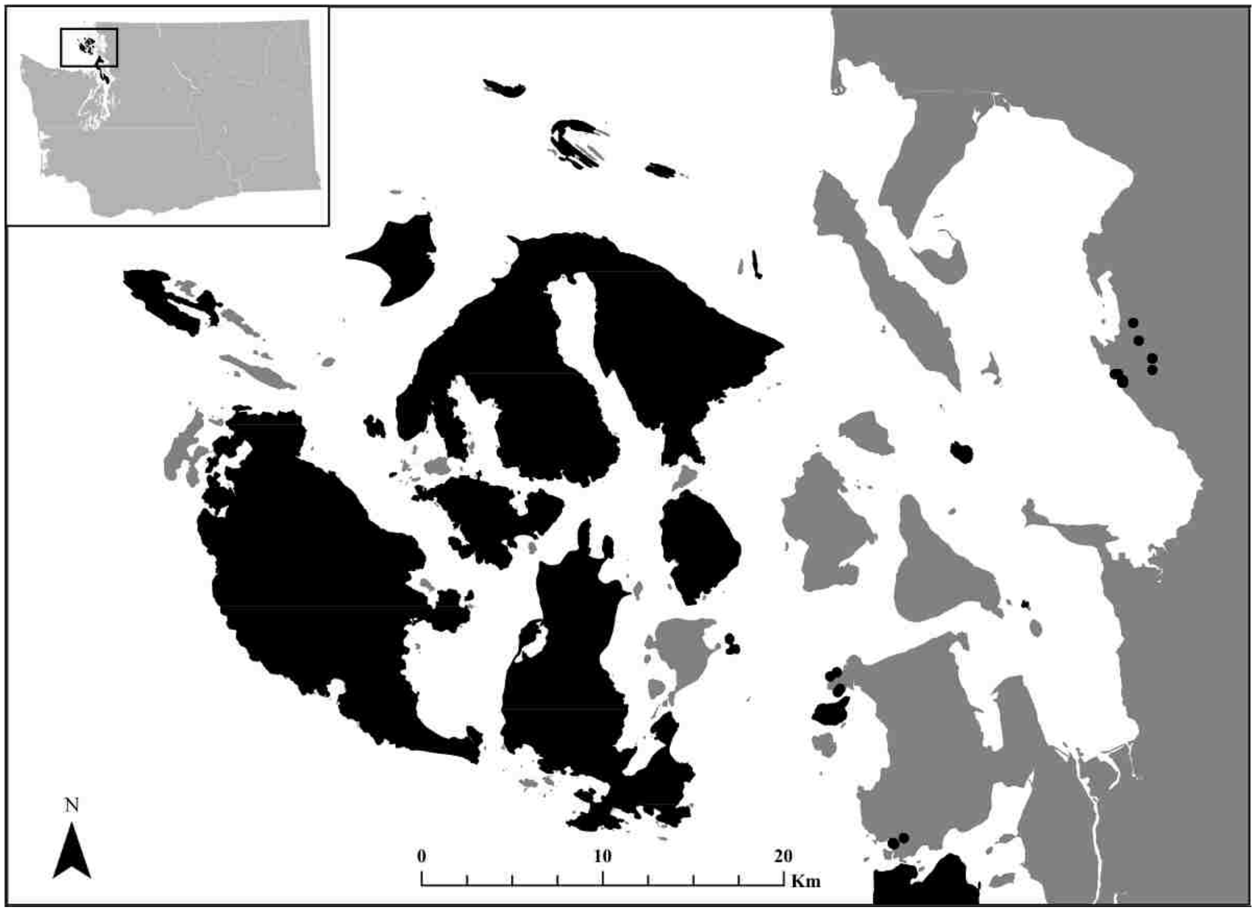

Figure 1.1. Map of the study area in the San Juan Archipelago and the Northwest coast of Washington State, USA. Surveyed islands (in *black*) and mainland survey sites (*dots*).

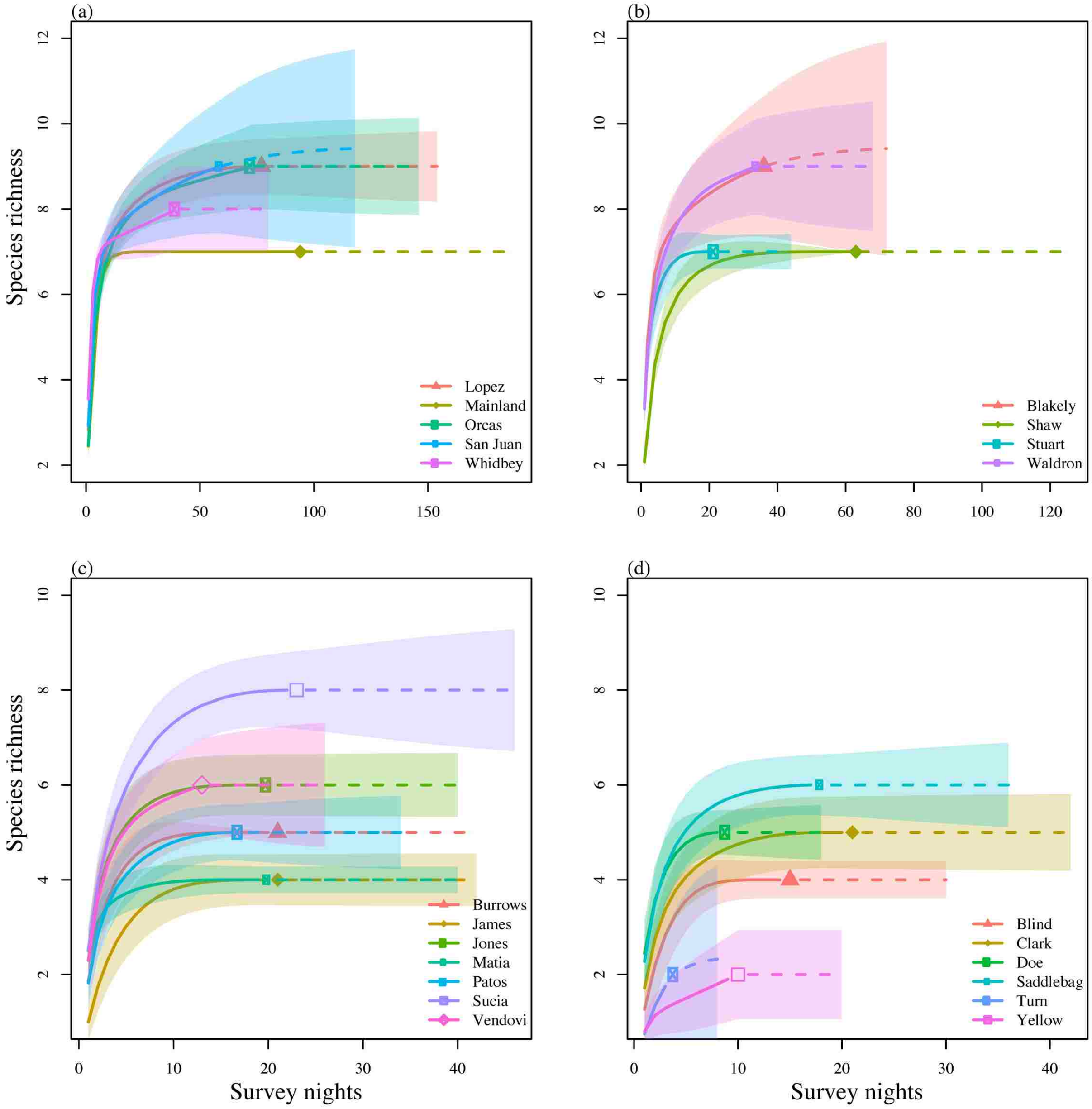

Figure 1.2. Species accumulation curves of bat species richness (Chao 2) for 21 islands in the San Juan Archipelago. Interpolated species richness is indicated by solid lines and extrapolated species richness (Chao 2, see methods) is indicated by dashed lined. Species accumulation curves are separated by island size as follows: (a) islands greater than 50 km^2 (b) islands between 50-5 km^2(c), and islands between 5-0.5 km^2(d) islands less than 0.5 km^2.

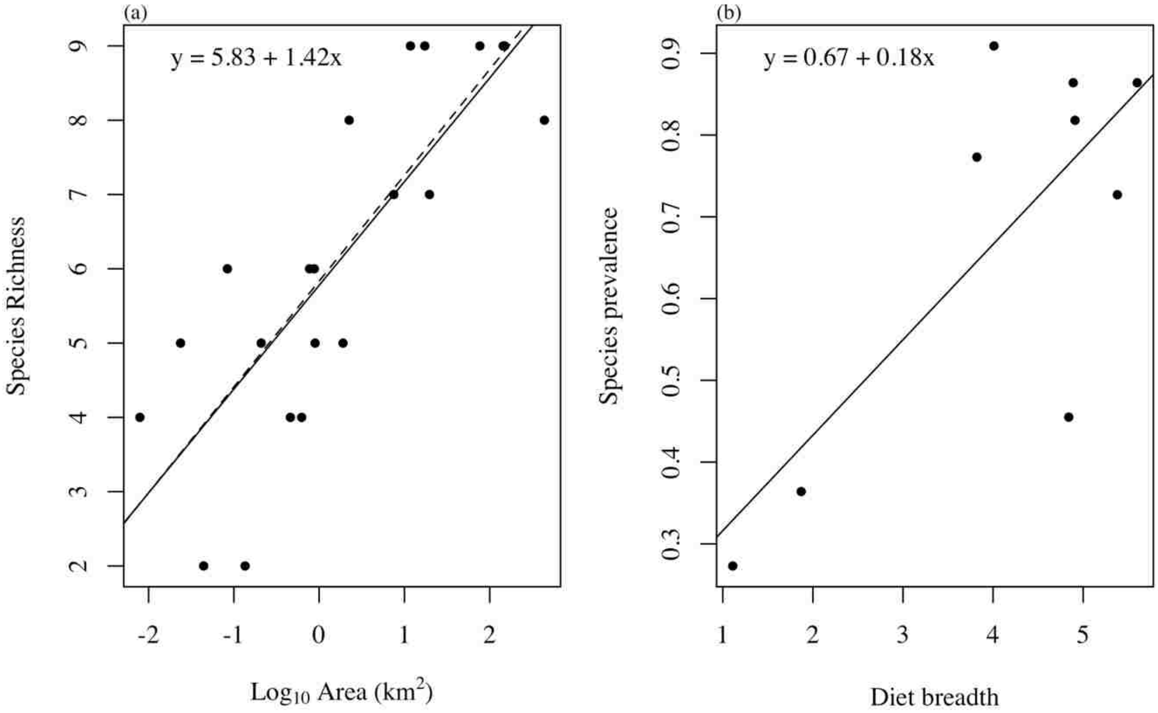

Figure 1.3. (a) Species-area relationship for observed species richness (solid line) and extrapolated Chao 2 species richness (dashed line) and (b) species prevalence-diet breadth relationship for bats among islands (n = 21) in the San Juan Archipelago.

Table 1.1. Islands surveyed throughout the San Juan Archipelago ranked by decreasing size. Island habitat characteristics include isolation from Washington mainland, snag density, old growth stand index, and percent canopy cover, which were collected from the LEMMA dataset, see *methods*. The number of recorded species and estimated total species richness (Chao 2 and first-order jackknife) are also indicated.

Island	**Area (km^2)**	**Isolation (km)**	**Snag density**	**Old growth stand index**	**Canopy Cover (%)**	**Recorded species**	**Chao 2**	**Jackknife 1**
Mainland	-	-	-	-	-	7	7.0	7.0
Whidbey	436.95	0.35	6.0	13.5	39.7	8	8.0	9.9
Orcas	149.39	8.95	10.7	25.8	62.8	9	9.0	11.0
San Juan	143.57	19.22	6.7	17.8	44.8	9	9.5	10.0
Lopez	76.54	8.45	5.1	16.4	45.8	9	9.0	8.0
Shaw	19.64	17.34	9.7	24.1	69.2	7	7.0	7.0
Blakely	17.33	7.90	13.1	31.8	68.4	9	9.5	10.0
Waldron	11.75	23.14	10.3	22.2	69.6	9	9.0	10.9
Stuart	7.50	35.58	18.4	26.0	68.2	7	7.0	7.0
Sucia	2.25	13.21	9.0	25.1	69.7	8	8.0	7.1
Burrows	1.90	0.42	11.1	23.0	66.5	5	5.0	5.0
Patos	0.90	15.84	9.5	23.0	68.6	5	5.0	4.2
Vendovi	0.88	3.82	13.6	25.1	71.6	6	6.0	7.8
Jones	0.77	27.86	12.9	30.8	77.8	6	6.0	6.0
Matia	0.62	9.68	13.0	26.1	70.9	4	4.0	4.0
James	0.46	5.17	8.2	23.1	61.1	4	4.0	4.0
Clark	0.21	7.36	10.3	23.8	62.4	5	5.0	5.0
Turn	0.14	20.14	12.0	31.0	76.1	2	2.4	2.9
Saddle bag	0.08	3.40	4.7	16.6	41.7	6	6.0	5.2
Yellow	0.04	26.38	6.4	10.7	15.1	2	2.0	3.7
Doe	0.02	13.47	11.4	30.4	65.1	5	5.0	4.3
Blind	0.01	19.84	0.0	0.0	0.0	4	4.0	4.0

Table 1.2. Species traits and prevalence among the San Juan islands. Diet breadth was calculated from Ober and Hayes (2008). Foraging guild was taken from Denzinger & Schnitzler (2013), Serugo-Trujillo *et al.* (*2018*), Fellers & Pierson (2002), or López-González *et al*. (2016). Body mass and forearm measurements were taken from field measurements, except in the case of *Lasiurus cinereus,* which was taken from Nagorsen (2002). Wing loading measurements were taken from Norberg and Rayner (1987).

Species	**Diet breadth**	**Foraging guild**	**Body mass (g)**	**Wing loading (N/m^2)**	**Forearm length (mm)**	**Island prevalence (%)**
Corynorhinus townsendii	1.11	Edge aerial	10.2	7.2	43.7	0.27
Eptesicus fuscus	4.01	Edge aerial	17.1	9.4	46.9	0.91
Lasiurus cinereus	3.82	Open aerial	28.4	16.5	54.5	0.77
Lasionycteris noctivagans	5.6	Open aerial	11.5	8.1	41.5	0.86
Myotis californicus	4.89	Edge aerial	4.5	4.8	31.8	0.86
Myotis evotis	4.91	Gleaner	6.3	6.1	37.4	0.82
Myotis lucifugus	4.84	Trawler	6.3	7.5	35.7	0.46
Myotis volans	1.87	Trawler	7.7	8.3	38.3	0.36
Myotis yumanensis	5.38	Trawler	5.4	7.8	34.5	0.73

Table 1.3. Results from Akaike information criterion (AIC) model selection for the candidate set of models explaining the relationship between species richness and island characteristics.

Model	r^2_{adj}	***AICc***	Δ ***AICc***	***w***
Area (km^2)	0.66	77.2	0	1
Canopy cover (%)	-0.01	100.2	23.5	0
Old growth stand index	-0.04	110.6	23.9	0
Isolation (km)	-0.03	100.7	24	0
Snag density	-0.05	100.9	24	0

Table 1.4. Results from Akaike information criterion (AIC) model selection for the candidate set of models explaining the relationship between species prevalence and species traits.

Model	r^2_{adj}	***AICc***	***Δ AICc***	***w***
Diet breadth	0.52	2	0	0.93
Body mass (g)	-0.08	9.2	7.23	0.03
Wing loading (N/m^2)	-0.13	9.6	7.63	0.02
Forearm (mm)	-0.14	9.6	7.66	0.02
Foraging guild	-0.12	25.7	23.75	0

Chapter 2. INFLUENCE OF LOCAL AND LANDSCAPE CHARACTERISTICS ON INSULAR BAT ACTIVITY

2.1 ABSTRACT

The loss and fragmentation of natural habitats are some of the greatest threats to terrestrial biodiversity. There is wide support for the positive influence of patch size on species richness. However there is also evidence that additional characteristics of habitat patches mediate species responses within fragmented landscapes, depending on their habitat requirements. In the present study, we investigated the relative importance and scale at which habitat characteristics influence activity of insectivorous bats within a temperate near shore archipelago using passive acoustic monitoring. We predicted that species that forage in more cluttered habitats (*Myotis* spp.) would be more active at more forested sites, and less active on more isolated islands. We also predicted that overall bat activity would be higher near fresh water resources and on larger islands and islands with a greater availability of potential roost sites (snags). At the island scale, we found that overall bat activity was higher on islands with a greater density of snags and on larger islands. *Myotis* spp. were most active at more forested sites, but showed no reduction of activity on more isolated islands. Proximity to fresh water sources emerged as the only site-scale habitat characteristic to significantly increase activity of *Myotis* spp and large bats. Our results suggest that small isolated forest patches have conservation value for bats, but that retention of open water sources, small forest patches, and larger tracts of habitat with a high abundance of potential roost sites (snags) are important conservation priorities.

2.2 INTRODUCTION

The loss and fragmentation of natural habitats are some of the greatest threats to terrestrial biodiversity (Dirzo et al. 2014, Newbold et al. 2015). The practice of conservation science is rooted in island biogeography theory (IBT), which proposes larger and less isolated habitat patches harbor more species than smaller less connected ones (MacArthur and Wilson 1967). Although there is wide support for the positive influence of patch size on species richness (Koh et al. 2002, Bommarco et al. 2010, Franzen et al. 2012), there is growing evidence that additional characteristics of habitat patches and the intervening matrix (e.g., open water, agriculture, urban development) mediate species and community responses to habitat fragmentation (Kupfer et al. 2006, Muñoz et al. 2013, Mendenhall et al. 2014a, 2014b, Ferrante et al. 2017).

The relative importance and scale at which habitat characteristics influence organism vary across species (Buskirk 2005, Terraube et al. 2016), taxonomic and functional groups (Mendenhall et al. 2014a, Wang et al. 2015, Mendes et al. 2017). High contrast matrixes surrounding forest patches are expected to disproportionately affect smaller species with low mobility (Muñoz et al. 2013, Mendenhall et al. 2014a, Pfeifer et al. 2017). For example, in Atlantic forest fragments, amphibian diversity, composition, and abundance are more influenced by structural characteristics of forest patches and the type of surrounding matrix than fragment size (Ferrante et al. 2017). In contrast, species with high dispersal ability are predicted to be better able to move between more isolated habitat patches (Marini et al. 2010). Even among highly mobile species, availability of resources within patches also influences species- or guild-specific distributions (Wang et al. 2015), abundances (Stracey and Pimm 2009) and activity patterns (Frey-Ehrenbold et al. 2013) within fragmented landscapes, depending on their habitat requirements. In birds and bats, species that forage in more open habitats tend to be less sensitive to habitat fragmentation than more forest dependent species (Estrada-Villegas et al. 2010, Wang et al. 2015, Terraube et al. 2016, Mendes et al. 2017). In bats, species are often grouped into foraging guilds based on shared characteristics in wing morphology and echolocation call design (Aldridge and Rautenbach 1987, Fenton and Bogdanowicz 2002, Schnitzler et al. 2003, Sleep and Bringham 2003, Denzinger and Schnitzler 2013). Bats with low aspect ratios, wing loading, and short, high frequency, broadband echolocation calls are more maneuverable and tend to forage in more structurally cluttered (e.g., forested) habitats. In contrast, species with higher wing loading and aspect ratios tend toward more rapid flight in open habitats where they use lower frequency echolocation calls to detect prey at greater distances. The relative importance of microhabitat and larger landscape scale characteristics also vary between bat foraging guilds (Frey-Ehrenbold et al. 2013, Mendes et al. 2017).

In the present study, we analyzed how island and site-scale characteristics influence patterns of bat activity in a naturally fragmented landscape–the San Juan Archipelago off the coast of Washington State. This is a mosaic landscape of near shore islands surrounded by a high contrast matrix (the Salish Sea, Fig. 2.1). The region has been found to support a community of nine bat species (Kelly *et al*., in review, Rodhouse et al., 2015). Within this community, the three largest species emit longer echolocation calls at lower frequencies and possess morphological traits (e.g., higher aspect ratios and wing loadings) associated with fast flight in open habitats (Denzinger and Schnitzler 2013). In contrast, the smaller (*Myotis*) species within the community emit shorter calls with higher frequencies, are more maneuverable, and generally considered to be more adapted to cluttered habitats (Sleep and Bringham 2003).

Since larger islands in the archipelago provide larger patches of habitats that are suitable for bats, and greater habitat complexity in general, we predicted that overall bat activity would be higher on larger islands. We also predicted that activity of *Myotis* spp. would be lower on more isolated islands because the adaptations of these species to cluttered habitats may make them less likely to commute across open water. In addition to island area and isolation, we predicted that bat activity would be higher on islands with a greater abundance of snags, which are known to be key roosting structures for bats in the region (Arnett and Hayes 2009, Rodhouse et al. 2015). At the site scale, we predicted that activity of *Myotis* spp. would be higher in more forested habitats, whereas activity of large bats would be higher in more open habitats. We also predicted that overall bat activity would be higher near fresh water resources, which provide important drinking or foraging opportunities for bats (Hall et al. 2016, Amorim et al. 2018). Finally, because there is mixed evidence that lunar illumination affects the activity of temperate bats species (Karlsson et al. 2002, Cryan and Brown 2007), we tested whether there is a relationship between bat activity and the lunar cycle (moon phase).

2.3 METHODS

2.3.1 *Study area*

Our study took place in the San Juan Archipelago of Northwestern Washington State, USA. The region's climate is affected by the rain shadow caused by neighboring coastal mountains, resulting in warm and dry summers (13 °C, 43mm) and mild wet winters (5 °C, 123mm) (Martin et al. 2011). Approximately 55% of the land area is forested and dominated by Douglas-Fir and Western Red Cedar (Tucker and King 2012). The remaining vegetation on the islands is primarily comprised of agricultural, grassland and riparian species (Tucker and King 2012). We carried out all fieldwork between June and September of 2015, 2016, and 2017.

2.3.2 *Acoustic surveys*

We carried acoustic surveys on 21 islands ranging in size from 0.01 to 436.95 km^2 (Fig. 2.1). Due to land access limitations on most islands, we could not establish a randomized site selection procedure. Instead, we opportunistically selected sites that represented the range of existing habitats. On each island, we selected between 1 - 11 sites to monitor bat activity. The number of sites increased with island size, and most islands had at least two survey sites. However, on two small islands (< 0.15 km^2) we could only establish one survey site due to logistical constraints. Eight of the surveyed islands contained open perennial fresh water sources (lakes and ponds), which provide important drinking and foraging sites for many bat species (Vindigni et al. 2009, Hall et al. 2016, López-González et al. 2016). We sampled within 30 m of a lake or pond edge on these eight islands (water sites). On a subset of islands (n = 16), we also sampled within 30 m of the coast line (coastal sites). The remaining sampling sites (dry inland sites) included forest gaps and edges, hiking trails, grassy knolls and fields, and were located at least 60 m away from any fresh water source or coastline, except on the smallest island in our study (Blind Island, Fig. 2.1) where the inland site was 50 m from the coast.

At each site, we recorded bat acoustic activity using a stationary Songmeter SM2+BAT ultrasonic recorder with an omnidirectional microphone (SMX-U1) (Wildlife Acoustics Inc., Concord, MA) mounted on a 3.7 m pole. In order to minimize acoustic reflections and maximize the probability of recording diagnostic “search phase” echolocation calls, we mounted microphones at least 3 m from any ‘clutter’ (Russo et al. 2018). We programmed recorders to record bat activity from 30 minutes prior to sunset until 30 minutes after sunrise each night. We set the trigger window for recordings to 2 s, with a maximum file length of 15 s, and recorded files in full-spectrum format. We deployed four ultrasonic recorders simultaneously on one to four islands, and recorded bat activity for 2-6 nights per sampling session, rotating the detectors around to all study sites; most sites were surveyed multiple years (Table S1.2).

2.3.3 *Data analysis*

We processed and filtered full spectrum acoustic files using Kaleidoscope Pro 4.2.0 (Wildlife Acoustics Inc., Concord, MA). In order to filter out any noise files from those containing bat echolocation calls, we required files to contain at least three calls (pulses of ultrasound; Loeb et al., 2015) with frequencies between 16-120 kHz, and call duration ranging from 2-50 ms. These characteristics match call sequences for Pacific Northwest bat species (Reichert et al. 2018). Using Kaleidoscope Pro, we converted all echolocation files to zero-crossing format using a division ratio of eight. We then used a custom filter in AnalookW 4.1 (C. Corben, Columbia, Missouri) to further process echolocation files. Using minimum frequency and duration of calls (Erickson and West 2003, Lausen et al. 2014, Luszcz and Barclay 2016), we classified sequences into two phonic groups: *Myotis* spp. (*M. californicus, M. evotis, M. lucifugus, M. volans,* and *M. yumanensis*) and 'large bats' (*Corynorhinus townsendii, Eptesicus fuscus, Lasiurus cinereus,* and *Lasionycteris noctivagans*). Because there can be a high degree of overlap in echolocation characteristics within these phonic groups, we used a conservative approach to call identification, taking into consideration the context of the recording (Russo et al. 2018). Additionally, these phonic groupings largely correspond to functional differences in maneuverability and foraging ecology among the species that form the bat community in the San Juan Archipelago (Denzinger and Schnitzler 2013, Hall et al. 2016), with the exception of *Corynorhinus townsendii,* a relatively large low frequency bat that is highly maneuverable, unlike the other species in this lower phonic group category (Fellers and Pierson 2002, Rodhouse et al. 2015). Although the echolocation characteristics of *C. townsendii* may be grouped within the large bat phonic group, this species emits low intensity calls that are rarely detected using acoustic monitoring techniques (Rodhouse et al. 2015). Therefore, we expect that this species would only represent a negligible component of the activity for this group. All but *C. townsendii* in the 'large bats' phonic group tend towards relatively fast flight, foraging in more open habitats (Sleep and Bringham 2003, Buchalski et al. 2013), and are associated with lower frequencies which travel further than higher frequencies. These faster, low frequency species benefit from long duration shorter bandwidth calls when searching for insect prey in uncluttered habitats, but will shift to use broader bandwidth, shorter duration, and often slightly higher frequency calls, when approaching any source of clutter (Broders et al. 2004). In contrast, *Myotis* spp. have slow maneuverable flight, which enables them to exploit more structurally cluttered habitats (Sleep and Bringham 2003, Owen et al. 2004) and thus coincides with production of shorter duration, higher frequency large band-width calls that allow for a high degree of resolution of a close range object (reviewed in Loeb et al. 2015).

As an index of relative bat activity, we analyzed the number of bat echolocation call files per night for all bat species combined, and for each of the phonic groups. We performed all statistical analyses in R v3.4.3 (R Core Team 2017). We developed candidate models explaining overall bat activity, activity of large bats, and activity of *Myotis* spp. The response variable was the nightly count of echolocation call files. The explanatory variables included characteristics at the scale of each island (area, isolation, and snag density) and each site (water, coast, and canopy cover; Table 2.1). Using ArcGIS 10.6 (ESRI, Redlands CA), we calculated island area (km^2) and island isolation (the distance from either the coastline of Washington or the nearest island > 20

km^2). We calculated the density of snags (trees/ha) ≥ 25 cm diameter at breast height and ≥ 2 m height for each island using a 30 m resolution forest structure dataset for the region (LEMMA 2014). For the site-scale models, we used the LEMMA forest structure dataset to calculate the percent canopy cover within a 30 m radius (2,827 m^2) of each survey site. Based on field deployment of detectors within 30 m of either water sources or the coastline, we included water and coastline as binary variables. Although the water sites ranged from small, heavily vegetated ponds less than one acre to lakes over 20 acres, we lacked the sample size to analyze these size classes separately. We used the package '*suncalc*' (Agafonkin and Thieurmel 2018) to calculate the moon phase (percentage illuminated fraction of the moon) on each survey night, and included this as a covariate in all models.

As appropriate for count data, we fit Poisson generalized linear mixed effects regression models (GLMMs) using the '*lme4*' package (Bolker et al. 2009, Bates et al. 2015). Our *a priori* candidate model set included an island model with variables at the island-scale (area, isolation, and snag density), a site model with variables at the site-scale (canopy, water, and coastal) and a global model with all of the site and island variables. We also included a null (intercept only) model in the candidate set, to evaluate model performance to a fixed baseline model (Nally et al. 2017). Prior to model fitting, we calculated Pearson correlation coefficients between all pairs of explanatory variables, none of which were highly correlated (all $r < |0.36|$, Table S1.3). We then standardized all continuous explanatory variables to have a mean of zero and a standard deviation of one. Because consecutive recording nights at a site could introduce temporal autocorrelation, we included date and site as random effect variables in all models. We evaluated initial models for evidence of overdispersion by calculating the ratio of summed Pearson residuals to residual degrees of freedom, and subsequently included an observation level random effect (OLRE) factor in order to account for overdispersion (Bolker et al. 2009, Harrison 2015). We then tested whether the ORLE controlled for overdispersion in models by evaluating the dispersion of simulated residuals using the Dharma package (Hartig 2019). We compared candidate models using Aikake's information criterion corrected for small sample size (*AICc*). We considered models with Δ*AICc* within two units of the model with the lowest *AICc* value to have considerable model weight (w_i), following Burnham & Anderson (2002). We also evaluated model fit by calculating the marginal (R^2_c, variance explained by fixed effects only) and conditional (R^2_m, variance explained by both fixed and random effects) variances explained by each candidate model (Nakagawa and Schielzeth 2013).

2.4 RESULTS

Between 2015 - 2017, we monitored nightly bat activity at 104 sites across 21 islands over 537 detector-nights. In total, we recorded of 59,158 bat echolocation files containing at least three echolocation pulses. We identified 69.3% (41,032) of echolocation files as *Myotis* spp. and 30.7% (18,126) as large bat species. We recorded bat activity on all surveyed islands. Activity was highly variable, ranging from 0 - 1,156 files per night for *Myotis* spp. and 0 - 404 files per night for large bats.

We found high support for the global GLMM regression model, which included both island and site-scale variables, in explaining activity of large bats and activity of all bats combined (Table 2.2). Activity of *Myotis* spp. was best explained by the site model (Table 2.2). The global model also received similar support (Δ*AICc* = 0.46), but only site-scale variables were significant predictors of *Myotis* spp. (Table 3) and regression parameter estimates for site-scale variables were nearly identical in the global and site models (Table S1.4). Across all candidate models, the variation in nightly bat activity explained by fixed effects (R^2_c) ranged from 9.36 to 26.71% (Table 2.2). However, the combined variation explained by both fixed and random effects (R^2_c) ranged from 74.12 to 78.01%. This suggests that much of the variability in the activity data resided in the random effects of survey night, site, and the observation-level random effect, which was included to account for overdispersion.

Results from the global models suggest differences in the relative importance of island and site characteristics between large bats and *Myotis* spp. (Table 2.2). Overall bat activity was positively related to island area ($P = 0.049$) and snag density ($P = 0.036$, Table 2.3), but was unaffected by island isolation ($P = 0.112$). Activity of large bats was also significantly higher on islands with greater snag density ($P < 0.01$) with less of an effect of island area ($P = 0.054$), and no effect from isolation ($P = 0.669$, Table 2.3). In contrast, island area ($P = 0.097$), isolation ($P = 0.118$), and snag density ($P = 0.287$) were not significant predictors of *Myotis* spp. activity (Table 2.3).

At the site-scale, overall bat activity was significantly higher near water ($P < 0.001$, Fig. 2.2), but was unrelated to canopy cover ($P = 0.273$, Table 2.3). Looking at the dynamics between phonics groups, large bat activity was significantly higher adjacent to fresh water sources ($P < 0.01$, Fig. 2.2), but negatively related to canopy cover ($P < 0.001$, Table 2.3). Activity of *Myotis* spp. was also significantly higher near water ($P < 0.001$, Table 2.3, Fig. 2.2) but positively related to canopy cover ($P < 0.001$). We did not find any statistically significant effect of moon phase on overall bat activity ($P = 0.061$) or large bat activity ($P = 0.256$), but *Myotis* spp. activity increased with moon illumination percentage ($P < 0.014$, Table 2.3). We did not find any significant differences in activity along coastlines for *Myotis* spp. ($P = 0.576$) large bats ($P = 0.201$), or overall bat activity ($P = 0.614$).

2.5 DISCUSSION

Within a naturally fragmented landscape, we found that bat activity overall is best explained a combination of site and island scale characteristics. At the island scale, we found greater overall bat activity on larger islands, but we did not find any reduction in bat activity on more isolated islands in this near shore archipelago. We also found that islands with a greater density of roosting sites (snag density) had higher overall bat activity, and more large bat activity in particular. Our results suggest that large bats and *Myotis* spp. respond differently to habitat characteristics at the site scale. We found activity of large bats tended to be higher at sites with more open habitats (e.g., lower canopy cover), and that *Myotis* spp. were most active at more forested sites, which was consistent with our predictions based on their maneuverability and foraging ecology. Moreover, our results show that large bats are influenced by a combination of site and larger landscape (island scale) characteristics*,* whereas *Myotis spp*. are most influenced by characteristics at the site scale. Proximity to fresh water sources emerged as the only site-scale habitat characteristic to significantly increase activity of both phonic groups (Table 2.3, Fig. 2.2). This is consistent with previous studies demonstrating the importance of standing water as a critical resource for bats (Adams and Thibault 2006, Vindigni et al. 2009, Dixon 2011, Hall et al. 2016).

Access to water sources is essential for bats to meet their physiological, foraging, and reproductive requirements (Kurta et al. 1989, Zsebok et al. 2013). During lactation, daily water flux more than doubles in Big brown bats, and drinking represents a significant portion of their water intake (Kurta et al. 1989, 1990). Bats must drink in flight, and nightly drinking bouts are 13 times higher in lactating Fringed myotis than in non-reproductive individuals (Adams and

Hayes 2008). Moreover, proximity to water is an important factor for roost site selection in many reproductive bat species in arid environments (Rabe et al. 1998), but less so in wetter regions (Rancourt et al. 2007). Unlike much of the Pacific Northwest, the San Juan islands are much drier owing to the rain shadow caused by neighboring coastal mountains (Erickson and West 2002, Adamus 2011). Therefore, water may be a more limiting resource in this insular landscape than in other areas in the region, especially for reproductive females. However, because we lack phenological data in this study and it is impossible to determine sex or reproductive condition based on acoustic data, we could not assess a direct mechanism linking reproductive trends with activity near water.

In addition to drinking, open water sources also provide valuable foraging habitat for many insectivorous bat species (Bringham et al. 1992, Frick et al. 2007b, Ober and Hayes 2008). Several species in the genus *Myotis* are known to forage extensively over water (Almenar et al. 2006, Fukui et al. 2006, Ober and Hayes 2008, Zsebok et al. 2013). Our results suggest that the positive effect of water was much higher for *Myotis* spp. than for large bats. Our regression estimates predict that activity of *Myotis* spp. is over four times higher adjacent to water sources, whereas large bat activity is 1.5 times higher at fresh water sites (Table 2.3). It is possible that large bats are active at water primarily for drinking, and that the relatively larger increases we observed in *Myotis* spp. activity reflect foraging bouts over the water surface. However, it is also possible that differences in activity could be partly explained by characteristics of the water bodies we surveyed. Larger, less maneuverable bat species are more active around large bodies of water that are more structurally open (Vindigni et al. 2009, Hall et al. 2016, Meyer and Rocha 2018). For example, in an experimental reduction of water surface area, Hall et al., (2016) found reduced activity and drinking attempts by larger and less maneuverable bat species. In contrast, they did not find any change in the activity of maneuverable species (e.g., *Myotis*). Thus, activity of large bats may have also been influenced by the size or structural characteristics of the water sources we surveyed. Although lakes are restricted to the largest islands, small man-made ponds are far more numerous throughout the islands (Adamus 2011). The relative importance of these smaller water sources for bats warrants further investigation.

Despite the fact that perennial fresh water sources are absent from many of the smaller islands we surveyed, we did not find that island size significantly influenced the activity of either phonic group. Rather, island size emerged as a significant factor only when we analyzed the combined activity of all bats (Table 2.3). In a previous study, we found that species richness was strongly influenced by island size in this system (Kelly *et al.,* in review), whereas the results presented here suggest that area is a relatively weak predictor of bat activity at this scale. We also did not find any evidence that island isolation reduces bat activity overall, or activity of either phonic group. These results are consistent with a previous study on the activity of neotropical insectivorous bats in a land-bridge island system (Estrada-Villegas et al. 2010). Although Estrada-Villegas et al. (2010) also found compositional differences in bat communities across islands, they did not find that small isolated islands reduced the activity levels of forest-dependent bats or species that forage in open habitats. Moreover, they found that open space foraging bats were more active on islands than in mainland interior forests. This suggests that, even in fragmented landscapes with a high contrast matrix (e.g., open water), small and isolated habitat patches have conservation value, especially for species that forage in more open habitats.

Within anthropogenically fragmented habitats, forest cover frequently emerges as an important predictor of bat activity (Johnson et al. 2008, Dixon 2011, Frey-Ehrenbold et al. 2013, Kelly et al. 2016). However, this response is often species, guild, or scale-specific (Mendes et al.

2017). Consistently, we found that both large bats and *Myotis* spp. were active on all surveyed islands, but *Myotis* spp. were significantly more active at forested sites and large bats were more active at more open sites. As a group, *Myotis* spp. activity is often associated with greater canopy cover at the microhabitat scale (Erickson and West 2003, Smith and Gehrt 2010, Blakey et al. 2019), whereas the species in our large bat phonic group have been reported to respond to certain aspects of forest characteristics in a scale-dependent fashion (Gert and Chelsvig 2004, Dixon 2011, Blakey et al. 2019). For example, in a highly urbanized landscape, Gert and Chelsvig (2004) found that activity of *Eptesicus fuscus* and *Lasionycteris noctivagans* was positively related to the amount of woodland cover within two kilometers. In contrast, an analysis of bat activity related to fire regime in the Sierra Nevada, occupancy rates of *E. fuscus*, *L. noctivagans*, and *Lasiurus cinereus* were all negatively related to the percentage of canopy cover within 100 m (Blakey et al. 2019). Although these studies took place in very different contexts, both of these findings are consistent with our results and suggest that activity of large bats may respond to forest cover at the larger landscape scale, even though they may selectively use more open microhabitats.

Even though the activity of large bats was negatively related to canopy cover at the site scale, we did find a significant positive effect of snag density on their activity and overall bat activity at the island scale (Table 2.3). All of the species in the large bat phonic group are known to roost in trees, and snags are considered a key roosting structure for many temperate bat species (Rabe et al. 1998, Rancourt et al. 2007, Rodhouse et al. 2015). *Myotis* spp. also extensively roost in snags, but their activity seems to be better predicted by local habitat structure as opposed to larger landscape features (Erickson and West 2003). Nevertheless, and considering that snags only occur within forested lands, our results further indicate the general importance of forests for bats. Moreover, many open space foraging bats are known to forage above the canopy (Adams et al. 2009, Marques et al. 2016), thus it is possible that species in the large bat phonic group were active at forested sites but at heights beyond the range of our detectors (Patriquin et al. 2003, Owen et al. 2004).

The opposing effect of site-scale forest cover (canopy-cover) on large bats and *Myotis* spp. activity likely prevents it from emerging as a significant predictor of combined bat activity. This suggests that combining overall bat activity may obscure guild-specific responses to local and landscape scale habitat variables. Considering this, it is important to acknowledge that our choice of phonic groupings also could have influenced our results. Because of the high overlap in call parameters between species within each of our phonic groups (Thomas et al. 1987, O'Farrell et al. 2000, Lausen et al. 2014), we used a conservative approach to classifying echolocation calls. This is a common practice in this type of research (Buchalski et al. 2013, Veres et al. 2013, Frey-Ehrenbold et al. 2013, Claireau et al. 2019, Lawson et al. 2019). Moreover, previous studies in the region have also grouped *Myotis* spp. and large bats into 'high' and 'low' frequency groups, respectively (Erickson and Adams 2003, Luszcz and Barclay 2016). An advantage of grouping species based on echolocation call similarity is that, if they are also similar in foraging ecology (Schnitzler et al. 2003, Denzinger and Schnitzler 2013) or morphology (Norberg and Rayner 1987), then groupings likely reflect functional differences between species. However, many bat species are highly flexible in their foraging ecology (Faure and Barclay 1994) and echolocation calls (Jakobsen and Surlykke 2010), which complicates inferences based on acoustic data alone (Russo et al. 2018).

We found high variation in nightly bat activity within and between sites, which was likely driven by environmental variables affecting both detectability and bat activity. For example, temperature, windspeed, and fog density have all been shown to influence bat activity (Erickson and West 2002, Ciechanowski et al. 2007, Cryan and Brown 2007). The effects of weather conditions on bat activity are known to vary among the species in our study. For example, *M. evotis* is thought be more tolerant of cooler and wetter conditions than other species because of its ability to glean prey from vegetation (Burles et al. 2009). Although we did not measure weather conditions, the random site and night effects in our models accounted for a large portion of the variation in all of our models (Table 2.2). These combined effects likely capture much of the variation that was due to unmeasured spatiotemporal variables. The night variable likely accounted for nightly weather variation, which is presumably temporally auto-correlated. Additionally, further site scale variation could have been driven by differences in structural vegetation characteristics, such as canopy height (Bader et al. 2015) or understory vegetation (Humes et al. 1999), or other habitat conditions. For example, activity of many bat species is positively affected by the amount of forested edges, which may provide shelter from wind or increase insect abundance (Magura et al. 2001, Ethier and Fahrig 2011, Jantzen and Fenton 2013).

Moonlight is also thought to affect bat activity because it could increase the risk of predation by making bats more visible to nocturnal, visually-oriented predators (Appel et al. 2017). We did not find any bat activity reduction around the full moon, and our results suggest that activity of *Myotis* spp. was greater during that part of the moon cycle. Our results corroborate the findings of Karlsson et al. (2002) and Hecker & Bringham (1997), which suggest that activity of temperate bats is unaffected by moonlight. Lunar phobia has been documented in some bat species (Lang et al. 2006, Cryan and Brown 2007, Appel et al. 2017), but Salda & Munguía-rosas (2013) found that this phenomenon is more prevalent in tropical bat species than in temperate species, and less prevalent in species that forage in more cluttered habitats. However, because we did not simultaneously measure cloud cover or the timing of moonrise and moonset, it is unclear how much this trend related to actual moonlight. For example, even during the full moon, there is likely less moon illumination below the canopy within forests than more open areas. Thus, *Myotis* spp. may also be selectively using more forested areas around the full moon (Hecker and Bringham 1997).

In conclusion, we examined how site and island characteristics influence relative activity patterns of temperate bats in a near shore, naturally fragmented landscape. We found that the two bat phonic groups examined were active even on very small and isolated islands. Our results underscore the importance of considering guild (e.g., phonic groups) and scale specific responses of bats to habitat characteristics (Estrada-Villegas et al. 2010, Caryl et al. 2016, Mendes et al. 2017), and suggests that conservation of open water sources, small forest patches, and larger tracts of habitat with a high abundance of potential roost sites (snags) are important for bat activity. Future research should investigate the behavioral and ecological mechanisms through which each of these characteristics may directly promote diverse bat communities within natural and anthropogenically fragmented landscapes.

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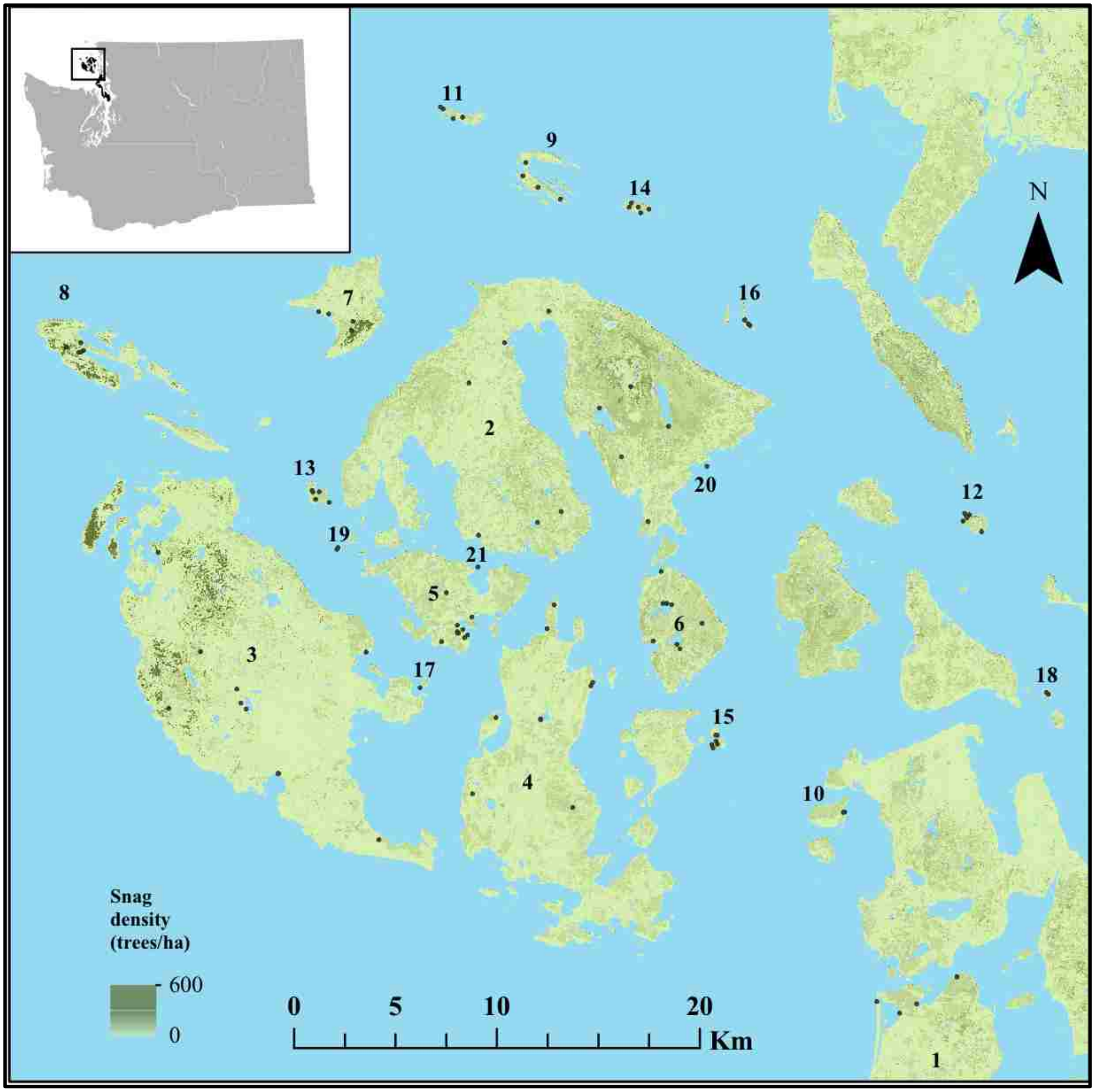

Figure 2.1. Map of the study area and 104 recording sites (dots) across 21 islands located in the San Juan Archipelago of Northwestern Washington State. Study islands are numbered in descending order of their size: 1) Whidbey Island, 2) Orcas Island, 3) San Juan Island, 4) Lopez Island, 5) Shaw Island, 6) Blakely Island, 7) Waldron Island, 8) Stuart Island, 9) Sucia Island, 10) Burrows Island, 11) Patos Island, 12) Vendovi Island, 13) Jones Island, 14) Matia Island, 15) James Island, 16) Clark Island, 17) Turn Island, 18) Saddlebag Island, 19) Yellow Island, 20) Doe Island, and 21) Blind Island.

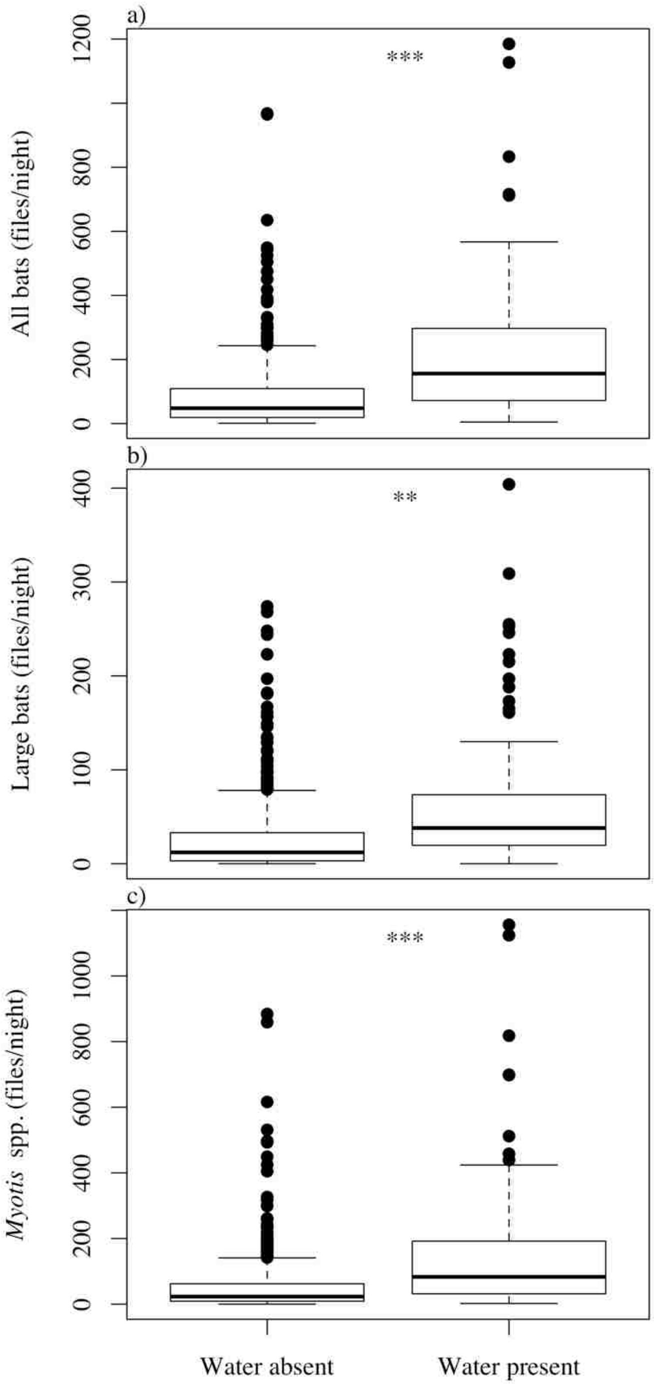

Figure 2.2. Nightly activity (echolocation call files/night) of bats on the San Juan Islands at sites where fresh water sources (e.g., lakes, ponds, or streams) were absent or present for: (a) all species combined (b) large bats and (c) Myotis spp. We assessed differences in overall and each phonic group's activity patterns by fitting generalized linear mixed-effects models (see Methods), and are indicated by (**) for $P < 0.01$ and (***) for $P < 0.001$.

Table 2.1. Description of island and site variables used to fit generalized linear mixed-effects models of nightly activity patterns of bats at 104 sites and 21 islands in the San Juan Archipelago of Northwestern Washington State.

Variable	Definition of variable	Prediction
Moon	Percent moon phase	Decrease overall bat activity
Island		
Area	Island area (km^2)	Increase overall bat activity
Iso	Isolation from mainland Washington or any large island (> 20km^2)	Decrease bat activity of *Myotis* spp. no effect on large bats
Snag	Density of snags (any dead or dying trees) > 25cm DBH and 2 m tall per hectare	Increase overall bat activity
Site		
Water	A recording site located within 30 m of a fresh water source (pond, lake, or stream)	Increase overall bat activity
Coast	A recording site located within 30 m of a the coastline	Increase overall bat activity
Canopy	Percent canopy cover within 30 m of recording site	Increase activity of *Myotis* spp. and decrease activity of large bats

Table 2.2. Model selection for nightly activity of all bats, large bats, and *Myotis* spp. across 104 sites and 21 islands in the San Juan Archipelago.

Model	K	AICc	Δ_i	w_i	R^2_m	R^2_c
All bats						
Area + iso + snag + coast + water + canopy + moon	**11**	**5781.3**	**0**	**0.92**	24.33%	74.59%
Area + iso + snag + moon	8	5801.4	20.10	0	12.27%	74.12%
Coast + water + canopy + moon	8	5786.1	4.75	0.08	18.66%	74.33%
null (intercept only)	4	5812.1	30.81	0	-	-
Large bats						
Area + iso + snag + coast + water + canopy + moon	**11**	**4450.4**	**0**	**0.96**	20.03%	78.01%
Area + iso + snag + moon	8	4456.8	14.87	0	9.36%	77.99%
Coast + water + canopy + moon	8	4456.8	6.44	0.04	13.59%	78.02%
null (intercept only)	4	4469.6	19.23	0	-	-
Myotis spp.						
Area + iso + snag + coast + water + canopy + moon	11	5217.7	0.3	0.46	26.71%	76.50%
Area + iso + snag + moon	8	5243.8	26.36	0	12.27%	74.13%
Coast + water + canopy + moon	**8**	**5217.4**	**0**	**0.54**	23.46%	76.31%
null (intercept only)	4	5253.5	32.9	0	-	-

Table 2.3. Regression parameter estimates (± *SE*) for the global generalized linear mixed-effects models explaining nightly activity of all bats, large bats, and *Myotis* spp. across 104 sites and 21 islands in the San Juan Archipelago of Washington State. Significance is indicated by (*) for P < 0.05, (**) for P 0.01, and (***) for P < 0.001.

Variable	All bats	Large bats	*Myotis spp.*
Moon	0.11± 0.06	0.09 ± 0.08	**0.17 ± 0.06***
Island:			
Area	**0.21 ± 0.10***	0.28 ± 0.13	0.20 ± 0.13
Iso	0.15 ± 0.11	0.05 ± 0.12	0.17 ± 0.11
Snag	**0.20 ± 0.09***	**0.37 ± 0.12****	0.12 ± 0.11
Site:			
Water	**1.24 ± 0.24***	**0.91 ± 0.32****	**1.45 ± 0.28*****
Coast	-0.11 ± 0.22	-0.38 ± 0.30	0.15 ± 0.27
Canopy	0.10 ± 0.06	**-0.43 ± 0.13*****	**0.40 ± 0.11*****

Chapter 3. PRIMARY PRODUCTIVITY EXPLAINS SIZE VARIATION ACROSS THE PALLID BAT'S (*ANTROZOUS* PALLIDUS) WESTERN GEOGRAPHIC RANGE)

3.1 ABSTRACT

1. Body size is associated with many aspects of the life history, ecology, and physiology of animals. Within a species, body size can vary substantially across space and time, and the mechanisms generating these patterns have been the focus of evolutionary and ecology research.
2. Bergmann's Rule predicts a negative relationship between body size and temperature across the geographic range of endothermic animals; larger animals have a lower surface to volume ratio, which would allow for greater heat conservation. Despite the broad support for this pattern, its underlying mechanisms are heavily debated. Numerous alternative explanations have been proposed to explain why larger animals are found in colder climates, and vice versa, including heat dissipation, environmental seasonality, and resource availability.
3. We used the Pallid bat, *Antrozous pallidus*, as a model to evaluate Bergmannian size patterns and the relative support for major explanatory hypotheses of geographic body size variation. We tested the hypothesis that geographic size variation is predicted by productivity, as opposed to seasonality, heat conservation or dissipation, or some combination of these processes. Additionally, we investigated the potential ecomorphological consequences of size variation in Pallid bats by determining if skull shape (an indicator of bite performance) varies with size.

4. Whereas we did find that Pallid bat populations in northern latitudes are composed of larger individuals, our results suggest that net primary productivity and, to a lesser extent heat conservation, best explains size variation throughout the western range of this species. We also found that skull shape in Pallid bats changes in tandem with skull size, with larger bats having cranial traits associated with greater bite force production. The results of our study indicate that variation in resource availability may be a key factor underlying spatial patterns in size, morphology and, possibly, feeding performance within wide-ranging bat species.

3.2 INTRODUCTION

Body size is tightly associated with the life history, ecology, and physiology of animals (Lindstedt and Boyce 1985, Isaac 2005, Porter and Kearney 2009). Within a species, adult body sizes can vary substantially across space and time, and the mechanisms generating these patterns have been the focus of evolutionary and ecology research for centuries (Bergmann 1848, Scholander 1955, Mayr 1956, Ashton 2002a). Of the most debated ecogeographic ‘rules’, Bergmann’s Rule (1847, translation in James 1970), predicts a negative relationship between body size and temperature in endothermic animals. In its original formulation, Bergmann proposed that among these animals, a larger body size is selected for in colder environments due to its lower surface to volume ratio, which minimizes heat loss (Mayr 1956). Whereas thermoregulation was the original mechanism proposed, latitude is frequently used as a proxy when testing for conformity to Bergmann’s Rule (reviewed in Ashton *et al.* 2000).

Bergmann’s rule is broadly supported in endothermic vertebrates (i.e., individuals are larger at higher latitudes and/or in habitats with lower temperatures; e.g., Ashton 2002a; Meiri & Dayan 2003; Blackburn & Hawkins 2004), and has also been invoked to explain latitudinal size gradients for various ectothermic vertebrates (Lindsey 1966, Ashton 2002b, Ashton, K and Feldman 2003, Rypel 2014), and arthropods (Arnett and Gotelli 1999, Blanckenhorn and Demont 2004, Stillwell et al. 2007, Shelomi 2012, Parsons and Joern 2014). However, there are many taxa that do not exhibit these size clines (for reviews, see Ashton et al. 2000; Meiri & Dayan 2003), as well as little support for the hypothesis that thermoregulation underlies clinal variation in body size (Scholander 1955; McNab 2010). Additionally, many ectotherms are characterized by reverse Bergmannian clines (Ashton, K and Feldman 2003), which seem to be the product of season length limiting growth (e.g., Blanckenhorn & Demont 2004).

Several alternative processes have been proposed to explain the pattern predicted by Bergmann's Rule, including heat dissipation, and coping with environmental seasonality or changes in resource availability. James (1970) reformulated Bergmann's hypothesis and suggested that pressures for more efficient heat dissipation drive body size variation. Under this scenario, selection would favor a smaller body size in warm and humid environments (Correll et al. 2015). Conversely, Rosenzweig (1968) argued that primary productivity, and thus resource availability, influences body size. In this case, decreased food availability in environments with low primary productivity is predicted to limit body size. However, Boyce (1978) suggested that environmental seasonality explains patterns of body size variation; larger individuals are more resilient to the periods of food shortages that are associated with more seasonal environments.

More recently, McNab (2010) proposed a generalized 'resource rule' in which the combined effect of prey size, food abundance and availability drive patterns of intraspecific body size variation across space and time. In the context of global climate change, the productivity hypothesis has gained increased support for explaining recent temporal changes in body size among mammals (Yom-Tov 2003, Eastman et al. 2012, Tomassini et al. 2014) and birds (Cooch et al. 1991, Leafloor et al. 1998). Additionally, precipitation frequently emerges as a key predictor of geographical size variation, leading to the conclusion that productivity or resource availability are major drivers of this pattern (Bodganowicz 1980, Cardini et al. 2007, Blois et al. 2008, O'Keefe et al. 2013). However, given that environmental variables are frequently intercorrelated, understanding the mechanism generating 'Bergmannian' size gradients requires contrasting multiple hypotheses simultaneously in order to gauge the relative contribution of different ecological or physiological processes (Ashton et al. 2000).

In the present study, we use the Pallid bat, *Antrozous pallidus* (Le Conte 1856), as a model to evaluate the hypothesis that differences in primary productivity explain geographic variability in body size. The Pallid bat is a geographically widespread species in the Family Vespertillionidae, occurring throughout Western North America (Martin and Schmidly 1982). Despite its extensive size variability across its range, previous studies have failed to identify clear geographic patterns, or associations between body size and environmental factors in this species (Martin and Schmidly 1982). The Pallid bat is heterothermic and uses torpor on a daily basis to minimize thermoregulatory costs (Vaughan and Shea 1976). Although little information exists in their winter hibernation phenology (Orr 1954), torpor depth and duration are strongly influenced by ambient temperature conditions throughout their range (O'Shea and Vaughan 1977, Rambaldini and Brigham 2008b). The Pallid bat is generally considered a gleaning insectivore, relying on auditory cues to find large ground dwelling arthropods (e.g., crickets, beetles, scorpions, centipedes; O'Shea, Vaughan & Shea 1977), but its diet and foraging habits are highly variable throughout its range (Herrera et al. 1993, Johnston and Fenton 2001, Frick et al. 2014). In addition to arthropods, Pallid bats have been documented to consume small vertebrates (Lenhart et al. 1894, O'Shea and Vaughan 1977), and are unique among vespertillionids by being the only species known to exhibit facultative nectarivory and frugivory (Howell 1980, Frick et al. 2009, 2013, Aliperti et al. 2017). The exploitation of cardon cacti (*Pachycereus pringlei*) has been observed exclusively in populations from Baja California, Mexico, thus it remains unclear whether or not this foraging strategy is widespread across areas where the Pallid bat co-occurs with other columnar cacti. Given the Pallid bat's broad geographic distribution across a wide latitudinal range and diverse habitats, thermal ecology, varied diet and foraging behavior, and extensive size variation, this species is an ideal model to assess whether resource availability is associated with size variation across their range.

Here, we first assessed whether Pallid bats conform to Bergmann's Rule, characterized by larger individuals at northern portions of its range. We then tested the hypothesis that geographic size variation is driven by differences in primary productivity (and thus resource availability), as opposed to seasonality or temperature, or some combination of these factors. Consistent with findings in other endothermic vertebrates (Wolverton et al. 2009, Gür and Kart Gür 2012, Morales-castilla et al. 2012, Goodall and Crespo 2013, Correll et al. 2015) and ectothermic species (invertebrates; Pearson & Knisley 1985; Arnett & Gotelli 1999), we predicted that larger bats would be found in areas with higher annual net primary productivity (NPP). We also evaluated the potential ecomorphological influence of size variation in Pallid bats, in particular as it pertains to diet. Both size and cranial shape directly influence bite performance in mammals (e.g., bite force; Anderson, Mcbrayer & Herrel 2008; Freeman & Lemen 2010; Santana, Grosse & Dumont 2012; Santana & Miller 2016), and thus the spectrum of prey available for consumption (Aguirre et al. 2003, Marroig and Cheverud 2005, Santana et al. 2010). In several mammal groups, cranial morphology is known to change in tandem with changes in skull size within and among species, and such isometric or allometric patterns can lead to differences in feeding performance and diet (e.g., Marroig & Cheverud 2005, Christiansen & Adolfssen 2005, Santana & Cheung 2016). We tested the hypothesis that Pallid bats exhibit variation in skull shape that is associated with skull size. We predicted that larger individuals would exhibit skull features that enhance bite force, which would in turn enable them to have more generalized diets in areas of high productivity, where a wider range of prey types are expected to be available. Although we focus on a single predator species, our results have broader implications for understanding the mechanisms that drive body size variation among animals.

3.3 METHODS

3.3.1 *Specimens and geometric morphometric analysis*

Our sample was composed of 175 adult Pallid bat crania (male = 82, female = 93) spanning a latitudinal gradient across the western part of their range (Fig. 3.1, Table S1.5). Using a Canon Powershot SLR camera mounted on a copy stand, we obtained digital images (4000 x 3000 pixels) on lateral and ventral views of the cranium. We placed specimens on a custom platform to consistently align them for each view. We then digitized homologous and sliding semi-landmarks for the lateral and ventral cranium (Fig. 3.2, Table S1.6) using *tpsDIG v 2.22* (Rohlf 2006). To minimize measurement error resulting from landmark digitization, the same investigator carried out landmark placement for all specimens for the lateral and ventral cranium, respectively. We also selected a random subset of 10 specimens to perform landmark placement in triplicate on 3 separate occasions, from which we analyzed the repeatability of landmark placement.

To obtain size and shape variables from the digitized landmarks configurations, we carried out a Generalized Procrustes Analysis (GPA) using the package *'geomorph' v. 3.0.0* (Adams and Otárola-Castillo 2013) within *R v. 3.1.2* (R Core Team 2017). GPA removes the effects of rotation and scale from landmark data in order to obtain size and shape variables that are independent from one another (Rohlf and Slice 1990). We used centroid size (i.e. the square root sum of the squared distances of each landmark from the center of the landmark configuration) as a measure of cranium size and proxy for body size. Cranium centroid size is preferable to body mass as measure of body size because the latter varies substantially across nights and seasons in temperate bats (Coutts et al. 1973, Speakman and Rowland 1999). We used the set of Procrustes coordinates as shape variables, and we also extracted the aligned Procrustes residuals to characterize skull shape in the context of allometry analyses. Due to the redundancy of landmarks given the symmetry in the ventral view of the cranium, we extracted the symmetrical shape component using the function *bilat.symmetry* in the *geomorph* package (Adams and Otárola-Castillo 2013) for subsequent shape analyses.

3.3.2 *Environmental variables*

We acquired spatially-gridded environmental datasets to inform tests of the heat conservation and dissipation, seasonality, and productivity hypotheses. Using the geographic coordinates of the collection site recorded for each individual, we extracted the corresponding environmental variables for all individuals. We first downloaded current climate data (World Clim 1.4) from the WorldClim database (Hijmans et al. 2005) at 5 arc-minute resolution (approx. 10 km grids). The current climate dataset is composed of temperature and precipitation raster layers, which were generated using data from weather station monthly averages between the years 1960-1990 (Hijmans et al. 2005).

To test the seasonality hypothesis, we extracted values representing both annual temperature and precipitation variation (the annual standard deviation of mean monthly temperature and precipitation, respectively). We then evaluated the explanatory power of temperature and precipitation seasonality, and used an information theory approach to select a single seasonality variable with the greatest explanatory power (Burnham and Anderson 2002). We found that temperature seasonality provided a better fit to the size data ($\Delta AICc = 25$). Therefore, we used temperature seasonality in subsequent model comparisons.

For testing the heat dissipation and conservation hypotheses, we used the maximum temperature of the warmest month and minimum temperature of the coldest month, respectively, for each specimen. In order to account for potential coordinate errors in the specimen locality information, we applied a bilinear interpolation on these climatic variables. This method averages all values from the nearest 4 cells (10 km grids) of the specimen's locality.

The 'resource rule' (McNab 2010) predicts that body size is largely driven by the size, abundance, and availability of food resources. However, since detailed data on prey (e.g., arthropod) abundance are lacking for most bat species, indices such as net primary productivity (NPP), are frequently used as a proxy for resource availability (Kaspari et al. 2000, Zhao et al. 2005, Wolverton et al. 2009, Gür and Kart Gür 2012). Therefore, to evaluate the productivity hypothesis, we obtained annual NPP (g C m^{-2} $year^{-1}$) gridded data, at a resolution of 30 arc-seconds (approx. 1 km grids), from the MODerate Resolution Imaging Spectroradiometer (MODIS) MOD17A3 land product dataset (Zhao *et al.* 2005; http://www.ntsg.umt.edu). The MOD17 algorithm calculates gross primary productivity (GPP) using a combination of photosynthetically active radiation estimates from satellite data (MODIS), existing land cover classifications, and local climate data, while accounting for daily respiration and maintenance costs. The Annual NPP estimate is the sum of daily GPP, after accounting for plant growth and maintenance, and closely corresponds to other, independently-derived NPP estimates (Zhao et al. 2005). Therefore, as a proxy for local productivity to test the productivity hypothesis, we used the mean annual NPP averaged over all 13 years (2000-2013) for which the MOD17 estimates are available. For each specimen, we calculated average annual NPP within a 5.6 km radius, which was the mean coordinate uncertainty among specimens in our dataset and corresponds to estimated foraging ranges of Pallid bats (Baker et al. 2008). We extracted all environmental variables within *R* v. 3.1.2 (R Core Team 2017), using the package '*raster*' v. 2.3 (Hijman 2015).

3.3.3 *Data analysis*

Prior to investigating geographic size variability, we tested for any evidence of sexual size dimorphism by using Welch's two sample *t*-test. Male and female Pallid bats did not differ in size (see *results*), and therefore we pooled males and females for subsequent analyses. To test for a latitudinal trend in skull size, we carried out ordinary least squares (OLS) linear regression, using centroid size as the response variable and latitude as the explanatory variable. To evaluate the relative support for each of the four hypotheses (Table 3.1) explaining size variability in the Pallid bat, we generated a candidate set of models including the main effects of each environmental variable and additive combinations of main effects using OLS linear regression. In addition to OLS linear models, which do not account for spatial autocorrelation, we fit spatial simultaneous autoregressive (SAR) models (Cressie 1993) to account for spatial dependence in the data. Specifically, we used a spatial error model ($\mathrm{SAR}_{\mathrm{err}}$), which outperforms other SAR models in terms of parameter estimate precision, reduction of residual spatial autocorrelation, and type I error control (Kissling and Carl 2008). The $\mathrm{SAR}_{\mathrm{err}}$ model is an extension of an OLS regression: $\mathbf{Y} = \boldsymbol{\beta} + \lambda \mathrm{W} u + e$, with additional terms representing the spatial structure (λW) in the spatially-dependent error term (*u*). In this equation, W is the spatial weights matrix and λ is the spatial autoregressive coefficient (Cliff & Ord 1981; Kissling & Carl 2008). We defined the weights matrix (W) using row standardization, where we assigned equal weights to all neighboring sites within a 100 km radius. We then fit SAR_{err} models using the *errorsarlm* function in the 'spdep' package (Bivand et al. 2013).

To enable comparison of effect sizes among predictor variables, we first centered each explanatory variable by their respective mean and then scaled these values by the standard deviation from the mean. Prior to fitting multiple regression models, we calculated Spearman's rank correlation coefficient (*r*) between all pairs of environmental variables. If two variables were highly correlated ($r > 0.7$), we did not include both variables in the same statistical model (Table S1.7). We used Akaike's Information Criterion corrected for small sample size (*AICc*) to select the top OLS and SAR_{err} models from the full candidate set of models explaining size variation in the Pallid bat. We considered the minimum *AICc* score, *ΔAICc*, and relative Akaike weight (*w*) when ranking candidate models (Burnham & Anderson 2002; Diniz-filho, Rangel & Bini 2008). Finally, to assess residual spatial autocorrelation, we calculated Moran's *I* for distance bands of 100 km from the residuals of each top ranking OLS and SAR_{err} model using the *correlog* function in the 'pgirmess' package (Giraudoux 2015). We considered significant spatial autocorrelation when the *P*-value of the Moran's *I* coefficient was below $\alpha = 0.05$ after Bonferroni correction (Bivand et al. 2013).

To test for correlated changes in skull shape with skull size, we conducted Procrustes ANOVAs, with a randomized residual permutation procedure (10,000 permutations) for significance testing, using the *proc.D.allometry* function in the *'geomorph'* package (Adams and Otárola-Castillo 2013, Collyer et al. 2014). We first performed a Procrustes ANOVA to test for differences size-shape relationship between males and females. As these were not significant (*see* results), we pooled data from males and females to estimate the amount of variation in shape that is explained by co-variation with size.

3.4 RESULTS

We found no evidence of sexual size dimorphism when we used centroid size of the lateral or ventral views of cranium as proxies for *Antrozous pallidus* body size, (lateral cranium: $t = -0.57$, df = 173, $P = 0.57$, ventral cranium: $t = -0.27$, df = 173, $P = 0.78$). Our analysis of replicate error in landmark digitization suggested that repeatability of landmark placement was higher for the ventral cranium (92%) than the lateral cranium (84%). Therefore, here we present the results of size analyses for the ventral cranium (results were nearly identical for the lateral cranium, however; *results not shown*). When we evaluated the hypotheses proposed to explain geographic size variation in the pallid bat, spatial (SAR_{err}) models always outperformed equivalent aspatial models (OLS) on the basis of *AICc* and model fit (R^2) (Tables 3.2, S1.8). We focus on the results from spatial models below, although patterns were generally consistent whether or not we accounted for spatial dependency in the data (Figs. 3, 4).

Consistent with Bergmann's rule, we found that Pallid bats tend to be larger in the northern part of their range (Table 3.2). Among our full set of candidate models, the top ranking spatial model included environmental variables associated with three of the hypotheses: productivity, seasonality, and heat conservation ($w = 0.46$, Table 3.2, Figs. 3, 4). However, a second model representing the productivity and heat conservation hypotheses also received considerable support ($\Delta AICc = 0.16$, $w = 0.43$, Table 3.2). The top ranking aspatial model included the same environmental predictors (Table S1.8), however the equivalent spatial model had a higher R^2, a lower *AICc,* and no significant spatial autocorrelation pattern in its residuals (Fig. S1.1). The standardized coefficients for models testing the productivity (*NPP*) and heat conservation (*MinWinTemp*) hypotheses suggest that productivity has the largest effect on size variation in the Pallid bat (Fig. 3.3). Although seasonality was included in the top ranking model, the 95% confidence intervals of the coefficient value included zero and was not significant ($\beta = -0.41 \pm 0.25$, $P = 0.10$, Table 3.3, Fig 3.4).

The best-supported spatial model was consistent with the Productivity hypothesis; larger bats are found in areas of higher productivity (*NPP*) ($\beta = 0.95 \pm 0.20$, $P < 0.001$, Table 3.3, Fig 3a). NPP was the only univariate model that received any relative Akaike weight ($w = 0.08$) among the full set of candidate spatial models (Table 3.2). Our best supported spatial model was also consistent with the heat conservation hypothesis (*MinWinTemp*), although the standardized effect was less than NPP ($\beta = -0.55 \pm 0.20$, $P < 0.01$, Table 3.3, Fig 3.4). Interestingly, we found that minimum winter temperature alone had no significant effect on size in the Pallid bat ($\beta = -0.31 \pm 0.17$, $P = 0.07$), but that it was influential only after accounting for the effects of NPP and temperature seasonality (Table 3.2). We also found that size decreased with increasing maximum summer temperature (*MaxSumTemp*; Table 3.2), which is consistent with the heat dissipation hypothesis. However, among the full set of candidate models explaining size variation in the Pallid bat, maximum summer temperature received little *AICc* support (Table 3.2).

We also found a significant association between variation in the size and shape of the cranium. In the lateral view, we found that larger bats generally had a more pronounced sagittal crest and a more posteriorly projected intraparietal region ($SS = 0.01$, $MS = 0.01$, $df = 1$, $R^2 = 0.06$, $P < 0.001$, Fig. 3.5a). In the ventral view, larger bats tended to have broader zygomatic arches, shorter rostrum, and broader braincase ($SS = 0.003$, $MS = 0.003$, $df = 1$, $R^2 = 0.05$, $P <$

0.001, Fig. 3.5b). There were no difference in these size-shape relationships between males and females in the lateral (Procrustes ANOVA $P = 0.79$) or ventral (Procrustes ANOVA $P = 0.13$) views of the cranium.

3.5 DISCUSSION

The Pallid bat exhibits substantial geographic variation in body size and dietary ecology, and our objective was to identify the environmental factors that best explain this variation. We found that Pallid bats tend to be larger in the northern part of their range (Table 3.2). This pattern is consistent with latitudinal size clines observed in other mammals (Ashton et al. 2000, Meiri and Dayan 2003), birds (Ashton 2002a), and various ectothermic species, including reptiles (Ashton, K and Feldman 2003), amphibians (Ashton 2002b), and arthropods (Blanckenhorn and Demont 2004). Although we did find that larger bats inhabit more northern latitudes, the latitudinal trend was weak relative to combined effects of productivity and minimum winter temperature. Whereas heat conservation was the original mechanism proposed to explain this trend (Bergmann 1848, Mayr 1956), our results do not support this rationale; minimum winter temperature alone failed to explain a significant amount of body size variation in Pallid bats (Table 3.2, Fig. 3.3b). Instead, we found that the size cline in the Pallid bat is best explained by the combined effects of net primary productivity (NPP) and minimum winter temperature (Table 3.2). Our results strongly suggest that the latitudinal cline in Pallid bat size is related to variation in productivity, as opposed to temperature alone.

The productivity hypothesis has been invoked to explain both geographic and temporal size variation among mammals (Meiri et al. 2007, Gür and Kart Gür 2012, Goodall and Crespo 2013, Correll et al. 2015), birds (Leafloor et al. 1998, Morales-castilla et al. 2012), and arthropods (Arnett and Gotelli 1999, Stillwell et al. 2007). As the sole predictor of cranium size, NPP explained 54% of the variation, with only an additional 2% explained by the top ranked spatial model (Table 3.2). Therefore, our study demonstrates that the relationship between productivity and body size may extend to Chiroptera as well.

We also evaluated the support for alternative hypotheses (Table 3.1), in addition to productivity, in explaining geographic size variation in the Pallid bats. When we considered the combined effect of productivity and heat conservation, these emerged as important predictors, but productivity was still clearly the most influential in terms of its standardized effect on body size (Table 3.3, Fig. 3.4). In contrast, our results were not concordant with the seasonality hypotheses. Specifically, we found that Pallid bats tend to be smaller in more seasonal environments (Table 3.3, Fig. 3.3c). These results contradict the prediction from the seasonality hypothesis, which proposes that, because larger individuals have proportionally larger fat stores, they have greater overwinter fasting endurance in more seasonal environments (Boyce 1978, Lindstedt and Boyce 1985). It is possible that differences in measurement error among climate variables could have obscured our ability to identify trends (Hijmans et al. 2005). Additionally, our use of a skeletal metric (cranium size) as a measure of body size could have obscured a size-seasonality relationship; for example, body mass but not skeletal size is correlated with seasonality among Swedish moose (Sand et al. 1995). Nevertheless, skull size is a more appropriate metric for drawing generalizations about geographic size variability in temperate bats because their body mass can vary over 50% on a nightly basis (Coutts et al. 1973), and previous studies using linear measurements have found significant relationships between size and seasonality in mammals (Gür 2010) and insects (Stillwell et al. 2007).

Importantly, the thermal physiology of bats may also explain why body size can lack a significant relationship with seasonality; bats use torpor and hibernation to cope with periods of food shortage and/or seasonality (Ruf and Geiser 2015). Temperate bats show extensive flexibility in their use of daily torpor and hibernation phenology depending on their energetic state (Boyles et al. 2007, Rambaldini and Brigham 2008a, Matheson et al. 2010, Norquay and Willis 2014), and thus behavioral and physiological responses may be more important than morphological or size adaptations for coping with highly seasonal environments. Among some insects, body size appears to be limited by the length of the growing season in seasonal environments (Roff 1980, Chown and Klok 2003, Blanckenhorn and Demont 2004). Thus, changes in the length of the growing period, rather than overwintering starvation resistance, may be more influential in determining adult body size among heterothermic mammals, such as Pallid bats (Lindstedt and Boyce 1985). Future studies comparing body size gradients among bat species that differ seasonal torpor patterns could help clarify whether the degree of heterothermy mediates the relative influences of growing season length and fasting endurance on body size.

At a coarse scale, using proxies such as NPP to test the productivity hypothesis allowed us to distinguish between the two broad mechanisms proposed to explain geographic size variation in Pallid bats, thermoregulation (heat conservation and dissipation hypotheses) and food resource availability (seasonality and productivity hypotheses). The fact that productivity is most closely related to size variation in the Pallid bat (Fig. 3.4) is consistent with growing evidence that resource availability drives both geographic (Wolverton et al. 2009, Goodall and Crespo 2013, Correll et al. 2015) and temporal (Yom-Tov 2003, Zalewski and Bartoszewicz 2012, Tomassini et al. 2014) patterns of intraspecific size variation. The geographic trends were robust despite the fact that climate data and specimen age were not temporally matched. Our

Pallid bat samples were originally collected between 1918-2010, but the climate and NPP data we acquired did not span this entire range, and we had to use averaged annual estimates (*see* methods). Although we cannot provide a causal link between body size and NPP, arthropod biomass is positively correlated with productivity (Kaspari et al. 2000, Sweet et al. 2015) and thus increased body size in Pallid bats could be the result of higher prey availability. More detailed dietary information throughout the range of the Pallid bat is necessary to gain a thorough understanding of how food resource availability may be associated with changes in body size.

We also found that differences in cranial morphology are significantly associated with differences in size in Pallid bats (Fig. 3.5). Larger bats exhibit cranial morphologies that may allow them to consume relatively larger and harder prey (Freeman 1984, Aguirre et al. 2003, Freeman and Lemen 2010, Santana et al. 2010, Santana and Cheung 2016) (Fig. 3.5). Broader zygomatic arches and a more pronounced sagittal crest can accommodate larger temporalis (jaw closing) muscles that can produce more forceful bites (Christiansen and Adolfssen 2005, Santana et al. 2010, Senawi et al. 2015). Similarly, a relatively shorter and wider rostrum allows for more forceful bites and a greater resistance to torsional forces when chewing hard prey (Dumont et al. 2005, Freeman and Lemen 2010, Santana et al. 2010). Qualitatively, these morphological trends could explain some of the geographic variation in Pallid bat diets that have been described by previous studies (Johnston and Fenton 2001). Comparing the diet of Pallid bat populations from the California central coast and Death Valley, Johnston & Fenton (2001) found considerable diet variability between populations; bats in the coastal population (which experience high NPP; Fig. 3.1) consume harder and larger prey and hard parts of the prey, which are culled by bats in the inland desert population (low NPP). The correlated changes in cranial size and shape described here indicate that Pallid bats from the coastal population can feed on relatively larger and more mechanically challenging prey not only because of their larger size, but also because of allometric cranial features that enhance bite force production.

Our study suggests that productivity, a proxy for food resource availability, is a key predictor of geographic body size variability in the Pallid bat. This adds to the growing evidence that resource availability may be responsible for body size variation in space (Wolverton et al. 2009, Goodall and Crespo 2013, Correll et al. 2015) and time (Arnett and Gotelli 1999, Yom-Tov 2003, Eastman et al. 2012, Tomassini et al. 2014). Importantly, our results underscore the importance of evaluating multiple environmental parameters, as opposed to just latitude or temperature, when attempting to explain patterns of geographic size variation (Ashton et al. 2000). Additionally, our research emphasizes the importance of size variation in generating morphological and ecological diversity within a species.

3.6 ACKNOWLEDGEMENTS

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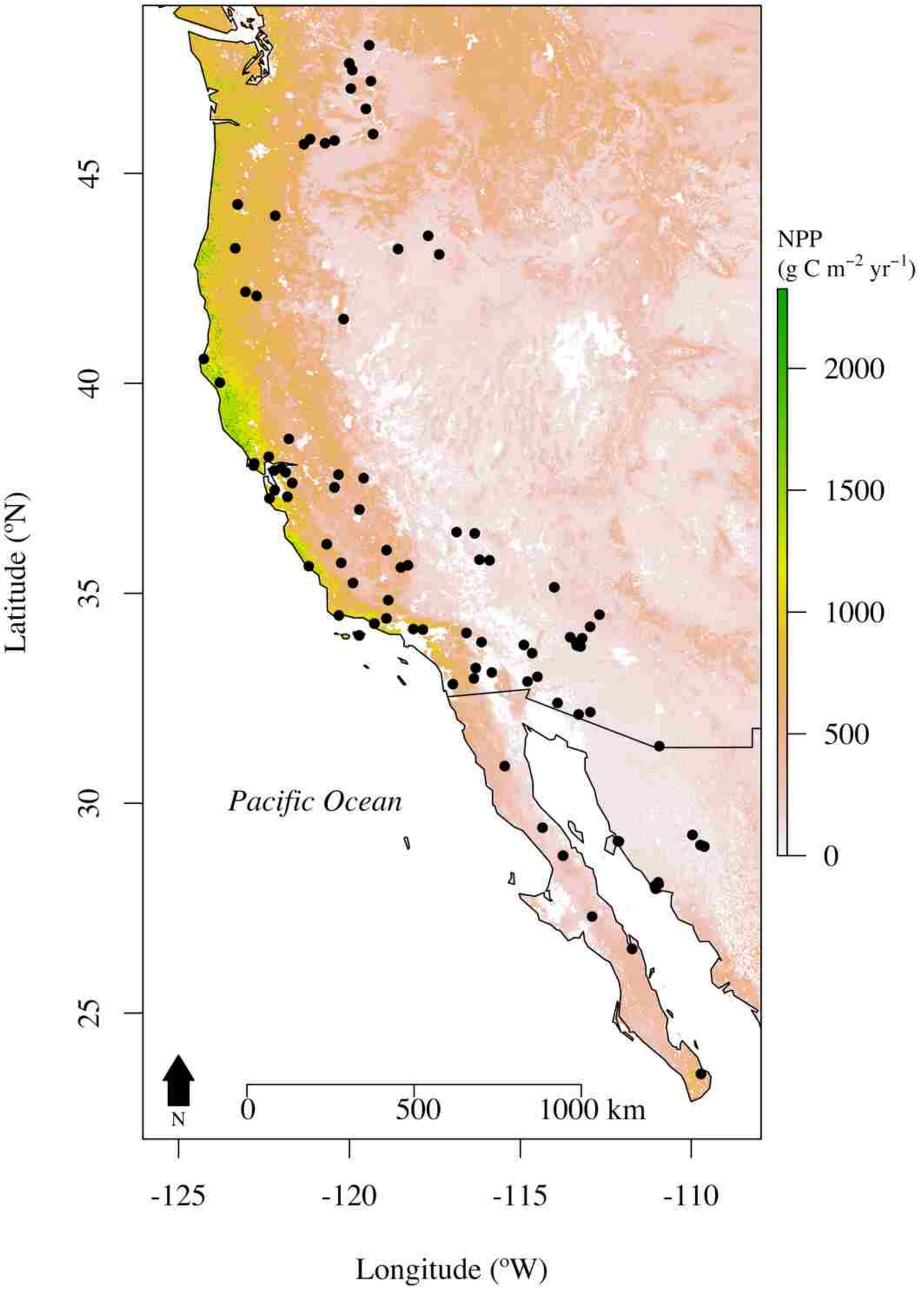

Figure 3.1. Collection localities for Pallid bat, *Antrozous pallidus,* specimens (black circles). Colors on the map represent mean annual net primary productivity (g C m^{-2} year^{-1}), obtained as gridded data from the MODerate Resolution Imaging Spectroradiometer (MODIS) MOD17 land product dataset (*see* methods).

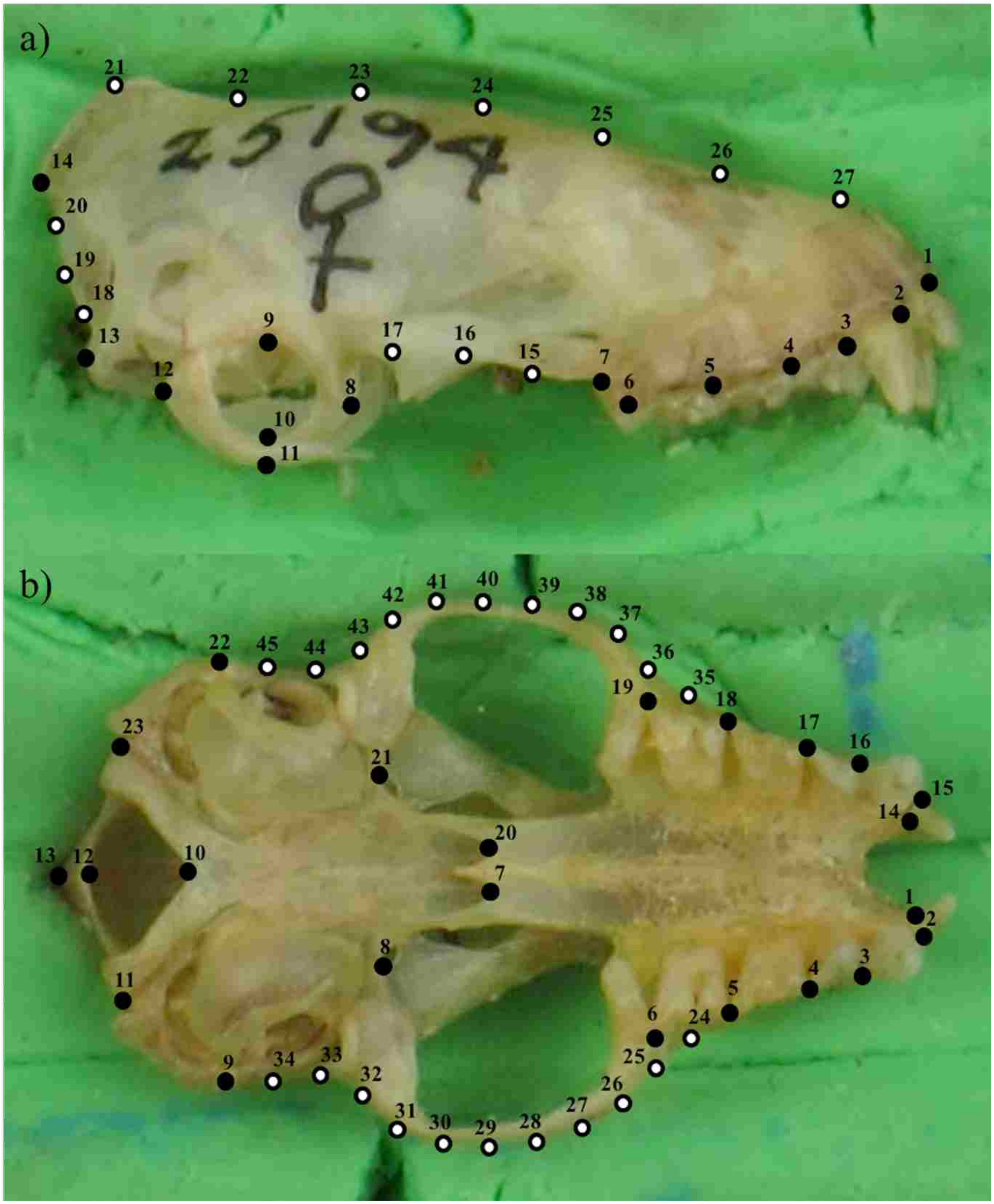

Figure 3.2. Landmark configuration for the (a) lateral and (b) ventral views of the cranium of the Pallid bat. Black circles indicate homologous landmarks and white circles indicate curve-sliding semi-landmarks (placed equidistantly between homologous landmarks).

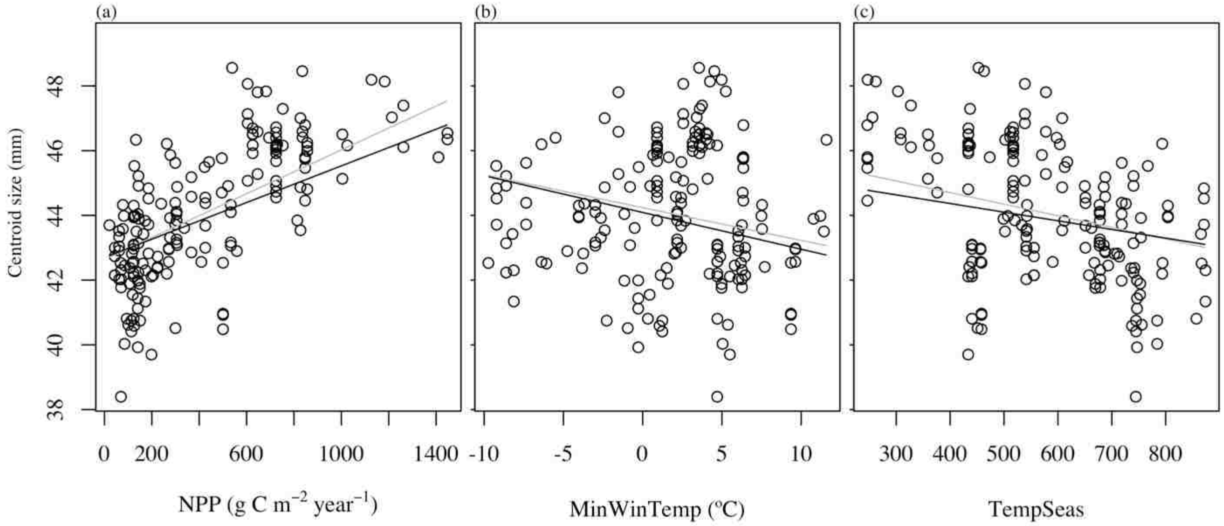

Figure 3.3. Fitted relationships between centroid size of the Pallid bat cranium and environmental variables from the top *AICc* ranked aspatial (grey lines) and spatial (black lines) models explaining size variation in the Pallid bat: (a) Net primary productivity (productivity hypothesis), (b) Minimum temperature of the coldest month (heat conservation hypothesis), and (c) Temperature seasonality (seasonality hypothesis).

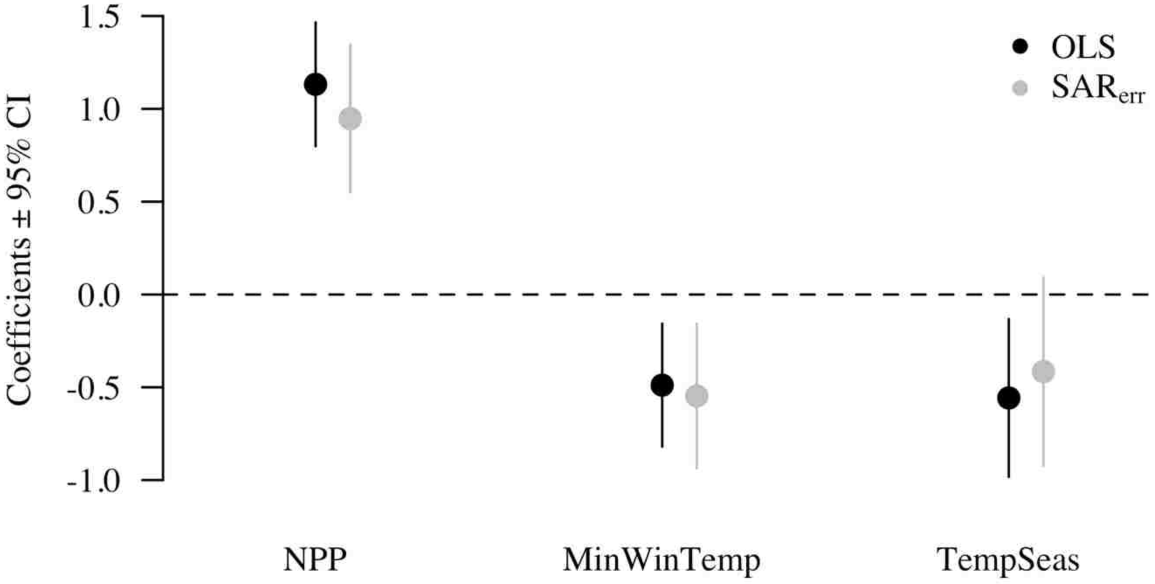

Figure 3.4. Coefficient estimates ± 95% confidence intervals for the environmental variables in the top *AICc* ranked OLS and SAR$_{err}$ models explaining size variability in the Pallid bat. To allow comparisons among effect sizes, variables were first scaled and centered prior to statistical model fitting.

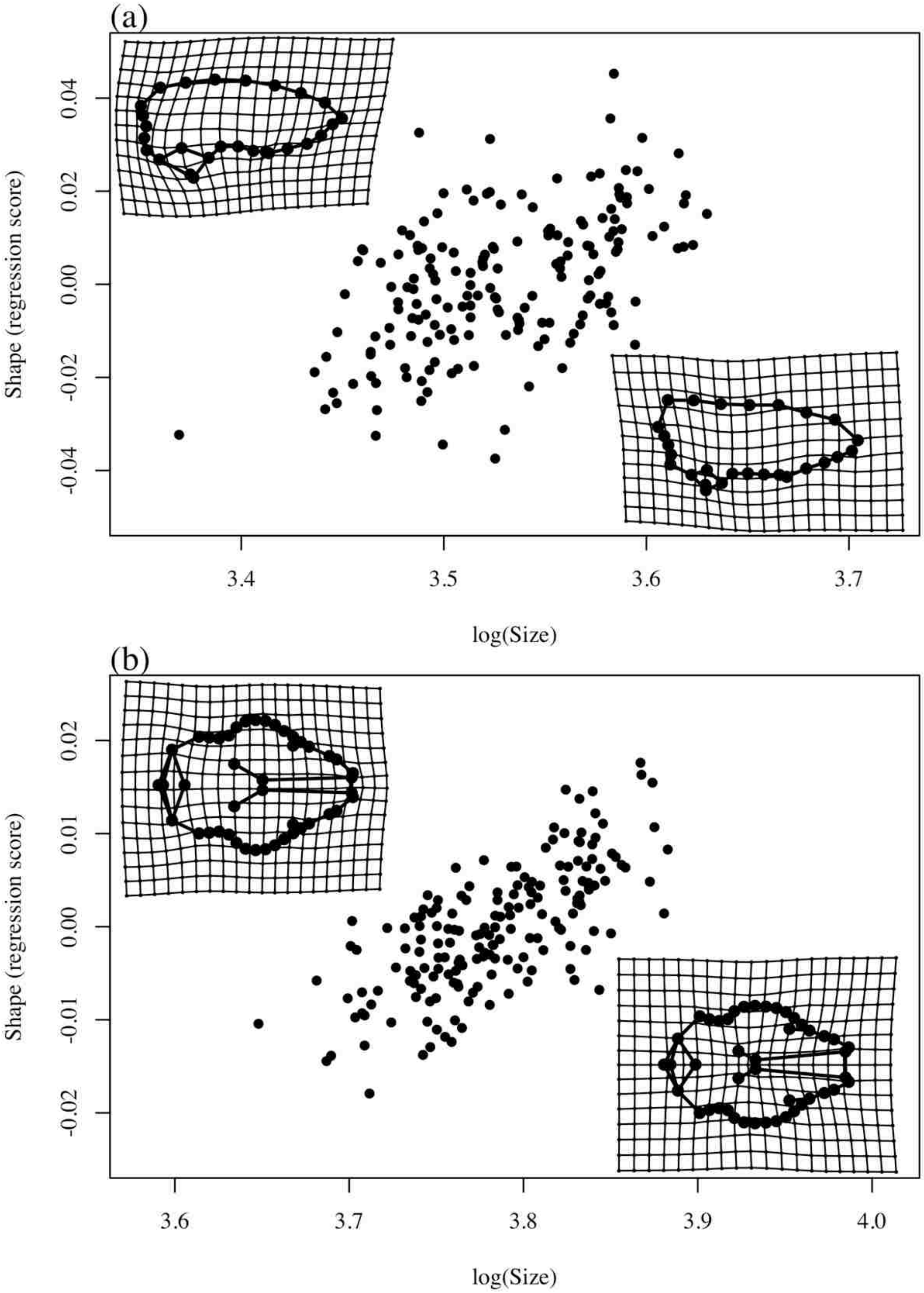

Figure 3.5. The relationship between size ($\log_{10}$ centroid size) and shape in the (a) lateral and (b) ventral cranium views of the pallid bat. Deformation grids are shown to illustrate the shape of the smallest (left) and largest (right) specimens relative to the average shape.

Table 3.1. Summary of major hypotheses proposed to explain Bergmannian size patterns, the predicted trends, and environmental variables used to test each hypothesis in this study.

Hypothesis	Prediction	Environmental Variable	Description
Heat conservation	Size increases as temperature decreases	*MinWinTemp*	Minimum temperature of the coldest month
Heat dissipation	Size decreases with humidity and environmental temperature	*MaxSumTemp*	Maximum temperature of the warmest month
Seasonality	Size increases with seasonality	*TempSeas*	Temperature seasonality
Productivity	Size increases with productivity and resource availability	*NPP*	Mean annual net primary productivity

Table 3.2. Spatial (SAR_{err}) model selection results for variables predicting cranium centroid size in the Pallid bat. The top model is indicated in bold. See Table 1 and methods for details about model variables.

SAR Model	R^2	*AICc*	*Δ AICc*	*w*	*λ*
NPP + MinWinTemp + TempSeas	**0.56**	**618.2**	**0**	**0.46**	**0.42**
NPP + MinWinTemp	0.55	618.3	0.16	0.43	0.48
NPP *(Productivity)*	0.54	621.7	3.53	0.08	0.43
NPP + TempSeas	0.54	623.7	5.49	0.03	0.44
TempSeas + MaxSumTemp + MinWinTemp	0.53	630.7	12.57	0	0.64
Latitude	0.51	633.7	15.56	0	0.66
TempSeas + MinWinTemp	0.51	634.5	16.24	0	0.55
MaxSumTemp *(Heat dissipation)*	0.48	642.2	24.04	0	0.59
TempSeas + MaxSumTemp	0.48	643.4	25.24	0	0.56
MaxSumTemp + MinWinTemp	0.48	644	25.85	0	0.61
TempSeas *(Seasonality)*	0.47	647.2	29.08	0	0.62
MinWinTemp *(Heat conservation)*	0.46	647.9	29.74	0	0.69

Table 3.3. Coefficient estimates for variables included in the top ranked spatial (SAR_{err}) model predicting variation in cranium centroid size in the Pallid bat.

Variable	β	*SE*	*P*
NPP	0.95	0.20	<0.001
MinWinTemp	-0.55	0.20	<0.01
TempSeas	-0.41	0.25	0.1

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SUPPLEMENTARY TABLES & FIGURES

Table S.5.1. Survey effort for islands surveyed throughout the San Juan Archipelago, ranked by decreasing size. Call file total indicates the number of bat call sequence files that were identified to species, see *methods*. The capture total indicates the number of individuals captured.

Island	**Acoustic sites**	**Acoustic nights**	**Call file total**	**Mist Net sites**	**Mist Net nights**	**Capture total**	**Years surveyed**
Mainland	11	85	258	5	9	25	2015-2017
Whidbey	4	36	148	2	4	34	2015-2017
Orcas	11	58	190	13	15	87	2014-2017
San Juan	9	42	187	14	17	128	2014-2017
Lopez	8	67	261	5	10	64	2015-2017
Shaw	10	55	178	4	8	44	2015-2016
Blakely	8	30	115	4	6	51	2015-2017
Waldron	4	28	137	2	6	49	2015-2017
Stuart	5	17	87	4	5	27	2015-2016
Sucia	5	19	59	2	4	62	2015-2016
Burrows	2	15	43	-	-	-	2016-2017
Patos	4	13	36	2	4	30	2015-2016
Vendovi	5	8	28	4	5	57	2014-2016
Jones	5	16	62	2	4	19	2015-2017
Matia	5	16	46	2	4	9	2016
James	5	17	29	3	4	3	2015-2016
Clark	4	18	41	2	3	10	2015-2017
Turn	1	4	3	-	-	-	2016
Saddle bag	2	18	50	-	-	-	2016-2017
Yellow	2	10	9	-	-	-	2016-2017
Doe	1	9	27	-	-	-	2016-2017
Blind	2	15	26	-	-	-	2016-2017

Table S1.2. Survey effort at 104 acoustic monitoring sites across 21 islands located in the San Juan Archipelago of Washington State. Islands are numbered in descending order of their size. Sites are arbitrarily numbered and indicate the whether a there was a water source or coastline within 30 m of the site, and the percent canopy cover within a 30 m radius. For each island and site, we also include the number of survey nights, years surveyed, and the sum of nightly recorded bat passes for *Myotis* spp., large bats, and combined total bat echolocation files, see *methods*.

Island	Site	Water	Coast	Canopy (%)	Nights	Years	*Myotis* spp.	Large bats	Total
1. Whidbey					35	2015-2017	8040	621	8661
	1	0	1	0	14	2015-2017	1619	234	1853
	2	1	0	51	13	2015-2017	6080	255	6335
	3	0	0	78	4	2017	109	102	211
	4	0	1	4	4	2017	232	30	262
2. Orcas					59	2015-2016	4132	1499	5631
	1	0	0	69	6	2015-2016	380	39	419
	2	0	0	25	6	2015, 2017	379	143	522
	3	0	0	66	2	2016	41	45	86
	4	0	0	57	9	2015-2017	195	657	852
	5	0	0	49	9	2015-2017	351	119	470
	6	0	0	28	4	2015	438	54	492
	7	1	0	30	5	2015-2016	562	141	703
	8	0	0	61	7	2015-2016	97	19	116
	9	1	0	40	2	2016	212	22	234
	10	0	0	74	4	2015	115	22	137
	11	1	0	65	5	2016-2017	1362	238	1600
3. San Juan					43	2015-2016	3616	2156	5772
	1	1	0	1	5	2015	869	73	942
	2	0	0	0	6	2015-2016	99	195	294
	3	0	1	6	4	2015	44	6	50
	4	0	0	5	3	2015	16	17	33
	5	1	0	70	7	2015-2016	1621	1350	2971
	6	0	0	4	5	2016	218	217	435
	7	1	0	0	5	2016	393	235	628
	8	0	0	27	5	2015-2016	139	25	164
	9	0	0	89	3	2015	217	38	255
4. Lopez					67	2015-2017	3518	2851	6369
	1	1	0	4	10	2015-2017	85	305	390

2	1	0	55	16	2015-2017	1291	655	1946
3	0	0	4	5	2015	373	455	828
4	0	0	61	5	2015-2016	175	108	283
5	0	0	79	15	2015-2017	223	305	528
6	0	1	0	4	2017	246	268	514
7	0	0	13	10	2015-2017	781	649	1430
8	0	0	0	2	2017	344	106	450
5. Shaw				56	2015-2016	1068	1854	2922
1	0	1	41	4	2015	49	237	286
2	0	0	23	3	2016	14	58	72
3	0	0	47	8	2015-2016	67	61	128
4	0	0	0	1	2015	2	11	13
5	0	0	22	3	2015	51	230	281
6	0	0	13	4	2015	28	55	83
7	0	0	0	6	2016	9	296	305
8	1	0	9	10	2015-2016	596	412	1008
9	0	0	89	6	2016	73	36	109
10	0	0	9	3	2015	100	370	470
11	0	0	90	8	2015-2016	79	88	167
6. Blakely				26	2015-2017	3043	1366	4409
1	0	0	72	2	2015	158	38	196
2	0	0	70	5	2015, 2017	299	268	567
3	1	0	32	3	2015	522	93	615
4	1	0	47	3	2017	688	679	1367
5	0	1	7	2	2015	211	118	329
6	0	0	20	3	2015	53	122	175
7	0	0	84	5	2015, 2017	1029	36	1065
8	0	1	18	3	2017	83	12	95
7. Waldron				28	2015-2017	2453	2248	4701
1	0	1	0	7	2015-2017	89	241	330
2	1	0	0	7	2015-2017	225	1235	1460
3	0	0	38	7	2015-2017	129	219	348
4	0	0	75	7	2015-2017	2010	553	2563
8. Stuart				17	2015-2016	3135	1060	4195
1	0	1	0	3	2015-2016	85	259	344
2	0	0	83	3	2015	158	30	188
3	1	0	72	4	2015-2016	964	297	1261
4	0	0	77	2	2016	482	26	508
5	0	0	58	5	2015-2016	1446	448	1894
9. Sucia				20	2015-2016	1163	581	1744

1	0	0	10	6	2015-2016	59	177	236
2	0	0	0	2	2016	43	195	238
3	0	0	41	2	2016	201	54	255
4	0	0	41	4	2015	389	123	512
5	0	0	83	6	2015-2016	471	32	503
10. Burrows				27	2016-2017	2795	227	3022
1	0	1	54	11	2017	1430	199	1629
2	0	0	88	16	2016-2017	1365	28	1393
11. Patos				13	2015-2016	723	504	1227
1	0	0	89	4	2015-2016	458	5	463
2	0	0	47	4	2015-2016	167	357	524
3	0	1	4	2	2015	5	52	57
4	0	1	21	3	2015-2016	93	90	183
12. Vendovi				12	2015-2016	1418	322	1740
1	0	1	15	2	2015	21	4	25
2	0	1	6	3	2015-2016	188	57	245
3	0	0	92	3	2015-2016	689	66	755
4	0	0	45	1	2016	326	149	475
5	0	0	10	3	2016-2015	194	46	240
13. Jones				16	2015, 2017	291	960	1251
1	0	0	59	2	2017	48	292	340
2	0	0	89	4	2015, 2017	51	229	280
3	0	0	41	2	2015	102	176	278
4	0	1	42	4	2015, 2017	60	58	118
5	0	0	77	4	2015, 2017	30	205	235
14. Matia				16	2016	2098	325	2423
1	0	0	79	4	2016	305	152	457
2	0	0	85	2	2016	138	13	151
3	0	0	87	2	2016	359	9	368
4	0	0	72	4	2016	138	110	248
5	0	0	85	4	2016	1158	41	1199
15. James				19	2015-2016	225	460	685
1	0	1	26	4	2015-2016	33	196	229
2	0	0	13	4	2015-2016	75	232	307
3	0	0	88	2	2015	44	0	44
4	0	1	15	3	2015-2016	17	25	42
5	0	0	85	4	2015-2016	34	5	39
6	0	0	74	2	2015	22	2	24
16. Clark				19	2015-2017	347	554	901
1	0	1	0	1	2015	61	12	73

	2	0	0	63	3	2015-2016	67	143	210
	3	0	1	0	2	2016	32	274	306
	4	0	0	0	13	2015-2017	187	125	312
17. Turn					5		44	13	57
	1	0	0	26	5	2016	44	13	57
18. Saddlebag					19	2016-2017	1523	291	1814
	1	0	0	66	6	2017	851	80	931
	2	0	0	31	13	2016-2017	672	211	883
19. Yellow					15	2016-2017	173	35	208
	1	0	0	25	5	2017	70	4	74
	2	0	1	0	10	2016-2017	103	31	134
20. Doe					10	2016-2017	1083	144	1227
	1	0	1	42	10	2016-2017	1083	144	1227
21. Blind					15	2016-2017	144	55	199
	1	0	0	0	10	2016-2017	91	34	125
	2	0	1	0	5	2017	53	21	74

Table S.1.3. Pearson correlation coefficients between explanatory variables used to explain nightly activity of bats in the San Juan Islands. Significance is indicated by (*) for P < 0.05, (**) for P < 0.01, and (***) for P < 0.001.

	Area	Iso	Snag	Water	Coast	Canopy	Moon
Area	-	-0.16	-0.29***	0.24***	0.07	0.04	0.14**
Iso		-	0.25***	-0.17***	0.03	-0.1*	-0.15***
Snag			-	-0.11**	0.01	0.32	-0.13**
Water				-	-0.22***	-0.08	0.02
Coast					-	-0.36***	-0.02
Canopy						-	-0.08
Moon							-

Table S.1.4. Regression parameter estimates (± SE) for site model explaining nightly activity of Myotis spp. across 104 sites and 21 islands in the San Juan Archipelago. Significance is indicated by (*) for P < 0.05, (**) for P < 0.01, and (***) for P < 0.001.

Variable	*Myotis spp.*
Water	**1.56 ± 0.28*** **
Coast	0.14 ± 0.27
Moon	0.16 ± 0.07*
Canopy	**0.46 ± 0.11*** **

Table S.1.5. Museum name and specimen numbers for *Antrozous pallidus* specimens.

Museum	**Specimen Number**
Los Angeles County Museum	LACM:Mamm:543
Los Angeles County Museum	LACM:Mamm:544
Los Angeles County Museum	LACM:Mamm:8929
Los Angeles County Museum	LACM:Mamm:8930
Los Angeles County Museum	LACM:Mamm:9570
Los Angeles County Museum	LACM:Mamm:9668
Los Angeles County Museum	LACM:Mamm:9685
Los Angeles County Museum	LACM:Mamm:11659
Los Angeles County Museum	LACM:Mamm:11660
Los Angeles County Museum	LACM:Mamm:11663
Los Angeles County Museum	LACM:Mamm:13208
Los Angeles County Museum	LACM:Mamm:30244
Los Angeles County Museum	LACM:Mamm:69527
Los Angeles County Museum	LACM:Mamm:69531
Los Angeles County Museum	LACM:Mamm:72858
Museum of Southwestern Biology	MSB:Mamm:18323
Museum of Southwestern Biology	MSB:Mamm:18808
Museum of Southwestern Biology	MSB:Mamm:18809
Museum of Southwestern Biology	MSB:Mamm:19039
Museum of Southwestern Biology	MSB:Mamm:19043
Museum of Southwestern Biology	MSB:Mamm:24974
Museum of Southwestern Biology	MSB:Mamm:38742
Museum of Southwestern Biology	MSB:Mamm:42581
Museum of Southwestern Biology	MSB:Mamm:42582
Museum of Southwestern Biology	MSB:Mamm:43110
Museum of Southwestern Biology	MSB:Mamm:43839
Museum of Southwestern Biology	MSB:Mamm:43841
Museum of Southwestern Biology	MSB:Mamm:53820
Museum of Southwestern Biology	MSB:Mamm:54946
Museum of Southwestern Biology	MSB:Mamm:60893
Museum of Southwestern Biology	MSB:Mamm:83770
Museum of Southwestern Biology	MSB:Mamm:161032
Museum of Southwestern Biology	MSB:Mamm:161044
Museum of Southwestern Biology	MSB:Mamm:161047
Museum of Southwestern Biology	MSB:Mamm:161048

Museum of Southwestern Biology	MSB:Mamm:161049
Museum of Southwestern Biology	MSB:Mamm:161050
Museum of Southwestern Biology	MSB:Mamm:161070
Museum of Southwestern Biology	MSB:Mamm:161085
Museum of Southwestern Biology	MSB:Mamm:161088
Museum of Southwestern Biology	MSB:Mamm:161089
Museum of Southwestern Biology	MSB:Mamm:161091
Museum of Southwestern Biology	MSB:Mamm:161095
Museum of Southwestern Biology	MSB:Mamm:161099
Museum of Southwestern Biology	MSB:Mamm:161104
Museum of Vertebrate Zoology	MVZ:Mamm:5244
Museum of Vertebrate Zoology	MVZ:Mamm:7340
Museum of Vertebrate Zoology	MVZ:Mamm:10696
Museum of Vertebrate Zoology	MVZ:Mamm:18788
Museum of Vertebrate Zoology	MVZ:Mamm:18789
Museum of Vertebrate Zoology	MVZ:Mamm:22091
Museum of Vertebrate Zoology	MVZ:Mamm:22093
Museum of Vertebrate Zoology	MVZ:Mamm:22097
Museum of Vertebrate Zoology	MVZ:Mamm:22098
Museum of Vertebrate Zoology	MVZ:Mamm:71625
Museum of Vertebrate Zoology	MVZ:Mamm:71626
Museum of Vertebrate Zoology	MVZ:Mamm:71627
Museum of Vertebrate Zoology	MVZ:Mamm:71634
Museum of Vertebrate Zoology	MVZ:Mamm:71636
Museum of Vertebrate Zoology	MVZ:Mamm:72100
Museum of Vertebrate Zoology	MVZ:Mamm:82137
Museum of Vertebrate Zoology	MVZ:Mamm:82139
Museum of Vertebrate Zoology	MVZ:Mamm:82140
Museum of Vertebrate Zoology	MVZ:Mamm:82141
Museum of Vertebrate Zoology	MVZ:Mamm:82142
Museum of Vertebrate Zoology	MVZ:Mamm:90573
Museum of Vertebrate Zoology	MVZ:Mamm:90575
Museum of Vertebrate Zoology	MVZ:Mamm:94700
Museum of Vertebrate Zoology	MVZ:Mamm:96091
Museum of Vertebrate Zoology	MVZ:Mamm:97534
Museum of Vertebrate Zoology	MVZ:Mamm:101942
Museum of Vertebrate Zoology	MVZ:Mamm:101948
Museum of Vertebrate Zoology	MVZ:Mamm:101990

Museum of Vertebrate Zoology	MVZ:Mamm:102223
Museum of Vertebrate Zoology	MVZ:Mamm:102232
Museum of Vertebrate Zoology	MVZ:Mamm:103196
Museum of Vertebrate Zoology	MVZ:Mamm:103197
Museum of Vertebrate Zoology	MVZ:Mamm:103210
Museum of Vertebrate Zoology	MVZ:Mamm:103215
Museum of Vertebrate Zoology	MVZ:Mamm:103893
Museum of Vertebrate Zoology	MVZ:Mamm:105205
Museum of Vertebrate Zoology	MVZ:Mamm:105206
Museum of Vertebrate Zoology	MVZ:Mamm:106846
Museum of Vertebrate Zoology	MVZ:Mamm:108007
Museum of Vertebrate Zoology	MVZ:Mamm:108008
Museum of Vertebrate Zoology	MVZ:Mamm:108009
Museum of Vertebrate Zoology	MVZ:Mamm:109494
Museum of Vertebrate Zoology	MVZ:Mamm:109505
Museum of Vertebrate Zoology	MVZ:Mamm:109509
Museum of Vertebrate Zoology	MVZ:Mamm:109520
Museum of Vertebrate Zoology	MVZ:Mamm:109555
Museum of Vertebrate Zoology	MVZ:Mamm:109846
Museum of Vertebrate Zoology	MVZ:Mamm:109847
Museum of Vertebrate Zoology	MVZ:Mamm:109848
Museum of Vertebrate Zoology	MVZ:Mamm:109849
Museum of Vertebrate Zoology	MVZ:Mamm:109850
Museum of Vertebrate Zoology	MVZ:Mamm:110684
Museum of Vertebrate Zoology	MVZ:Mamm:110685
Museum of Vertebrate Zoology	MVZ:Mamm:110686
Museum of Vertebrate Zoology	MVZ:Mamm:110687
Museum of Vertebrate Zoology	MVZ:Mamm:110688
Museum of Vertebrate Zoology	MVZ:Mamm:110689
Museum of Vertebrate Zoology	MVZ:Mamm:110690
Museum of Vertebrate Zoology	MVZ:Mamm:110691
Museum of Vertebrate Zoology	MVZ:Mamm:110692
Museum of Vertebrate Zoology	MVZ:Mamm:110693
Museum of Vertebrate Zoology	MVZ:Mamm:110694
Museum of Vertebrate Zoology	MVZ:Mamm:110695
Museum of Vertebrate Zoology	MVZ:Mamm:110701
Museum of Vertebrate Zoology	MVZ:Mamm:110702
Museum of Vertebrate Zoology	MVZ:Mamm:110703

Museum of Vertebrate Zoology	MVZ:Mamm:110704
Museum of Vertebrate Zoology	MVZ:Mamm:112450
Museum of Vertebrate Zoology	MVZ:Mamm:112454
Museum of Vertebrate Zoology	MVZ:Mamm:114446
Museum of Vertebrate Zoology	MVZ:Mamm:114450
Museum of Vertebrate Zoology	MVZ:Mamm:114451
Museum of Vertebrate Zoology	MVZ:Mamm:122057
Museum of Vertebrate Zoology	MVZ:Mamm:122295
Museum of Vertebrate Zoology	MVZ:Mamm:122877
Museum of Vertebrate Zoology	MVZ:Mamm:134289
Museum of Vertebrate Zoology	MVZ:Mamm:146575
Museum of Vertebrate Zoology	MVZ:Mamm:146578
Museum of Vertebrate Zoology	MVZ:Mamm:183565
Museum of Vertebrate Zoology	MVZ:Mamm:189928
Museum of Vertebrate Zoology	MVZ:Mamm:227947
Puget Sound Museum	PSM:Mamm:7698
Puget Sound Museum	PSM:Mamm:8969
Puget Sound Museum	PSM:Mamm:8970
Puget Sound Museum	PSM:Mamm:8971
Puget Sound Museum	PSM:Mamm:8972
Puget Sound Museum	PSM:Mamm:8973
Puget Sound Museum	PSM:Mamm:13276
Puget Sound Museum	PSM:Mamm:13277
Puget Sound Museum	PSM:Mamm:13278
Puget Sound Museum	PSM:Mamm:13279
Puget Sound Museum	PSM:Mamm:13280
Puget Sound Museum	PSM:Mamm:13281
Puget Sound Museum	PSM:Mamm:13282
Puget Sound Museum	PSM:Mamm:13283
Puget Sound Museum	PSM:Mamm:13284
Puget Sound Museum	PSM:Mamm:13285
Puget Sound Museum	PSM:Mamm:13286
Puget Sound Museum	PSM:Mamm:13300
Puget Sound Museum	PSM:Mamm:13301
Puget Sound Museum	PSM:Mamm:13302
Puget Sound Museum	PSM:Mamm:20711
Puget Sound Museum	PSM:Mamm:20712
Puget Sound Museum	PSM:Mamm:20713

Puget Sound Museum	PSM:Mamm:20715
Puget Sound Museum	PSM:Mamm:20716
Puget Sound Museum	PSM:Mamm:20717
Puget Sound Museum	PSM:Mamm:20718
Puget Sound Museum	PSM:Mamm:20720
Puget Sound Museum	PSM:Mamm:20721
Puget Sound Museum	PSM:Mamm:20722
Puget Sound Museum	PSM:Mamm:20723
Puget Sound Museum	PSM:Mamm:20724
Puget Sound Museum	PSM:Mamm:21284
Puget Sound Museum	PSM:Mamm:21285
Puget Sound Museum	PSM:Mamm:21286
Puget Sound Museum	PSM:Mamm:22221
Puget Sound Museum	PSM:Mamm:24240
Puget Sound Museum	PSM:Mamm:24241
Puget Sound Museum	PSM:Mamm:24242
Puget Sound Museum	PSM:Mamm:27318
Puget Sound Museum	PSM:Mamm:27325
Puget Sound Museum	PSM:Mamm:27327
Burke Museum of Natural History and Culture	UWBM:Mamm:32505
Burke Museum of Natural History and Culture	UWBM:Mamm:32507
Burke Museum of Natural History and Culture	UWBM:Mamm:32510
Burke Museum of Natural History and Culture	UWBM:Mamm:32512
Burke Museum of Natural History and Culture	UWBM:Mamm:32513
Burke Museum of Natural History and Culture	UWBM:Mamm:76199
Burke Museum of Natural History and Culture	UWBM:Mamm:77941

Table S.1.6. Landmarking protocol for the lateral and ventral skull of *Antrozous pallidus.*

Lateral skull:

1. Most anterior point at the base of the 2nd incisor
2. Most anterior point at the base of the canine
3. Most anterior point at the base of the 1st premolar
4. The point between the 1st premolar and 1st molar, at the base
5. The point between the 1st and 2nd molar, at the base
6. The point between the 2nd and 3rd molar, at the base
7. The end of the tooth row at the base of 3rd molar, at the base
8. The most posterior and ventral point of the squamosal
9. The most dorsal point of the external auditory meatus
10. The most ventral point of the external auditory meatus
11. The most ventral point of the auditory bulla
12. The most posterior point of the auditory bulla
13. The most posterior point of the occipital chondyle
14. The most posterior point of the skull at the sagittal and lambdoidal crests
15. Semi-landmark placed equidistant between landmark 7 & 8
16. Semi-landmark placed equidistant between landmark 7 & 8
17. Semi-landmark placed equidistant between landmark 7 & 8
18. Semi-landmark placed equidistant between landmark 13 & 14
19. Semi-landmark placed equidistant between landmark 13 & 14
20. Semi-landmark placed equidistant between landmark 13 & 14
21. Semi-landmark placed equidistant between landmark 14 & 1
22. Semi-landmark placed equidistant between landmark 14 & 1
23. Semi-landmark placed equidistant between landmark 14 & 1
24. Semi-landmark placed equidistant between landmark 14 & 1
25. Semi-landmark placed equidistant between landmark 14 & 1
26. Semi-landmark placed equidistant between landmark 14 & 1
27. Semi-landmark placed equidistant between landmark 14 & 1

Ventral skull:

1. The most anterior & medial point of the 2nd incisor, at the base (L)
2. The most anterior and lateral point of the 2nd incisor, at the base (L)
3. The most posterior and lateral point of the canine, at the base (L)
4. The most posterior and lateral point of the 1st premolar (L)
5. The most posterior and lateral point of the 1st molar (L)
6. The most posterior and lateral point of the 2nd molar. (L)
7. The most posterior point of the palate (L)
8. The most medial point of the mandibular fossa (L)
9. Most lateral point of the parietal arm/squamosal suture (L)

10. The most anterior point of the foramen magnum at midline
11. The most lateral point of the occipital chondyle (L)
12. Most posterior point of the foramen magnum, at midline
13. The most posterior point of the skull
14. The most anterior & medial point of the 2nd incisor, at the base (R)
15. The most anterior and lateral point of the 2nd incisor, at the base (R)
16. The most posterior and lateral point of the canine, at the base (R)
17. The most posterior and lateral point of the 1st premolar (R)
18. The most posterior and lateral point of the 1st molar (R)
19. The most posterior and lateral point of the 2nd molar. (R)
20. The most posterior point of the palate (R)
21. The most medial point of the mandibular fossa (R)
22. Most lateral point of the parietal arm/squamosal suture (R)
23. The most lateral point of the occipital chondyle (R)
24. Semi-landmark placed equidistant between landmark 5 & 9
25. Semi-landmark placed equidistant between landmark 5 & 9
26. Semi-landmark placed equidistant between landmark 5 & 9
27. Semi-landmark placed equidistant between landmark 5 & 9
28. Semi-landmark placed equidistant between landmark 5 & 9
29. Semi-landmark placed equidistant between landmark 5 & 9
30. Semi-landmark placed equidistant between landmark 5 & 9
31. Semi-landmark placed equidistant between landmark 5 & 9
32. Semi-landmark placed equidistant between landmark 5 & 9
33. Semi-landmark placed equidistant between landmark 5 & 9
34. Semi-landmark placed equidistant between landmark 5 & 9
35. Semi-landmark placed equidistant between landmark 18 & 22
36. Semi-landmark placed equidistant between landmark 18 & 22
37. Semi-landmark placed equidistant between landmark 18 & 22
38. Semi-landmark placed equidistant between landmark 18 & 22
39. Semi-landmark placed equidistant between landmark 18 & 22
40. Semi-landmark placed equidistant between landmark 18 & 22
41. Semi-landmark placed equidistant between landmark 18 & 22
42. Semi-landmark placed equidistant between landmark 18 & 22
43. Semi-landmark placed equidistant between landmark 18 & 22
44. Semi-landmark placed equidistant between landmark 18 & 22
45. Semi-landmark placed equidistant between landmark 18 & 22

Table S.1.7. Spearman rank correlation coefficients for environmental variables corresponding to each hypothesis: minimum temperature of the coldest month (*MinWinTemp*), maximum temperature of the hottest month (*MaxSumTemp*), standard deviation of annual temperature range (*TempSeas*), and mean annual net primary productivity (*NPP*).

	NPP	*MaxSumTemp*	*TempSeas*	*MinWinTemp*
NPP	1	-0.75	-0.54	-0.12
MaxSumTemp	-0.75	1	0.46	0.33
TempSeas	-0.54	0.46	1	-0.62
MinWinTemp	-0.12	0.33	-0.62	1

Table S.1.8. Aspatial (OLS) model selection results for cranium centroid size in the Pallid bat. The top model is indicated in bold. For each model, the significance of the coefficient estimates is indicated as follows: (*) $P < 0.05$, (**) $P < 0.01$, (***) $P < 0.001$. See Table 1 and methods for details about model variables.

OLS Model	R^2	*AICc*	*Δ AICc*	*w*
NPP + MinWinTemp + TempSeas	**0.51**	**629.9**	**0**	**0.82**
NPP + MinWinTemp	0.49	634.7	4.78	0.08
NPP *(Productivity)*	0.49	634.7	4.84	0.07
NPP + TempSeas	0.49	636.5	6.57	0.03
TempSeas + MaxSumTemp + MinWinTemp	0.4	668.7	38.78	0
TempSeas + MinWinTemp	0.39	669.5	39.62	0
TempSeas + MaxSumTemp	0.39	669.1	39.19	0
MaxSumTemp + MinWinTemp	0.38	674.7	44.77	0
MaxSumTemp *(Heat dissipation)*	0.35	680.8	50.88	0
TempSeas *(Seasonality)*	0.21	711.6	81.69	0
Latitude	0.1	733.6	103.7	0
MinWinTemp *(Heat conservation)*	<0.01	754.7	124.83	0

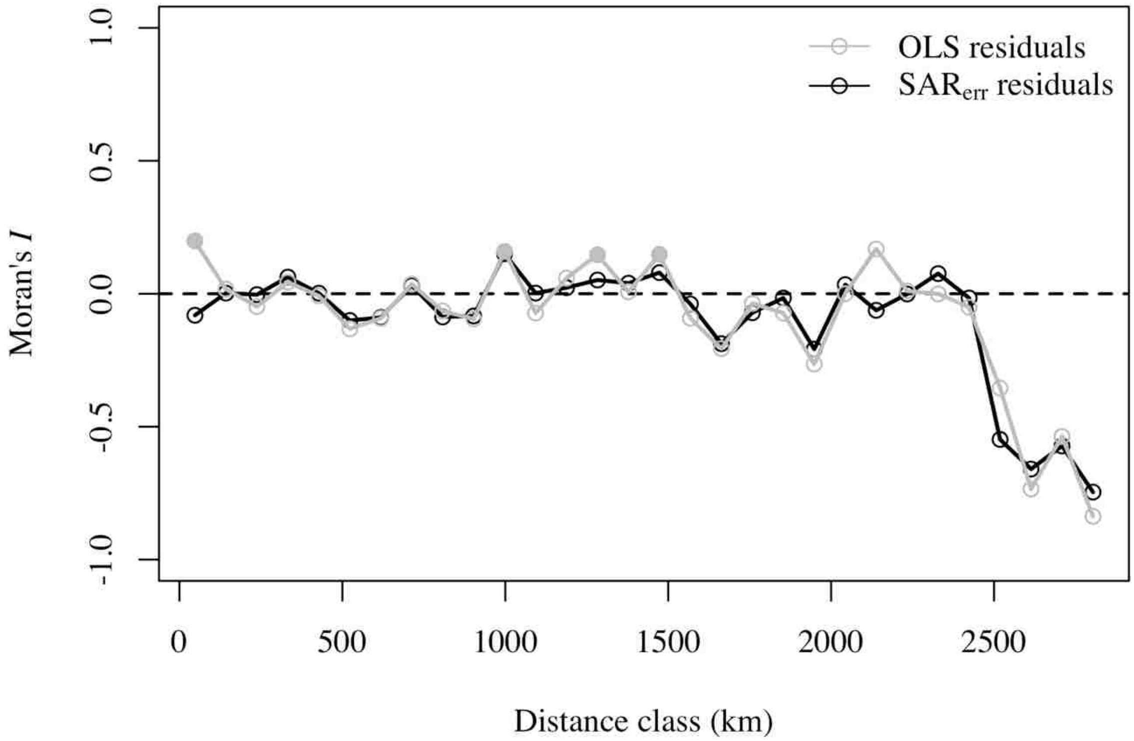

Figure S.1.1 Correlograms of Moran's *I* calculated for distance bands of 100 km from the top-ranked AICc aspatial (OLS) and spatial (SAR$_{err}$) model residuals. Filled circles indicate significant autocorrelation (see *methods* for details).

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PUBLICATIONS

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