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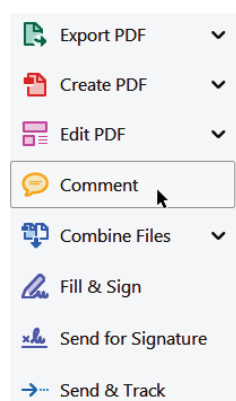
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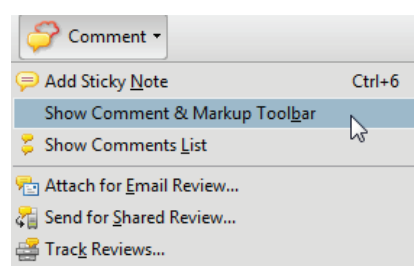
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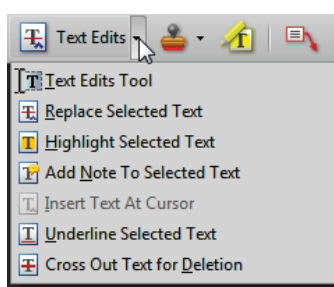
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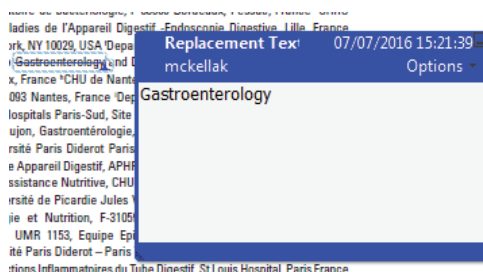
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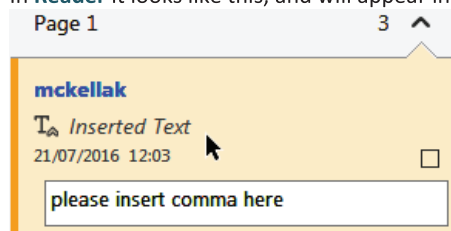#### POP-UP NOTES
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Implications of forest management practices for sex-specific habitat use by *Nycticeius humeralis*

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North American bats are experiencing declines in part due to anthropogenic impacts resulting in habitat loss and disturbance. In eastern deciduous forests, bats rely on forest resources for all or part of the year. Therefore, to promote conservation of bats, it is essential to determine whether current forest management techniques are compatible with habitat use by bats. We evaluated the relative effect of landscape characteristics, including forest management variables, on sex-specific foraging habitat of an insectivorous forest-dwelling bat species, the evening bat (*Nycticeius humeralis*), and predicted areas of suitable habitat for *N. humeralis*. A total of 18 variables were assessed using a maximum-entropy (Maxent) machine-learning approach: eight land use–land cover classes, three stand types, two topography measures, normalized difference vegetation index, and four forest management variables. Females showed the highest probability of presence closer to stands treated with prescribed fire, whereas males showed the highest probability of presence closer to reforested stands. In general, males exhibited more flexibility than females in their habitat selection. The Maxent model further indicated that habitat associated with suitability of > 70% was ~4 times larger for males than females, and predicted an additional area of suitable foraging habitat where no presence locations had been recorded. Our modeling approach may be suitable for other researchers to derive models appropriate for a wide range of bat species.

Key words: bats, Chiroptera, habitat selection, maximum entropy, Ozarks, prescribed fire, timber harvest

Insectivorous bats play an important ecological role, providing valuable services such as pest management, while also serving as ecosystem indicators due to their sensitivity to a wide range of environmental stressors (Jones et al. 2009). Many bat species in North America heavily rely on forest resources for food, commuting, roosting, and reproduction. Forest management practices are used for various reasons, including improving the health of the forest, attracting certain wildlife species, and producing timber products. These management techniques may have positive or negative effects on insectivorous bats that are dependent on forest resources. Thus, conservation scientists and managers require tools that simultaneously examine how numerous variables, including forest management techniques, influence the distribution of bats of a particular species. For example, forest management can improve habitat by reducing clutter that complicates the flight of some bats (Grindal and Brigham 1999; Patriquin and Barclay 2003; Owen et al. 2004). Prescribed burning, specifically, can also promote growth of new foliage necessary to increase insect prey for bats (Grindal et al. 1999; Jung et al. 2012; but see Armitage and Ober 2012; Cox et al. 2016). Alternatively, forest management can both create and destroy important roosting habitat (Parnaby et al. 2010, 2011). The evening bat (*Nycticeius humeralis*), like several other bat species, inhabits managed forest stands (Menzel et al. 1998; Istvanko et al. 2016). Previous studies have addressed the effects of some forest management practices (Boyles and Aubrey 2006; Miles et al. 2006; Perry et al. 2007) but were unable to address an entire suite of management practices.

Nycticeius humeralis is a common insectivorous bat species that is broadly distributed throughout the southeastern United States. Particular aspects of its ecology make it an appropriate model for developing tools that address the impact of habitat

2.5 variables, including the influence of management techniques, on its distribution. For example, *N. humeralis* can be locally abundant, is easy to capture, and has a relatively small home range for a bat species (Morris et al. 2011). *Nycticeius humeralis* commonly roosts beneath exfoliating bark and within snags, cavities,
2.10 or crevices of both live and dead trees in mature stands (Menzel et al. 2001; Boyles and Aubrey 2006; Boyles and Robbins 2006; Istvanko et al. 2016), typically near water (Kalcounis-Rüppell et al. 2005). The species has a low aspect ratio associated with low maneuverability during flight, and a high wing loading for
2.15 fast flight speed (Findley et al. 1972; Saunders and Barclay 1992), which would indicate a low tolerance to clutter. Nonetheless, *N. humeralis* is considered a flexible forager and forages along forest edges and riparian areas, above the canopy, in open habitat, and within the forest (Clem 1993; Menzel et al. 1998, 2000;
2.20 Carter et al. 2004; Morris et al. 2010).

Although sex differences in roosting ecology of *N. humeralis* have been addressed (e.g., Menzel et al. 1999, 2001; Miles et al. 2006; Istvanko et al. 2016), information on sex-specific foraging behavior in this species is scant (but see Morris et al.
2.25 2011; Istvanko et al. 2016). Male and female insectivorous bats have differing energetic requirements due to demands placed on females during pregnancy and lactation in addition to reduced maneuverability of females during pregnancy (Hamilton and Barclay 1994; Grinevitch et al. 1995). Reduced
2.30 use of torpor by females during pregnancy and lactation subsequently increases energetic demands and requires greater prey consumption (Kurta et al. 1989), which can cause differential expression of spatial use and foraging habitat. Female bats show preference for higher-quality, homogenous patches
2.35 of uncluttered habitat (Lintott et al. 2014; Rocha et al. 2017), suggesting that sex-specific use of habitat is driven by a need for more efficient foraging by females. Additionally, females show stronger fidelity to core foraging areas that are closer to the roost (Grinevitch et al. 1995; Istvanko et al. 2016), provide
2.40 larger prey (Mata et al. 2016), or are higher-quality foraging habitat (Wilkinson and Barclay 1997).

Radiotelemetry has allowed researchers to estimate bat home ranges and study habitat use. Unique to radiotelemetry, as opposed to other methods for sampling bats, is the genera-
2.45 tion of multiple spatial points from one individual. However, most approaches for analyses of habitat use require presence and absence data for models to estimate absolute probabilities of occurrence (i.e., the absolute probability that a species will occur in a defined unit). Therefore, the validity of these models
2.50 depends on the quality of absence data, which are difficult to obtain, especially for volant animals (MacKenzie 2005; Pearce and Boyce 2006). Alternatively, presence-only models, by producing a relative probability (i.e., the sum of probability values of all locations in the study area equals one), can avoid
2.55 the high costs of sampling throughout their home range to obtain true representation of absence. Among presence-only models, a maximum-entropy machine-learning approach (hereafter Maxent—Phillips et al. 2004, 2006) has demonstrated higher predictive ability than other approaches (Elith et al. 2006). The
2.56 Maxent model explicitly assumes that presence locations are

2.57 compared with a sample of available habitats for the species. Presence data generated via radiotelemetry result in a biased nonrandom sample, as points are spatially autocorrelated. Thus, the success of Maxent models with radiotelemetry data requires accounting for the spatial and temporal sampling bias of pres-
2.60 ence records relative to identification of available locations across the landscape.

As current management practices determine future forest conditions, a knowledge of the influence of past habitat management on present bat distributions affords managers the
2.65 ability to create future high-quality bat habitat. Our goals were to comprehensively evaluate sex-specific foraging habitat use by *N. humeralis* in a forest with a history of management practices (e.g., burning, harvest, reforestation, and silviculture) and known habitat characteristics (e.g., land use–land cover,
2.70 stand type, vegetation density, and topography), and to predict areas of suitable habitat for *N. humeralis*. To achieve this goal, we applied Maxent modeling to foraging data collected by radiotelemetry and corrected for sampling bias. We predicted that areas managed by prescribed burn or timber harvest,
2.75 creating more open habitats, would be selected for foraging more than unmanaged areas. Because our data were collected during lactation and postlactation, we also predicted that there would be sex-specific differences in areas selected for foraging.

Materials and Methods

2.80

Study area.—Our study area, located in the USDA Forest Service (USFS) Sylamore Ranger District, Ozark–St. Francis National Forest, is ~10 km northwest of Mountain View, Arkansas (Fig. 1). The Sylamore Ranger District encompasses
2.85 ~53,000 ha within the counties of Stone, Searcy, Marion, Baxter, and Izard in the Ozark Highlands ecoregion of north-central Arkansas. This district is largely composed of limestone and sandstone ridges in hardwood, pine, and mixed forests. Wildlife management practices in the Sylamore are a cooper-
2.90 ative effort between the Arkansas Game and Fish Commission and the USFS to enhance wildlife habitat. Timber management practices range from small regeneration cuts to seed tree and shelterwood cuts. Prescribed burning is conducted in timber patches to reduce fuel and stimulate vegetative growth.
2.95 Wildlife management practices in the area are primarily focused on white-tailed deer (*Odocoileus virginianus*) and turkey (*Meleagris gallopavo*) populations, with some large field systems being managed for bobwhite quail (*Colinus virginianus*) and eastern cottontail rabbits (*Sylvilagus floridanus*). More
2.100 recently, intensive management has also targeted habitat enhancement for Indiana bats (*Myotis sodalis*—Perry et al. 2016).

Field methods.—We obtained foraging data for a total of 32 individual *N. humeralis* (17 females and 15 males) in June–August of 2013 and 2014, captured with triple-high and
2.105 single-high mist nets. Basic characteristics such as sex, relative age (juvenile or adult), and reproductive condition (females: nonreproductive, lactating, or postlactating; males: reproductive or nonreproductive) were recorded. We attached 0.33-g VHF transmitters (Model LB-2X, Holohil, Carp, Ontario,
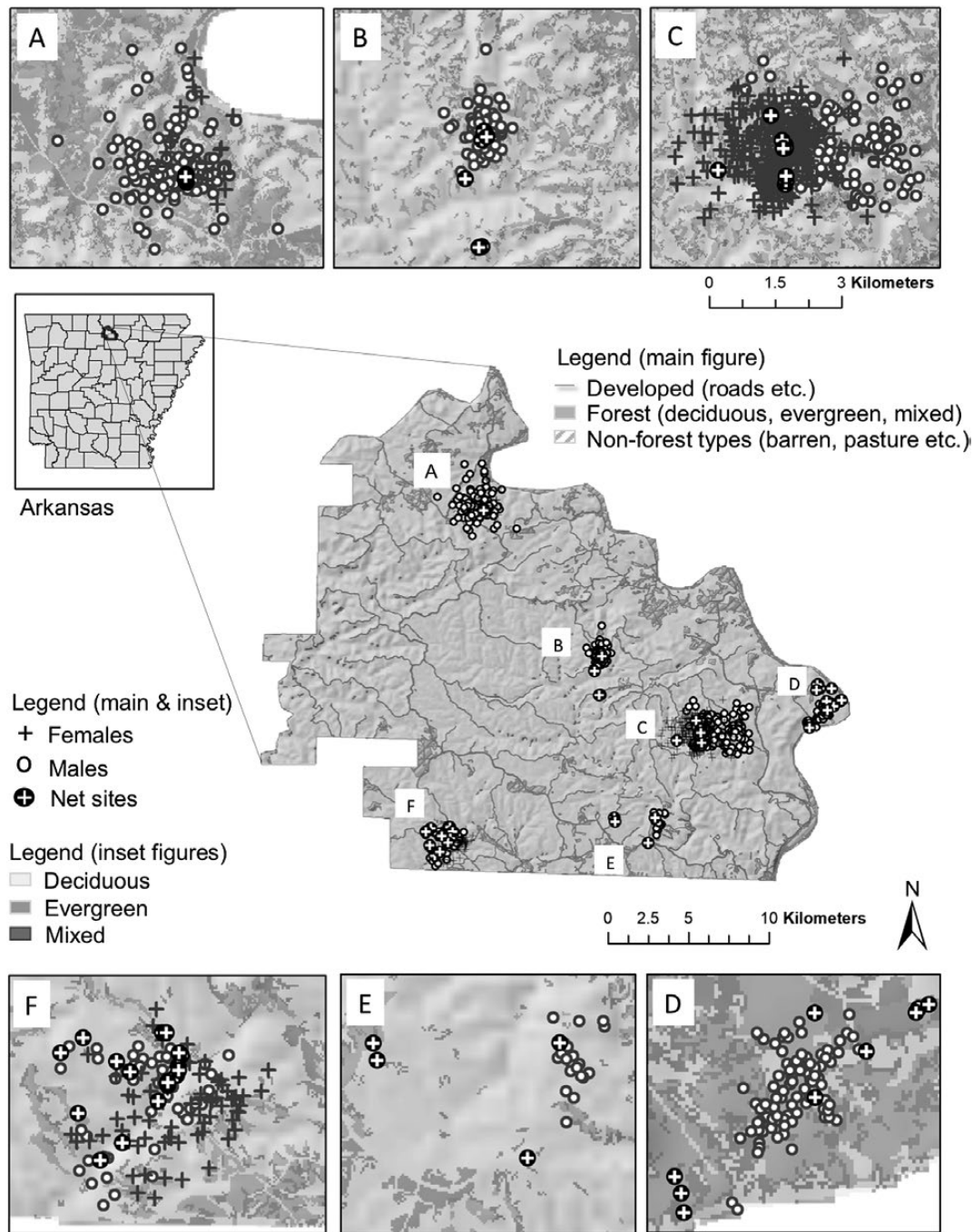2.110

AQ2

Fig. 1.—Net sites and sex-specific presence locations of radiotracked *Nycticeius humeralis* in the Sylamore Ranger District, Arkansas. Insets show magnified view of six clusters of presence locations.

Canada) to the back of bats using Perma-Type or Skin Bond surgical cement. All female *N. humeralis* used in the study were lactating or postlactating when transmitters were attached. To avoid inhibiting foraging maneuverability, transmitter weight never exceeded 5% of the captured individual's body mass (Brigham 1988), and handling time never exceeded 15 min to minimize capture-related stress. Bats were tracked daily using TRX-1000s receivers (Wildlife Materials, Murphysboro, Illinois) and 5-element folding Yagi antennas (Wildlife Materials) during their first foraging bouts of the night, beginning when bats emerged from their roosts and ending when all

bats returned. Foraging locations were estimated by triangulation in 2-min intervals and each bat was monitored for an average of 6 days after capture and ~2 h per night during the first foraging bout. As a result, we collected a total of 1,223 presence foraging locations (719 GPS points for females and 504 GPS points for males). Further details of field methods are described in Istvanko et al. (2016). Methods conformed to guidelines of the American Society of Mammalogists for use of wild mammals in research (Sikes et al. 2016).

Correction to sampling bias.—Sampling bias may be derived from two factors. First, the locations of net sites were

not random, as a large portion of study area (west-central portion of the district) was inaccessible, and we also relied on our prior knowledge of where evening bats had been captured in past years (e.g., near water features such as a small pond or road ruts that hold water). Second, *N. humeralis* has a relatively small home range and short commuting and foraging distance (Duchamp et al. 2004; Morris et al. 2011; Istvanko et al. 2016), which would produce a clustering of presence points from a radiotelemetry approach, imposing an important constraint in species distribution modeling. Because clustering of presence was unavoidable, we applied three methods to account for spatial sampling bias derived from radiotracked presence records: 1) We excluded all presence points from the date of release to reduce the spatial and temporal influence of the release site, as well as to ensure abnormal behavior associated with capture-related stress was not included in the analyses. 2) To avoid biased weights by individuals in the model, we subsampled 20 presence points per individual. These 20 presence points were systematically selected to limit spatial and temporal autocorrelation within data using two criteria: a) any two consecutive points should be at least 5 min apart, and b) any two points from an individual should be at least 100 m apart. 3) We manipulated the background sampling effort using a "bias file" approach matching environmental variables' sampling bias similar to the presence points. This correction approach has been extensively tested and suggested by Kramer-Schadt et al. (2013) and Phillips et al. (2009). In practice, we first counted the presence points on 30-m by 30-m grids over the study area. Each grid containing presence points was then given a value of "1." If no bat was detected in a grid, the grid was assigned a value 0.1 to indicate a 10th of the sampling effort. We then summed the grid values using a 3 × 3 moving window to create the *bias file*. For each sex, 2,000 grid locations of environmental variables were then proportionately selected according to manipulated sampling bias information from the bias file.

Environmental variables.—We considered a total of 18 environmental variables: eight site-specific, land use–land cover classes (Barren, Crop, Developed, Herbaceous, Pasture, Shrubland, Water [permanent sources], and Wetlands); three stand types (Deciduous, Evergreen, and Mixed forest stands); four management practices conducted between 2004 and 2013 (fire history records [FH], silviculture-treated stands [Silvic], reforested stands [RF], and harvested stands [Harv]); two topographic variables (Slope and Elevation); and the normalized difference vegetation index (NDVI; Table 1).

To develop continuous variables, all predictor variables except NDVI and topography variables were converted to distance-based variables. A distance-based quantification method measures the distance from a given land cover, stand type, or management polygon. A land cover data set was obtained from the 2011 National Land Cover Database (NLCD, amended 2014 edition, https://www.mrlc.gov/sites/default/files/metadata/landcover.html) data set. This land cover data set was validated by high-resolution aerial photographs from Digital Globe taken during 2014, provided by ArcGIS, and produced an overall accuracy of 91.2% (Kappa coefficient = 0.79), assuring

Table 1.—Description of environmental variables used in the Maxent model. **AQ4**

Category	Variable (abbreviation)	Unit
Land cover	Distance to barren land (Barren)	Meters
	Distance to crop land (Crop)	
	Distance to developed land (Developed)	
	Distance to herbaceous land (Herbaceous)	
	Distance to pasture land (Pasture)	
	Distance to shrubland (Shrubland)	
	Distance to water (Water)	
	Distance to wetlands (Wetlands)	
Stand type	Distance to deciduous stands (Deciduous)	Meters
	Distance to evergreen stands (Evergreen)	
	Distance to mixed stands (Mixed)	
Forest management practices	Distance to burned stands (Fire history; FH)	Meters
	Distance to silviculture-treated stands (Silvic)	
	Distance to reforested stands (RF)	
	Distance to harvested stands (Harv)	
Vegetation density	Normalized difference vegetation index (NDVI)	Unitless (between −1 and 1)
Topography	Slope (Slope)	Degree
	Elevation	Meters

the accuracy of land cover classes used in the study area. Forest management practices between 2004 and 2013 were determined at the stand level, through the Forest Service Activity Tracking System (FACTS) database within the Natural Resource Manager (NRM) suite of applications (https://www.fs.fed.us/nrm/index.shtml). Individual treatments used and the corresponding area affected by each forest management practice are described in Table 2. The NDVI was calculated as the difference between near-infrared and red band from a Landsat 7 image taken on 11 July 2014. An NDVI map was used as proxy for tree canopy density, with higher NDVI considered to have a denser canopy cover than lower NDVI. Slope and elevation were obtained from the National Elevation Dataset (NED) at resolutions of 1 arc-second (resampled at 30 m). All environmental variables were processed into 30-m by 30-m raster resolution and checked for multicollinearity. If the correlation between any two variables exceeded absolute Pearson's *r*-value of 0.75, we retained the variable with the least correlation with the other variables.

Maxent model.—To examine forest characteristics and management influences on sex-specific differences in habitat suitability for *N. humeralis*, we applied a Maxent modeling approach to females and males separately. The details of the Maxent approach have been extensively explained in the literature (see Phillips et al. 2004, 2006; Merow et al. 2013). Maxent's strengths in habitat modeling include its reliable prediction accuracy for presence-only data, and a built-in jackknife test to evaluate the importance of individual variables and its parameter configuration capabilities (Yi et al. 2016). Maxent finds the maximum entropy in a geographic data set of species presence in relation to background environmental variables, and iteratively improves model fit determined by the gain, which is a

Table 2.—Description of forest management variables.

Forest management practice	Treatment	Total area	Description of variable
Silviculture	Precommercial thin and Tree release and weeding	95 km²	Selective felling, deadening, or removal of trees from a young stand, designed to free young trees from undesirable, competing vegetation
Harvest	Commercial thin and Shelterwood establishment cut	133 km²	Intermediate harvest designed to reduce stand density to enhance forest health and tree growth
Reforestation	Seed trees, Fill-in, and Replant trees	67 km²	Establishment of forest stands
Fire history	Prescribed fire and Wildland fire use	145 km²	The application of the appropriate management to naturally ignited wildland fires in predefined designated areas

likelihood statistic that maximizes the probability of presence. We used built-in auto-configuration that tunes the parameters (i.e., feature functions and a regularization coefficient) against an international data set using an empirical algorithm based on sample size (Phillips and Dudík 2008). Although the default parameterization may not produce the best result, especially when the sample size is small (Morales et al. 2017), different parameter options can be tested following a practical guide by Merow et al. (2013). However, our relatively large data set (540 presence locations) was well-suited for the default setting.

We used three statistics to evaluate the model performance and contributions of environmental variables by randomly setting aside 25% of the sample records for a testing data set: 1) the area under the receiver-operating-characteristic (ROC) curve (AUC), 2) the jackknife test, and 3) the response curves generated per predictor (Phillips et al. 2009). The AUC, a metric used for evaluating model fit in Maxent (Fielding and Bell 1997; Liu et al. 2011), is an arbitrary threshold measuring predictability accuracy based only on location rankings. The AUC metric can be interpreted as the probability that a randomly chosen presence location is ranked higher than a randomly chosen background point, with an AUC value of 0.5 representing random probability (Merow et al. 2013). We interpreted model performance categorized as failing (0.5 to 0.6), poor (0.6 to 0.7), fair (0.7 to 0.8), good (0.8 to 0.9), or excellent (0.9 to 1—Swets 1988). We then used a jackknife test to determine the contribution of each variable to the probability of *N. humeralis* presence. For the jackknife test, 75% of presence points are used as training data and the remaining 25% are used as test data. The jackknife test result gives two levels of interpretation: 1) each variable tested independently, with the variable that yields the highest gain containing the most useful information, and 2) with each variable removed from the full set of variables; the variable set that yields the lowest gain indicates that the removed variable contains the most useful information. We also produced variable response curves that measure the relationship of the probability of presence for the study species and each environmental variable, while keeping all other environmental variables at their average sample value. We interpreted only those variables that showed a strong, monotypic pattern within a 1-km distance and with a probability of presence > 0.5.

Finally, the Maxent model produced a logistic map output of habitat suitability for the species. Suitability values were converted to percentages ranging from 0 to 100 per grid. The

Maxent software package (Gomes et al. 2018, version 3.1) in R (R Core Team 2017) was used for the model development and generating sex-specific predictive habitat maps for *N. humeralis*.

Results

Model performance and contributions of the variables.—A total of 540 presence locations were used in the model (i.e., 20 presence points each for 14 females and 13 males, respectively; three females and two males were excluded due to an absence of required presence points). For females, 14 environmental variables out of 18 were used; strong correlations (Pearson's $r > 0.75$) were found between Mixed and Evergreen, Barren and Pasture, Silvic and Harv, Silvic and RF, and Harv and RF (Supplementary Data SD1). We retained the Mixed variable over Evergreen, the Pasture variable was retained over Barren, and the Silvic variable was retained over RF and Harv. For males, 15 environmental variables out of 18 were used with the same means of variable selection as females; the RF variable was retained over Silvic and Harv, and the Mixed variable was retained over Evergreen (Supplementary Data SD2). All other combinations of variables had a Pearson's $r < 0.75$.

The calculated ROC showed higher AUC values for females (> 0.9) than males (> 0.8) for both training and test data sets. The highest AUC (0.92) occurred with the female training data set (Table 3). According to Swets's classification, our model prediction accuracy was "excellent" and "good" for females and males, respectively. The jackknife test showed that for females, FH had the highest gain when used independently, followed by Pasture and Shrubland (Fig. 2A). For males, RF had the highest gain, followed by Shrubland and FH (Fig. 2B). Notably, Developed yielded the lowest gain (< 0.1) regardless of sex. For both females and males, when the variable set was tested with a given variable removed from the full data set, the results were consistent with the independent test, which further confirmed the reliability of model results.

Response of variables to suitability.—For females (Fig. 3A), the predicted probability of presence (i.e., suitable habitats) gradually increased closer to FH and Herbaceous but increased with greater distance from Mixed. Elevation and Shrubland showed the highest probability at an intermediate distance; the highest probabilities of presence were at an elevation of 200 to 300 m, and 300 to 500 m distance to Shrubland. For males (Fig. 3B), the predicted probability of presence gradually increased

Table 3.—Area under the curve (AUC) values for training and test data sets for female and male *Nycticeius humeralis* in the Sylamore Ranger District, Arkansas.

	AUC (training data set, 75% of occurrence used)	AUC (test data set, 25% of occurrence used)
Female	0.924	0.901
Male	0.874	0.850

closer to RF and Crop, and to a lesser extent, FH, Herbaceous, and Pasture. The probability of presence for Shrubland, similar to the result for females, was highest at an intermediate distance (400 to 600 m). Regardless of sex, probability of presence was highest at close proximity to Water but decreased immediately to its lowest at 1,000 m before gradually increasing again with distance. NDVI, Developed, and Wetlands showed no strong patterns with probability of presence.

Sex-specific habitat suitability maps.—Within the Sylamore Ranger District, several locations were identified for both sexes as high suitability (> 0.7) of foraging habitat (Fig. 4): the mid-east, northeast, and southwest portion of the district, which also reflected presence locations used in the model. However, the Maxent model also identified, for both sexes, additional areas of suitable foraging habitat where no presence locations had been recorded: for females, an approximately 8-km^2 cluster in the mid-west, a 4-km^2 patch on the northwest corner, and a 3-km^2 patch on the west border of the district; and for males, clusters of ~3 km^2 in the northern and western portions of the district and a 4-km^2 patch on the southern part of the Sylamore district (Fig. 4). Habitat associated with a high suitability (> 0.7) was nearly four times larger for males (33 km^2) than for females (9 km^2).

Discussion

We comprehensively examined the relative effect of forest management practices and key landscape characteristics on the sex-specific foraging range of *N. humeralis* in the Sylamore Ranger District of the Ozark National Forest. Although foraging locations are associated with roost site locations due to the short commuting distances of *N. humeralis* (compare figure 1 from Istvanko et al. 2016, with Fig. 1 above), our modeling results showed that close proximity to burned sites (i.e., FH variable) was an important determinant for both females and males. However, the contribution of distance to burned sites was much higher for females than males; contributions evaluated by regularized gain were nearly double for females. This strong preference for females to forage near burned sites may be attributed to differences in sex-specific physiological requirements (Levin et al. 2013), that is, the need for females to increase prey intake during the highly energy-demanding period of reproduction (Kurta et al. 1989; Encarnação and Dietz 2006). This energy hypothesis is supported by the potential benefits of prescribed burning. Recently burned habitat opens the canopy and enhances herbaceous growth that subsequently favors colonization of insects (Lacki et al. 2009), and more severe fire may stimulate aquatic productivity, driving a pulse in insect availability, in turn encouraging bat activity (Malison and Baxter 2010). In some studies, however, abundance of insects appeared not to respond to fire, and thus were weakly associated with bat activity (Armitage and Ober 2012; Cox et al. 2016). The variability of fire thus influences differential prey response (Swengel 2001) and subsequent bat activity.

Several variables, including topography variables and NDVI, showed little influence on probability of presence. Although Levin et al. (2013) indicated that male *Rhinolophus microphyllum* prefer foraging at higher and cooler elevations than females, in our study, no substantial relationship was found with elevation. Our study sites only had a maximum difference of ~300 m in elevation, which did not produce large temperature gradients. Similarly, although Suarez-Rubio et al. (2018) found a negative effect of clutter or canopy complexity on bat activity, the NDVI variable was consistently unimportant in our models. We used NDVI as an index of clutter, but a more detailed measure of vegetative clutter, such as those derived from LiDAR (Light Detection and Ranging), would be necessary to fully capture the effects of forest structure (Froidevaux et al. 2016). For females, however, an association with an intermediate distance to Shrubland and negative responses to variables associated with forest covers (e.g., Deciduous and Mixed) suggests a preference for less cluttered habitat. This result aligns with *Myotis lucifugus* in North Dakota that selected edge habitats near open areas and water resources (Nelson and Gillam 2016). Thus, our results reinforce the management recommendation of open areas near edges, offering protection in proximity to shrubs and tree lines, for the management of female *N. humeralis*.

Our results also highlight subtle but important differences in areas of habitat suitability between males and females. Sexual segregation during foraging and differences in home range size have been reported specifically in *N. humeralis*, in that females have larger home ranges than males (Istvanko et al. 2016). Studies on sex-specific use of foraging habitat by other bat species also report more flexibility in selection of foraging areas by males than females. For example, female parti-colored bats (*Vespertilio murinus*) have more restricted foraging ranges than males and rely heavily on lakes (Safi et al. 2007), which may be because their preferred prey occur over large water bodies and open areas (Jaberg et al. 1998). Senior et al. (2005) and Barclay (1991) also suggest that male insectivorous bats forage in poor-quality habitat when excluded from high-quality habitat by energetically constrained females, resulting in larger foraging ranges. This hypothesis may further explain our result that male *N. humeralis* showed higher presence near reforested stands than burned sites. Male *N. humeralis* may have been excluded by females from the more open burned sites, and were thus pressured to forage near poorer-quality reforested stands. Although reforested stands likely provide adequate prey abundance and availability due to growth of new foliage, the habitat may have been more cluttered and thus difficult for larger female *N. humeralis* to navigate. Alternatively, the size of foraging areas of red bats (*Lasiurus borealis*) did not differ between sexes (Elmore et al. 2005), although reliable sources of water were available near most foraging areas. This may imply
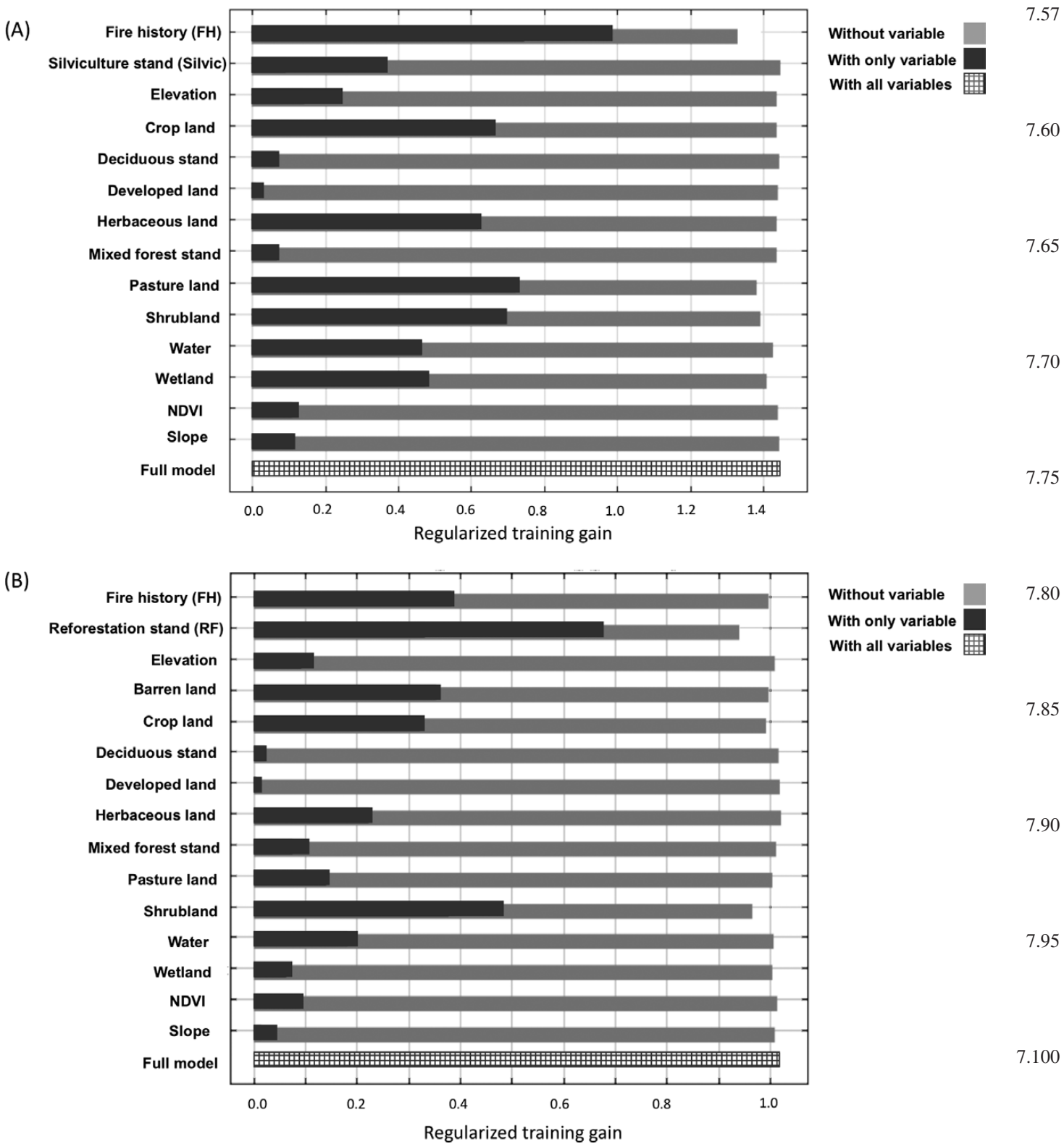
Fig. 2.—Results of the jackknife test of contributions of variables in modeling (A) female and (B) male *Nycticeius humeralis*'s habitat distribution in the Sylamore Ranger District, Arkansas. The regularized training gain describes how much better the Maxent distribution fits the presence data compared to a uniform distribution. The dark gray bars indicate the gain from using each variable independently, the light gray bars indicate the gain lost by removing the single variable from the full model, and the patterned bar indicates the gain using all of the variables.

that sex-specific foraging area is dictated by landscape context in addition to foraging requirements. In our study, the more restricted areas of habitat suitability for females suggest that males exhibit more flexibility in their habitat selection than females, likely because males have lower energetic demands than females during lactation, a period of peak energetic demand for females. Lactating
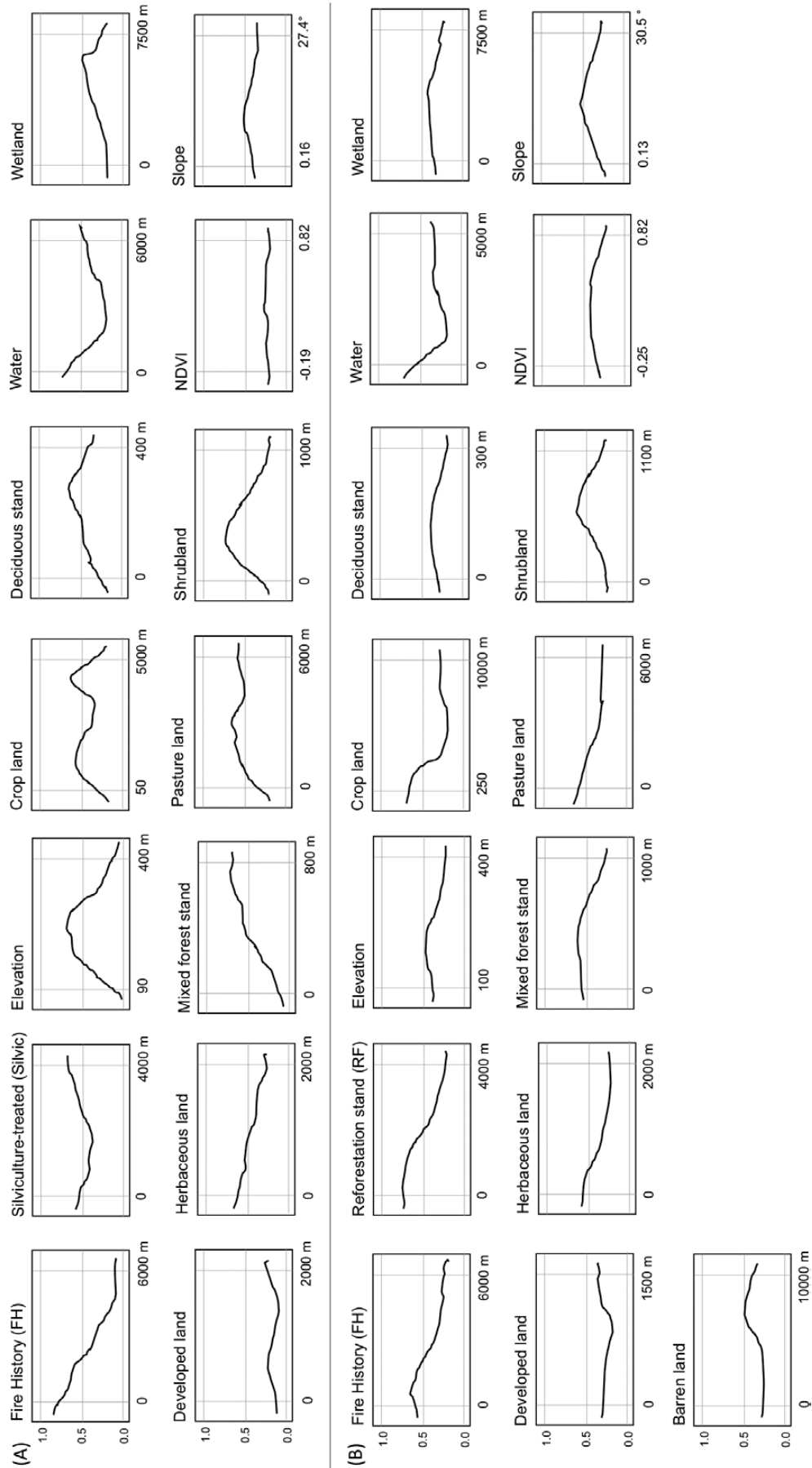
Fig. 3.—Response curves for environmental variables for (A) female and (B) male *Nycticeius humeralis.*
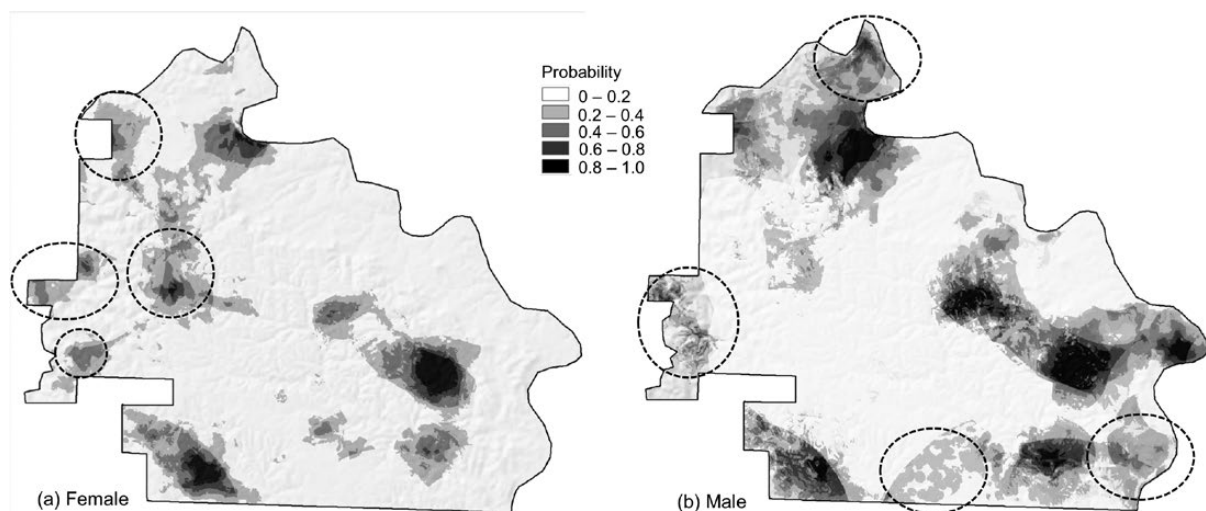
Fig. 4.—Habitat suitability maps generated by Maxent models for (A) female and (B) male *Nycticeius humeralis* in the Sylamore Ranger District, Arkansas. Darker hues represent higher probability of presence. Dashed lines indicate newly identified suitable foraging habitat.

insectivorous bats are also believed to have smaller home ranges than pregnant bats because nursing requirements at night constrain foraging distances (Henry et al. 2002). In our study, we grouped lactating and nonlactating females, and future studies may aim to determine home range size differences in these two groups.

Our methodology evaluating habitat suitability for *N. humeralis* provided new information on how forest management techniques influence their foraging habitat use. The generated habitat suitability maps can be used to predict areas of occupancy to be applied toward future conservation planning. The most influential variables for *N. humeralis* were Fire History and Reforestation, although models addressing other species of North American bats may wish to include different variables. For example, inclusion of ecogeographical variables such as large bodies of water or karst landscape features for conservation of cave-obligate species such as gray bats (*Myotis grisescens*) and Townsend's big-eared bats (*Corynorhinus townsendii*) may be preferential. Forest management regimes are important to consider depending on their positive or negative impact on all species living in a management area. However, *N. humeralis* may provide good proxies to evaluate the effects of these management strategies on other bat species.

Acknowledgments

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Correlation matrix for environmental variables for female *Nycticeius humeralis*. Values of Pearson's $r > 0.75$ are underlined. Each of the correlations is significant at $\alpha < 0.01$.

Supplementary Data SD2.—Correlation matrix for environmental variables for male *Nycticeius humeralis*. Values of Pearson's $r > 0.75$ are underlined. Each of the correlations is significant at $\alpha < 0.01$.

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