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Bat community dynamics and foraging activity patterns in young regenerating Southern pine plantations and mixed hardwood forests

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Bat community dynamics and foraging activity patterns in young
regenerating Southern pine plantations and mixed hardwood forests

A Senior Honors Thesis submitted to the Faculty of Longwood University in
fulfillment of the requirements for the degree of

Bachelors of Science with Honors


Biological Sciences

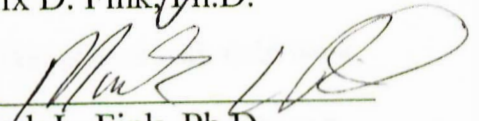
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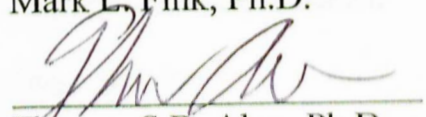
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Bat community dynamics and foraging activity patterns in young regenerating Southern pine
plantations and mixed hardwood forests

Prepared according to *Journal of Wildlife Management* guidelines

ABSTRACT

Forests of the southeastern U.S. are changing rapidly in species composition and extent of forest cover due to increasing conversion to pine (*Pinus* sp.) plantations, intensifying management practices, and expanding urbanization and sprawl. Questions related to the impacts of these changes on wildlife species are of great conservation interest and management relevance. Highly mobile species with large home ranges and complex habitat requirements, such as bats, may be especially vulnerable to increasing human modification of landscapes. However, the impacts of such modifications on bat species are poorly understood. I sought to evaluate bat community structure and foraging activity in regenerating managed pine and mixed hardwood systems in the central the Southern Appalachian Piedmont Ecoregion (SAPE) of Virginia. I conducted this research in the Appomattox-Buckingham State Forest in June-August 2006 and May-August 2007. I sampled sites in both hardwood and managed pine systems across a range of ages and management strategies. In each site we established a sampling array consisting of a bat detector and an associated insect sampling location. I assessed bat activity (1800 to 0700 hours) with Anabat II bat detector systems, calculated mean bat passes per hour, and identified calls to genus or species. I collected and analyzed insect samples and assessed vegetation attributes using standard procedures. To understand factors affecting bat activity, I used an Information Theoretic approach to evaluate support for a suite of a priori models that included measures of habitat attributes, climate conditions, and prey availability. Some key findings for my a priori models include: the importance of stand age on both bat and insect activity in my study sites as well as weather conditions, like lunar cycle, temperature, and humidity. My descriptive analyses suggested that there are species-specific effects for

certain members of the bat community and their 'preferred' insect prey orders between dominant vegetation type and stand age characteristics. Important management implications suggest the importance of having mixed-hardwood forest and pine plantations at various levels of succession to provide roosting and foraging locations for bat community members in the SAPE of Virginia, as well as to maintain high insect prey abundance.

INTRODUCTION

Forests of the southeastern U.S. are changing rapidly, both in terms of forest composition and extent of forest cover (Wear and Greis 2004). Compositional changes, driven in part by increasing conversion to pine (*Pinus* spp.) plantations and increasing management intensity, are expected to continue (Wear and Greis 2004, Allen et al. 2005). Concurrent to changes in composition, forest cover is decreasing as a result of urbanization and sprawl associated with human population growth (Wear and Greis 2002). Moreover, the nature and extent of impacts of global climate change on Southern forests are largely speculative (Moore et al. 2002), though further changes in composition and coverage are expected.

Questions related to the impacts of these changes on wildlife species are of great conservation interest and management relevance. Highly mobile species with large home ranges and complex habitat requirements, such as bats, may be especially vulnerable to increasing human modification of landscapes. Though some researchers suggest that forest dwelling bats are good indicators for forest ecosystem health (Fenton 1997, Elmore et al. 2005), the impacts of landscape modifications on bat species are poorly understood (e.g., Pierson 1998, Menzel et al. 2002b, Tibbels and Kurta 2003).

The Southeast region of the U.S. produces the most industrial timber in the world (Allen et al. 2005). Due to high production demands, natural forests are being converted to pine

plantations and management intensity within this region is increasing to insure the greatest output (Allen et al. 2005). These changes in forest composition present opportunities to evaluate how bat species are affected by these modifications. Studies in Mississippi's intensively managed pine plantations have examined bat community composition and species-specific habitat use within these landscapes (Miller 2003, Elmore et al. 2004, Elmore et al. 2005). In regards to the resident bat community, a large number of a few species Eastern red bats (*Lasiurus borealis*), big brown bats (*Eptesicus fuscus*), and Eastern pipistrelle bats (*Perimyotis subflavus*) and small numbers of the more "rare" species (i.e. Hoary bat (*Lasiurus cinereus*); Miller 2003, Elmore et al. 2005) were captured in these pine plantations. In regards to species-specific habitat use, these researchers asked questions related to distance between foraging and roosting locations and found that bats were roosting in "natural" forests near foraging locations in pine plantations to limit unnecessary energy use (Elmore et al. 2005). Roost sites were mostly within riparian buffers that contained mature hardwood trees (Elmore et al. 2005). Eastern red bats captured in these pine plantation-dominated landscapes roosted in mature hardwood trees 70% of the time (Elmore et al. 2004). These studies point to variation in bat use in forests of largely different compositions and suggest the importance of natural forest, specifically mature hardwood trees in riparian buffer zones, in intensively managed pine plantations.

Along with composition, cover changes are also occurring in the Southeast and wildlife species with specific habitat requirements have shown decreases in population size due to habitat loss and associated fragmentation (Graham 2002, Wear and Greis 2002). Studies determining how cover changes affect bat activity in these landscapes are of great importance due to the potential loss of roosting and foraging locations for forest dwelling bats (Pierson

1998). A study in Missouri evaluated site occupancy in a largely fragmented landscape and determined that landscape cover types within and around study sites (i.e., deciduous forest, non-forest, pine forests, ect.) affected which bat species were using these areas (Yates and Muzika 2006).

Aside from habitat modifications, studies have found variation among bat species in foraging patterns and dietary preferences due to basic biological characteristics of body size, wing morphology, and echolocation call structure (Freeman 1981, Thomas 1988, Fenton 1997, Bogdanowicz et al. 1999, Agosta et al. 2003, Carter et al. 2003, Whitaker 2004, Loeb and O'Keefe 2006, Kalcounis-Rueppell et al. 2007). This interspecific variation often manifests in unique patterns of habitat use. For example, generally species with larger wingspan-to-body ratios forage in more open areas. Additionally, these physical differences also affect prey specialization. Researchers examining diets of some bat species have found that along with physical characteristics, variation occurs among individuals, age, geographic regions, and time of the year (Barclay 1985, Aldridge and Rautenbach 1987, Feldhamer et al. 1995, Hamilton and Barclay 1998, Agosta et al. 2003, Agosta and Morton 2003, Carter et al. 2003, Whitaker 2004, Kalcounis-Rueppell et al. 2007).

In Virginia's Southern Appalachian Piedmont Ecoregion (SAPE; Bailey 1995), the bat community includes Eastern red bats (*Lasiurus borealis*), big brown bats (*Eptesicus fuscus*), Eastern pipistrelle bats (*Perimyotis subflavus*), evening bats (*Nycticeius humeralis*), little brown bats (*Myotis lucifugus*), Northern Myotis (*Myotis septentrionalis*), hoary bats (*Lasiurus cinereus*), and silver haired bats (*Lasionycteris noctivagans*; Durkee 2005). Some of these species are prey specialists. For example, big brown bats are generally Coleopteran specialists due to their cranial morphology that allows them to consume hard prey items

(Freeman 1981, Brigham 1990, Feldhamer et al. 1995). Eastern red bats and other *Lasiurus* spp. are Lepidopteran specialists, and Eastern pipistrelle bats tend to forage along streams or ponds for Dipterans (Aldridge and Rautenbach 1987, Hamilton and Brigham 1998, Agosta et al. 2003, Carter et al. 2003, Agosta and Morton 2003, Whitaker 2004, Elmore et al. 2005, Kalcounis-Rueppell 2007). In total, this results in a complex set of factors affecting bat activity: 1) various physical and behavioral adaptations over time and 2) landscape characteristics of forest composition and extent of cover that directly affect bats and – arguably as importantly– their insect prey.

Pierson (1998) asserts that to better understand how landscape alterations and habitat loss affect bat communities, studies should focus on how these changes affect prey availability. A recent study in the United Kingdom explored this exact question and found significant differences in bat foraging activity in organic and conventionally managed agricultural land (Wickramasinghe et al. 2004). The differences in bat activity were directly related to differences in insect abundance (Wickramasinghe et al. 2003), which in turn was directly related to the intensity of vegetation management and/or control (Wickramasinghe et al. 2004). A study in Canada's boreal forests had similar results: increased management intensity decreased insect abundance and thus bat use (Patriquin and Barclay 2003). These studies raised interesting questions about linking vegetation management practices to insect abundance and then relating both to bat activity. This research approach could help to explain bat community and activity in the changing Southeast.

The SAPE of Virginia offers opportunities to better understand the ecological relationships between forest management, prey availability, environmental variables, and bat activity as well as building on other recent studies that have taken place in the Southeast that

investigated how habitat characteristics affect bat communities (Menzel et al. 2002a, Carter et al. 2003, Miller 2003, Elmore et al. 2005, Loeb and O'Keefe 2006, Yates and Muzika 2006, Ford et al. 2006). This ecoregion is important because it has been identified as the area with the most actual and predicted forest loss in the entire Southeast (Graham 2002, Wear and Greis 2004), and there is an important need to investigate how changing forests systems affect bat communities so that sound conservation and management decisions can follow.

In developing my study, I sought to build on the research in agricultural systems in the United Kingdom by considering analogous systems in the SAPI's intensive pine plantations and more "natural" forest systems. My study addressed these issues by seeking to describe the bat community and quantify foraging activity in the Appomattox-Buckingham State Forest within this ecoregion from June-August in 2006 and 2007. I developed questions that investigated environmental variables such as temperature, humidity, barometric pressure, and lunar phase as potential drivers of both insect and bat activity in my sites (Parsons et al. 2003, Tibbels and Kurta 2003, Lang et al. 2006). Below I have listed specific study objectives and hypotheses:

Objectives:

- 1) To determine effects of habitat characteristics on insect availability and bat activity.
- 2) To determine effects of environmental conditions on insect abundance and bat activity.
- 3) To determine links between potential insect prey biomass and bat activity.
- 4) To determine temporal variations in both insect and bat activity.

Hypotheses:

- 1) Sites that have been recently disturbed will have greater vegetation diversity and therefore have the highest insect abundance and thus the most bat activity.
- 2) Nights with lower relative humidity, barometric pressure, and moonlight will have higher insect biomass and bat activity, while nights with the highest temperatures will have the highest insect abundance and bat activity.
- 3) Study sites with the greatest insect prey biomass will have the most bat activity.
- 4) Insect abundance and bat activity will vary by month and year, with August having the most insect and bat activity.

STUDY AREA

I conducted this research in the Appomattox-Buckingham State Forest (ABSF; Fig. 1) in Appomattox and Buckingham counties in the SAPE (Bailey 1995) of central Virginia during the summers of 2006 and 2007. The SAPE is largely forested (>80% forest cover in some counties; Wear and Greis 2004) and includes many intensively managed pine plantations. In the next few decades the SAPE is expected to lose more forest cover than any other region in the Southeastern U.S. (Wear and Greis 2004). Therefore, the ABSF's location within this ecoregion provides an interesting context for addressing research questions of wildlife habitat use in changing forest systems.

In the counties in which the ABSF is located, total cover and general composition of forested lands were determined by a forest inventory conducted by the U.S.D.A. Forest Service's Southern Research Station in 2001 (Rose 2001). Buckingham County encompasses a total of 373,760 acres, of which 307,269 acres (82%) were forested (Rose 2001). This forested acreage included 185,420 acres of hardwood forest, 92,157 acres pine

(*Pinus* spp.) forest, and 29,690 acres of mixed pine-hardwood forest (Rose 2001).

Appomattox County encompasses a total of 215,200 acres, of which 141,489 acres (65.7%) were forested (Rose 2001). Forested acreage included 67,138 acres of hardwood forest, 41,181 acres of pine (*Pinus* spp.) forest, and 33,170 acres of mixed pine-hardwood forest (Rose 2001). Industrial timber companies and other private landowners own the majority of forested land within these two counties (Rose 2001). The publicly owned ABSF encompasses over 19,000 acres that matrix of private land. Within this large public forest I selected 15 forested sites that were either managed for pine or mixed hardwoods at various stages of regeneration and management intensity (Table 1).

METHODS

Acoustic Sampling

I monitored bat activity using Anabat II bat detectors with Zero-Crossing Analysis Interference Modules with Compact Flash memory storage (CF ZCAIM; Titley Electronics). To protect my acoustic equipment, I housed each system (Anabat II and CF ZCAIM) in a plastic cooler with a 4-inch, 45°-angle polyvinyl chloride (PVC) elbow with detection cone directed upward (S. Amelon, pers. comm.). To further prevent water damage, inside the cooler I placed the systems in a one-gallon plastic bag with an opening for the microphone. When each system was set up in the field, each detector system was elevated in height by a tree stump or sticks to 0.1 m and 0.3 m above ground level. I used rechargeable Nickel-metal hydride (NiMH) AA and 9-V batteries to power my acoustic units in my 2006 season. In 2007, I changed to 12-V deep cycle marine batteries as power sources (Optima Batteries) using 12-V leads from Titley Electronics. In the second season I also modified my acoustic housing with drainage holes to further prevent water damage.

In each season, I identified one detector location in each site that allowed for an unobstructed detection cone. In 2006, I monitored bat activity in 9 sites (Table 1) from mid-June through late August. There were 7 sampling rounds, each lasting 3 ± 1 days, depending on weather conditions. In each round, a site was sampled once for bat activity. Data were downloaded from the compact flash card each morning. Due to the change in power source in 2007, I continuously monitored 9 sites (Table 1) from early June through late August with one acoustic system at each site. I checked systems weekly or bi-weekly to download data and monitor charge levels on the batteries. Batteries with charge levels $< 10.5V$ were brought in from the field to be recharged.

I analyzed bat echolocation calls using Analook software (Titley Electronics). To minimize error, I used a filter that removed call files that contained only insect noise (S. Amelon, pers. comm.). I identified calls to species where possible and otherwise to genus using call structure characteristics and frequency ranges from a call library (S. Amelon, unpub. data). Files that contained a bat call of < 3 call sequences were marked as “unidentified bat.” I also determined bat activity by hour (i.e., 1801-1900, 1901-2000, etc.) to evaluate variation in site use throughout the night.

Insect Sampling

In each study site, I identified one or more insect sampling locations that were approximately 50m from the bat detector location. In 2006, I sampled sites for insects from mid-June to late August. In each of the 7 sampling rounds discussed previously for bats, insects were collected twice: one night with a bat detector on site and another without. In 2007, insects were sampled from late July through late August in 3 sampling rounds in which each site was sampled for one night.

I collected insect samples using Universal Black Light Traps with Photoelectric Switches (BioQuip Products, Inc.) powered by 12-V batteries. The trap design funneled insects into a glass jar that contained an Insect Guard Jr. Kill strip (Prozap). Insect samples were retrieved each morning after a sampling night, transferred to unique one-gallon plastic bags labeled with sample information, and placed in a freezer for future processing. Prior to processing, I placed samples on standard cookie sheets and dried them for 24 hours at 60°C using a soil drying oven (Quincy Lab Incorporated). After samples were dried they were placed in air-tight plastic storage containers for later processing.

Prior to processing samples, I determined bat prey size limits by a literature search and found that 3 mm was a reasonable lower body size limit (Fenton and Barclay 1980) and 29 mm was a useful upper size limit (Barclay 1985). To remove those insects smaller than the lower size limit, I used a 2-mm U.S. Standard testing sieve (Dual Manufacturing). I placed each of the dried samples in the sieve and over a large sheet pan gently shook it 10 times following a set pattern. The insects that passed through the sieve's openings were weighed and recorded. Additionally I removed by hand those insects larger than the upper size limit and weighed them. This process resulted in 2 sets of insects outside the predicted prey size range; both sets were kept separated and stored with the rest of the sample.

I conducted another literature search to determine which insect orders were key prey items for bats in the region and determined that Lepidoptera, Coleoptera, Diptera, and Tricoptera where the most important orders (Freeman 1981, Shump and Shump 1982, Caceres and Barclay 2000, Agosta et al. 2003, Carter et al. 2003, Whitaker 2004). Thus, in further processing the samples of insects that were within the predicted prey size range, I separated them into 5 taxonomic categories: the 4 listed above and one "other" category. To

separate each sample, I used taxonomic keys, magnifying glasses, and a dissecting microscope to determine each insect's taxonomic category. Once separated, each taxonomic category was weighed, recorded, placed in a separate storage bag, and stored permanently with the rest of the complete sample.

Habitat Types

To better understand how bat activity and prey abundance varied with forest stand characteristics, I identified three key site descriptors: dominant vegetation type, relative age, and dominant vertical vegetation strata (Table 1). I characterized sites by dominant vegetation type to either pine (*Pinus* spp.) or hardwood (with multiple hardwood species). In 2006 and 2007, I studied 5 pine and 4 hardwood sites and 4 pine and 5 hardwood sites, respectively (Table 1). I further classified sites by relative age post-harvest: young (0-3 years), intermediate (10-12 years), and mature (with a full canopy). I sampled 5 young, 2 intermediate, and 2 mature sites in my first field season and 4 young, 1 intermediate, and 4 mature sites for my second season (Table 1). Recent studies have determined forest structure to be an important factor for predicting bat use in a site (Loeb and O'Keefe 2006, Yates and Muzika 2006), and therefore I also characterized sites by their dominant vertical vegetation strata: shrub-level (0 – 1.5 m), mid-level (2 – 3.5 m), canopy (>4 m), and mid-level and canopy-dominated sites (Table 1). As expected, age and dominant strata are closely linked (e.i., sites with dominant shrub-level vegetation were also young sites), but both were used due to the uniqueness of some of the mature sites. In 2006, I had 2 sites that contained co-dominant strata, of both mid-level and canopy, and one of those site types was sampled in 2007.

Data Analysis

I used an information theoretic approach (Burnham and Anderson 2002) to evaluate a series of hypotheses about the effects of habitat, environmental, and temporal factors on bat activity and insect abundance. From my hypotheses I developed a priori models to evaluate with 3 different data sets: bat activity, insect abundance, and a combined subset of samples with coupled bat and insect sampling nights. For both the bat and combined data sets, I used PROC GENMOD with a negative binomial distribution (SAS 9.1) suitable for irregularly distributed count data. For the insect data set, I used PROC GENMOD with a normal distribution (SAS 9.1).

For all data sets, I used a multi-staged strategy for model evaluation. In the first stage of the model selection procedure for the bat and insect data sets, I evaluated 3 model subsets, each of which corresponded to a particular hypothesis: habitat effects, environmental effects, and temporal effects (Table 2). In this first stage for the combined data set, I evaluated the three subsets listed above as well as a prey effects subset (Table 2). I identified models from each subset with the greatest support and used those for subsequent stages of model selection.

Due to the complexity of environmental effects variables, I employed a two-step approach to the first stage of model selection. I first evaluated environmental variables in 8 single-variable models (Table 2), and I used the results to determine which humidity, temperature, and lunar variable was best supported by each data set. I selected the best variable in each category and proceeded to complete the first stage of model selection using these variables multi-variable environmental effects models in the step 2 model set (Table 2).

I evaluated support for all models in each subset using Akaike's Information Criterion value for small sample sizes (AIC_c), ΔAIC_c , and AIC_c weight (w_i ; Burnham and Anderson 2002). The AIC_c value for a model is an unbiased maximum log-likelihood value because it takes into account the number of parameters (K) in the model (Burnham and Anderson 2002). I ranked all models from the lowest AIC_c to highest, and I calculated ΔAIC_c by subtracting the top model's AIC_c value from each subsequent model's AIC_c value. Models with ΔAIC_c values < 2 had substantial support along with the top model, while models with ΔAIC_c values > 10 have essentially no support (Burnham and Anderson 2002). I also calculated w_i values for each model within a subset following procedures outlined in Burnham and Anderson (2002). I identified models for the second stage of my model selection as those with ΔAIC_c values < 2 and w_i values > 0.20 . For brevity in my results for the first stage of model selection, I reported only habitat, environmental, prey, and temporal effects hypotheses model sets to the first model below the 2 ΔAIC_c threshold.

In the second stage of model selection, I combined the best supported models from each subset into a new model set. I combined them into multi-variable models representing biologically relevant hypotheses of simultaneous habitat, environmental, prey, and temporal effects. These models were evaluated as described above, and I reported all model results for this final stage of the selection process.

In addition to the results of my information theoretic approach to model selection, I also completed several descriptive statistical analyses to determine means for bat activity by species, insect abundance by taxonomic group, and environmental conditions. I also determined mean bat activity by hour for all species combined, and I reported those results by vegetation type and stand age.

RESULTS

In the multi-stage model selection procedure, the model best supported by the data differed for the bat activity, insect abundance, and combined data sets. For the bat activity data set, in the first stage of model selection I identified two models with good support: one for habitat effects (i.e., young-aged) and one for temporal effects (i.e., year; Table 3). No environmental effects variables had enough support to be carried through to stage 2. For this data set in the second stage of model selection, three models were well supported: 1) young and year; 2) young; and 3) year (Table 3).

For the insect abundance data set, in the first stage of model selection I identified five models with good support (Table 4). Two were habitat effects models: 1) young and 2) young and intermediate (Table 4). For this data set there was one environmental effects model (step 2) with support: fraction of moon and pressure (Table 4). Finally, my two temporal effects hypothesis models which received support were: 1) year and 2) year and julian date (Table 4). In the second stage of model selection for the multiple effects hypothesis model set, two models received support: 1) young, fraction of moon, and pressure and 2) young, intermediate, fraction of moon, and pressure (Table 4).

For the combined data set, in the first stage of the model selection procedure I identified five models with good support. There was one supported model for habitat effects: pine and young (Table 5). For this data set there were two supported models for environmental effects: 1) hour of moon, maximum humidity, and maximum temperature; and 2) maximum temperature and maximum humidity (Table 5). There was one supported model for prey effects: Coleopteran biomass (Table 5). Finally, one temporal effects model was supported: year (Table 5). In the second stage of model selection (i.e., multiple effects

hypothesis model set), two models were well supported: 1) pine, young, hour of moon, maximum temperature, and maximum humidity; and 2) pine, young, maximum temperature, and maximum humidity (Table 5).

In addition to the model selection procedures, I calculated means for bat activity by species or species group, insect abundance by taxonomic group, and environmental conditions. I sampled bat activity with acoustic detectors for a total of 105 sampling nights (17 in 2006, 88 in 2007). These efforts yielded 524 acoustic surveys (46 in 2006, 478 in 2007). The acoustic surveys resulted in variable numbers of call files (low of 1, high of 332). Through careful evaluation, I identified 71% of files to species or species group, and I categorized 29% of the total bat call files as “unidentified bat species.” In these acoustic surveys, I identified 5 species and 1 species group: Eastern red (*Lasiurus borealis*), big brown (*Eptesicus fuscus*), Eastern pipistrelle (*Perimyotis subflavus*), evening (*Nycticeius humeralis*), hoary (*Lasiurus cinereus*), and *Myotis* species group.

Mean activity varied by species (Table 6) as well as with vegetation type, stand age, and date (Table 6). Hardwood-dominated sites had higher total bat activity (i.e., all species combined) than pine plantations, and sites of intermediate age had the greatest total bat activity compared to young and mature sites (Table 6). Eastern red bats had higher mean activity in hardwood-dominated sites than pine plantations and the greatest activity in young sites compared to intermediate and mature sites (Table 6). Big brown bats had higher activity in pine plantations compared to hardwood sites (Table 6). Both big brown bats and Eastern pipistrelle bats had higher mean activity in intermediate-aged sites compared to young and mature sites (Table 6). Mean bat activity also varied by date and year; generally

there was greater mean activity for all community members in August for both years (Table 6).

In addition to daily and annual variation in bat activity, I also found important variation in mean bat activity throughout the overnight hours. Activity by hour differed in hardwood and pine sites (Fig. 2) and also in sites of different ages (Fig. 3). More specifically, activity peaked in hardwood sites as day roosting time approached (i.e., 0501-0600; Fig. 2). Bat activity in sites of intermediate age peaked in two time periods: one early in the overnight period (i.e., 2101-2200; Fig. 3) and one near the end of that period (i.e., 0501-0600; Fig. 3). In both young and mature sites, activity peaked as the day roosting time approached (i.e., 0501-0600; Fig. 3).

I determined insect abundance by measuring dry biomass for 5 taxonomic groups and calculated means in relation to habitat effects and temporal effects hypotheses (Table 7). Total prey biomass was higher in hardwood-dominated stands than pine plantations (Table 7). Young sites had higher total prey biomass compared to intermediate and mature sites, and August 2007 had the greatest mean total prey biomass for both sampling years (Table 7). Lepidopteran biomass was greater in hardwood-dominated sites than pine plantations, and Lepidopteran biomass was also greater in young sites compared to intermediate and mature sites (Table 7). Lepidopteran biomass also varied by month and year with the greatest mean biomass recorded for August 2007 (Table 7). Both mean Coleopteran and Trichopteran biomass were greater in pine plantation sites than hardwood sites, and both taxonomic groups also had greater biomass in young sites compared to intermediate and mature sites (Table 7). Mean Coleopteran biomass was the greatest in August 2007 (Table 7).

I determined environmental factors for sampling nights by recording climate and lunar data collected at the Farmville Airport, which is the nearest comprehensive weather station to the Appomattox-Buckingham State Forest. I calculated means for each environmental variable in relation to month and year (Table 8). Temperature variables (i.e., minimum, maximum, and mean) were highest in August of both sampling years (Table 8). July 2006 had the highest mean barometric pressure, fraction of the moon, and hours of moonlight for any month in the 2 summers (Table 8).

DISCUSSION

Results of the model selection procedures clearly indicated that each of my hypotheses – habitat effects, environmental effects, temporal effects, and prey effects – is supported by my data. I chose these hypotheses because all biologically influence both bat activity and insect abundance in the SAPE (Bailey 1995).

I predicted that habitat characteristics such as dominant vegetation type and stand age would affect bat activity, and this was supported by one of my 3 data sets. While I did not explore the direction of the effect (Table 5), my descriptive statistics suggest that the effect would be in favor of hardwood-dominated sites (Table 6). Elmore et al. (2004 and 2005) found that hardwood sites in an industrial pine landscape provided important roosting locations for some bat species in Mississippi and some of those species also are part of the SAPE bat community. In my descriptive analyses, I explored bat activity throughout the night using hourly intervals and found that there was early morning activity in hardwood-dominated sites that is probably linked to bats returning to diurnal roost locations; this is consistent with the Elmore et al. (2004 and 2005) findings.

Biologically site age should affect both bat and insect activity due to vegetation structure and diversity changes that occur with succession. In evaluating my habitat effects hypothesis with each data set, I found an important effect of young age of site vegetation on bat and insect activity. As mentioned above, mature sites are important areas for diurnal roosting locations for some species (Elmore et al. 2004). Young habitats recently disturbed by forest harvest lack a canopy and therefore are less cluttered, providing foraging habitat that allows for increased maneuverability for a range of bat species (Loeb and O'Keefe 2006, Yates and Muzika 2006). My model results from all three data sets agree with this assertion: younger sites are more open structurally and therefore allow for more foraging. These results agree with findings from Loeb and O'Keefe (2006) and Yates and Muzika (2006), which indicated that stand age affected bat activity in sites more than forest type. For my insect data set, there was an additional model that received support: young and intermediate-aged sites (Table 5). This further suggests the importance of stand age not only for bat activity but also as a predictor of high insect prey abundance.

Along with structural differences between age classes, I predicted that floral diversity would affect bat activity and insect abundance in study sites. I expected that young sites would have higher floral diversity due to the recent disturbance associated with forest harvest (Walker 1994). Because the canopy has been opened up, light can penetrate to the ground, stimulating the growth of fast growing weeds and other pioneer plants (Walker 1994). However, I did not measure vegetation diversity or density in my study sites. The habitat effects model selection results for all three data sets suggested the need to continue to explore the link between vegetation, insect abundance, and bat activity as found in both the United Kingdom and Canada studies (Patriquin and Barclay 2003, Wickramasinghe et al. 2003,

Wickramasinghe et al. 2004) to determine more clearly if there is similar effects in the SAPE of Virginia.

As a final point regarding stand characteristics, I determined mean total bat activity throughout the night by stand age using a descriptive analysis approach (Fig. 3). The results indicated that bat activity peaked at dawn in mature-aged sites. This further suggests that mature-aged sites are important for members of the SAPE's bat community as diurnal roosting locations. Young-aged sites should have the highest activity during early foraging hours; my results raised questions about high early morning activity in my young sites. This high activity in young-aged sites might be caused by members of the bat community returning to roost sites near or on the edges of these young-aged sites or even roost locations within these recently disturbed sites.

Environmental conditions like lunar cycle, temperature, and humidity affect bat activity and insect abundance. Previous studies have suggested an inverse relationship of the amount of moonlight and fraction of the moon with bat foraging activity (Crespo et al. 1972, Lang et al. 2006). As reported by Lang et al. (2006), nocturnal animals react differently to moonlight depending on their role in the ecosystem as predators, prey, or both. Generally increased visibility causes lower insect and bat activity in areas due to increased predation (Crespo et al. 1972, Lang et al. 2006). In examining my environmental effects hypothesis, I found that lunar variables of hours of moonlight and fraction of moon received support for all 3 data sets (Table 3, 4, and 5), which correlates with both Crespo et al. (1972) and Lang et al. (2006).

Along with the lunar cycle, activity levels for bats and insect abundance should increase as temperature increases because some energy required in maintaining body

temperature can be allocated to allow for increased foraging activity. Tibbels and Kurta (2003) found that temperature affected both insect abundance and bat activity in their studies. In my environmental effects hypothesis models, this interaction was supported for the insect abundance and combined data sets (Table 4 and 5) but not supported by the bat data set (Table 3).

Another factor that should biologically affect both bat activity and insect abundance is humidity. Nights with higher humidity without precipitation should have the higher bat activity due to decreased water loss. However, model results for the insect abundance and combined data sets (Table 4 and 5) showed support for humidity models while my bat activity data set did not (Table 3). A reason why climatic variables, like temperature and humidity, did not receive support potentially was due to the lack of site-specific climate data that would have elucidated microclimatic differences among sites.

Temporal variables are indicative of time-linked factors, like seasonality and reproduction, that affect bat activity and insect abundance. In the beginning of the summer female bats give birth, and by the end of the summer reproductively successful females have taught their offspring to fly (Kunz and Fenton 2003), thus increasing the foraging bat population. Bat activity may also vary among years, which could be a result of a hard winter or increased mortality caused by wind turbines in bat migration routes. I explored the temporal effects hypothesis and found that, for all 3 data sets, year received support (Table 3, 4, and 5). Because I did not determine the direction of the effect, I can not determine if activity in year 1 was less than or greater than year 2. An important consideration in interpreting that result is the uneven sampling between the two years. In my descriptive

analysis there were differences by month for mean bat activity, mean insect prey biomass, and some environmental variables.

Sites with high insect prey availability should have high bat activity levels as found in the United Kingdom and Canada studies (Patriquin and Barclay 2003, Wickramasinghe et al. 2003, Wickramasinghe et al. 2004). For my combined data set, I examined a prey effects hypothesis and found support that only Coleopteran abundance at a site affected bat activity (Table 5). I did not have support for total insect prey biomass, as found by both Patriquin and Barclay (2003) and Wickramasinghe et al. (2003 and 2004). While sample size for nights with both bat activity and insect abundance monitored at study sites may be too small to detect these effects, my descriptive statistics suggest some key trends. For example, Lepidopteran prey biomass and Eastern red bat activity were greater in both hardwood-dominated sites and young-aged sites (Table 6 and 7), and Coleopteran prey biomass and big brown bat activity were higher at pine-dominated sites than hardwood sites (Table 6 and 7), suggesting that there is a trend for positive association between species-specific activity and 'preferred' prey items.

Habitat, environmental, and temporal effects hypotheses are not independent of each other but rather interact to determine both bat activity and prey abundance in my study sites. Models within the multiple effects hypothesis model set explored these interactions of the top habitat, environmental, temporal, and prey effects models for all three data sets. Models that received support from my data under my multiple effects hypothesis for both my insect abundance and combined data sets were multivariable models containing top models from my environmental and habitat effects hypotheses. For my bat data set, I only ran multiple effects hypothesis models for habitat and temporal variables, and my most supported model

was young-aged sites and year. These results reiterate that there are multiple factors affecting bat and insect activity in the SAPE region of Virginia. For example, environmental conditions, like lunar activity and temperature, and stand age do not only independently affect bat and insect activity. This is evident because when used put in multi-variable models together they received more support from the data then they did independently, and thus are important in understanding ecological relationships within these ecoregion.

MANAGEMENT IMPLICATIONS

The strong relationship between stand age and bat activity suggested that forest stands disturbed recently by forest harvest provide an area with lower vegetation clutter, high insect prey abundance, and thus have higher bat activity. Mature sites are important landscape elements because they provide large trees for roosting. Dominant vegetation type is an important factor in some Eastern forest bat species' roosting ecology, and therefore should also be considered in developing overall management strategies for bat conservation. Thus, for proper management of regenerating mixed-hardwood forests and pine plantations, it is important to maintain sites at various levels for succession to provide foraging and roosting locations for bat community members as well as high insect prey abundance.

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Table 1. Stand information for 15 study sites in the Appomattox-Buckingham State Forest, Virginia, U.S.A., 2006 – 2007.

Management Unit and Stand Number	Site name	Stand type	Dominant Vegetation	Relative age	Sampling year(s)
Loth 04	Desert	Loblolly pine	Pine	Young	2006, 2007
Talbert 07	Glover	Virginia pine	Pine	Intermediate	2007
Harris 47	Harris	Mixed upland hardwoods	Mixed hardwoods	Mature	2006
Harris 47	Junction	Mixed upland hardwoods	Mixed hardwoods	Young	2007
Talbert 32	Lake	Loblolly pine	Pine	Mature	2007
Glover 20	Little HQ	Mixed upland hardwoods	Pine	Young	2006
Loth 22	Loth	Loblolly pine	Mixed hardwoods	Young	2006, 2007
Loth 23	Pre Loth SW	Mixed upland hardwoods	Mixed hardwoods	Mature	2006
Loth 23	Post Loth SW	Mixed upland hardwoods	Mixed hardwoods	Young	2007
Talbert 14	Skinny Pines	Shortleaf pine	Pine	Mature	2007
Walker 33	Slate	Loblolly pine	Pine	Intermediate	2006
Talbert 01	Snake	Mixed upland hardwoods	Mixed hardwoods	Mature	2007
Loth 10	View	Virginia pine	Pine	Intermediate	2006
4H 56	V-site	Loblolly pine	Mixed hardwoods	Young	2006, 2007
Abbitt 09	Weird	Pine hardwood	Pine	Young	2006

Table 2. A priori candidate models for the first stage of model selection procedure used to evaluate habitat, environmental, and temporal effects hypothesis for all data sets collected in the Appomattox-Buckingham State Forest, Virginia, U.S.A, 2006-2007. For the combined data set, a prey effects hypothesis was also evaluated. For categorical variables of vegetation type and age, hardwood and mature stands were the reference categories, respectively.

Candidate models

Habitat effects hypothesis:

Young

Intermediate

Pine

Young, intermediate

Pine, young

Pine, intermediate

Pine, young, intermediate

Environmental effects hypothesis (step 1):

Minimum humidity

Maximum humidity

Mean humidity

Minimum temperature

Maximum temperature

Mean temperature

Hours of moon

Fraction of moon

Environmental effects hypothesis (step 2):

Pressure

Pressure, lunar

Pressure, humidity

Pressure, temperature

Lunar, humidity

Lunar, temperature

Humidity, temperature

Pressure, lunar, humidity

Pressure, lunar, temperature

Pressure, humidity, temperature

Lunar, humidity, temperature

Pressure, lunar, humidity, temperature

Temporal effects hypothesis:

Year

Julian, year

Julian

Table 2. Continued. A priori candidate models for the first stage of model selection procedure, for all data sets.

Candidate models
Prey effects hypothesis:
Total prey biomass
Lepidoptera biomass
Coleoptera biomass
“Other” biomass
Lepidoptera biomass, Coleoptera biomass

Table 3. Model results for a priori candidate models used to evaluate hypotheses of habitat, environmental, and temporal effects on bat activity in the Appomattox-Buckingham State Forest, Virginia, U.S.A., 2006-007. Models were evaluated using a multi-stage approach in which models with $\Delta AIC_c < 2$ and $w_i > 0.20$ in stage 1 were used to populate the stage 2 model set. For categorical variables of vegetation type and age, hardwood and mature stands were the reference categories, respectively.

Model	K	n	AIC _c	ΔAIC_c	w_i
Habitat effects hypothesis:					
Young	2	524	-148151	0.00	0.679801
Null	1	524	-148153	1.96	0.254606
Young, intermediate	3	524	-148158	6.08	0.032484
Environmental effects hypothesis (step 1):					
Minimum humidity	2	524	-148151	0.00	0.210069
Minimum temperature	2	524	-148152	0.44	0.168736
Maximum humidity	2	524	-148152	0.46	0.166657
Mean humidity	2	524	-148152	0.99	0.128027
Fraction of moon	2	524	-148153	1.47	0.100750
Mean temperature	2	524	-148153	1.50	0.099140
Null	1	524	-148153	2.01	0.076865
Environmental effects hypothesis (step 2):					
Minimum temperature, pressure, minimum humidity, fraction of moon	5	524	-148148	0.00	0.196290
Pressure, minimum humidity, minimum temperature	4	524	-148149	0.51	0.152203
Fraction of moon, minimum humidity, minimum temperature	4	524	-148149	1.27	0.103867
Fraction of moon, pressure, minimum temperature	4	524	-148150	1.50	0.092611
Fraction of moon, pressure, minimum humidity	4	524	-148150	1.73	0.082824
Minimum humidity, minimum temperature	3	524	-148150	1.84	0.078082
Minimum humidity, pressure	3	524	-148150	1.94	0.074586
Minimum temperature, pressure	3	524	-148150	2.47	0.057143
Temporal effects hypothesis:					
Year	2	524	-148153	0.00	0.550845
Null	1	524	-148153	0.41	0.449155
Julian	2	524	-148348	195.41	2.03E-43
Multiple effects hypothesis – Stage 2:					
Young, year	3	524	-148151	0.00	0.444209
Young	2	524	-148151	0.47	0.351755
Year	2	524	-148153	1.56	0.204036
Null	1	524	-148153	2.43	0.131743

Table 4. Model results for a priori candidate models used to evaluate hypotheses of habitat, environmental, and temporal effects on insect biomass in the Appomattox-Buckingham State Forest, Virginia, U.S.A., 2006-2007. Models were evaluated using a multi-stage approach in which models with $\Delta AIC_c < 2$ and $w_i > 0.20$ in stage 1 were used to populate the stage 2 model set. For categorical variables of vegetation type and age, hardwood and mature stands were the reference categories, respectively.

Model	K	n	AIC _c	ΔAIC_c	w_i
Habitat effects hypothesis:					
Young	2	115	697.9159	0.00	0.312597
Young, intermediate	3	115	698.7848	0.87	0.202447
Intermediate	2	115	699.1141	1.20	0.171711
Pine, young	3	115	699.7642	1.85	0.124062
Pine, intermediate	3	115	700.8746	2.96	0.071206
Environmental effects hypothesis (step 1):					
Fraction of moon	2	115	685.6357	0.00	0.998152
Mean temperature	2	115	699.8085	14.17	0.000835
Environmental effects hypothesis (step 2):					
Fraction of moon, pressure	3	115	680.7348	0.00	0.740617
Mean temperature, pressure, fraction of moon	4	115	682.8396	2.10	0.258546
Temporal effects hypothesis:					
Year	2	115	699.2119	0.00	0.461696
Julian, year	3	115	700.33	1.12	0.263979
Julian	2	115	701.1167	1.90	0.178129
Null	1	115	702.349	3.14	0.096195
Multiple effects hypothesis – Stage 2:					
Young, pressure, fraction of moon	4	115	672.797	0.00	0.502012
Young, intermediate, pressure, fraction of moon	5	115	673.4797	0.68	0.356849
Pressure, fraction of moon, year	4	115	676.371	3.57	0.084068
Pressure, fraction of moon, year, Julian	5	115	677.5115	4.71	0.047532
Pressure, fraction of moon	3	115	680.7348	7.94	0.009485
Young, year	3	115	693.0958	20.30	1.96E-05
Young, year, Julian	4	115	693.585	20.79	1.54E-05
Young, intermediate, year	4	115	694.9228	22.13	7.87E-06
Young, intermediate, year, Julian	5	115	695.4939	22.70	5.92E-06
Young	2	115	697.9159	25.12	1.76E-06
Young, intermediate	3	115	698.7848	25.99	1.14E-06
Year	2	115	699.1519	26.35	9.50E-07
Year, Julian	3	115	700.33	27.53	5.27E-07

Table 5. Model results for a priori models used to evaluate hypotheses of habitat, environmental, prey, and temporal effects on bat activity from the combined data set in the Appomattox-Buckingham State Forest, Virginia, U.S.A., 2006-2007. Models were evaluated using a multi-stage approach in which models with $\Delta AIC_c < 2$ and $w_i > 0.20$ in stage 1 were used to populate the stage 2 model set. For categorical variables of vegetation type and age, hardwood and mature stands were the reference categories, respectively.

Model	K	n	AIC _c	ΔAIC_c	w_i
Habitat effects hypothesis:					
Pine, young	3	63	-27658.7	0.00	0.357932
Pine	2	63	-27660.5	1.88	0.139610
Pine, young, intermediate	4	63	-27660.6	1.90	0.138390
Young	2	63	-27660.7	2.07	0.127059
Environmental effects hypothesis (step 1):					
Maximum temperature	2	63	-27660.5	0.00	0.191434
Maximum humidity	2	63	-27660.7	0.21	0.172508
Minimum temperature	2	63	-27660.8	0.31	0.164275
Hour of moon	2	63	-27660.9	0.46	0.151949
Mean humidity	2	63	-27661.9	1.40	0.094902
Minimum humidity	2	63	-27662.0	1.48	0.091290
Null	1	63	-27662.5	2.03	0.069278
Environmental effects hypothesis (step 2):					
Hour of moon, maximum humidity, maximum temperature	4	63	-27657.4	0.00	0.411848
Maximum temperature, maximum humidity	3	63	-27658.5	1.18	0.228427
Maximum temperature, hour of moon	3	63	-27659.2	1.81	0.167021
Maximum humidity, hour of moon	3	63	-27659.3	1.89	0.159895
Null	1	63	-27662.5	5.16	0.031231
Temporal effects hypothesis:					
Null	1	63	-27662.5	0.00	0.672119
Year	2	63	-27664.0	1.44	0.327881
Julian	2	63	-27713.0	50.48	7.34E-12
Prey effects hypothesis:					
Null	1	63	-27662.5	0.00	0.391044
Coleoptera biomass	2	63	-27662.6	0.13	0.366880
"Other" biomass	2	63	-27665.0	2.37	0.119405
Multiple effects hypothesis – Stage 2:					
Pine, young, hour of moon, maximum temperature, maximum humidity	6	63	-27652.8	0.00	0.476345
Pine, young, maximum temperature, maximum humidity	5	63	-27654.4	1.54	0.220778

Table 5. Continued. Results for a priori models that examined hypotheses on bat activity from the combined data set.

Model	K	n	AIC _c	ΔAIC _c	w _i
Multiple effects hypothesis – Stage 2 continued:					
Coleoptera biomass, hours of moon, maximum humidity, maximum temperature	5	63	-27656.1	3.30	0.091328
Hours of moon, maximum humidity, maximum temperature	4	63	-27657.4	4.52	0.049594
Coleoptera biomass, Pine, young	4	63	-27658.2	5.38	0.032284
Coleoptera biomass, maximum temperature, maximum Humidity	4	63	-27658.3	5.47	0.030854
Maximum temperature, maximum humidity	3	63	-27658.5	5.70	0.027507
Pine, young,	3	63	-27658.7	5.82	0.0259
Hours of moon, maximum humidity, maximum temperature, year	5	63	-27659.5	6.70	0.016701
Maximum temperature, maximum humidity, year	4	63	-27659.8	6.93	0.014863
Pine, young, year	4	63	-27661.6	8.76	0.005977
Coleoptera biomass	2	63	-27662.6	9.81	0.003528
Coleoptera biomass, year	3	63	-27663.3	10.49	0.00251
Year	2	63	-27664.0	11.12	0.001835

Table 6. Bat activity (mean # of call files per night \pm SE) by species or species group for key habitat and temporal categories in the Appomattox-Buckingham State Forest, Virginia, U.S.A., 2006-2007.

		n	Total bat activity	<i>Eptesicus fuscus</i>	<i>Lasiurus borealis</i>	<i>Myotis</i> spp.	<i>Nycticeius humeralis</i>	<i>Perimyotis subflavus</i>	Unidentified bat species
Habitat effects hypothesis:									
Dominant Vegetation									
Pine		269	38.79±2.87	5.62±1.29	15.62±1.11	1.90±0.19	0.33±0.10	4.86±0.68	10.09±0.70
Hardwood		255	51.16±2.67	1.96±0.17	25.75±1.46	1.75±0.13	0.67±0.09	4.77±0.61	16.15±1.03
Stand Age									
Young		221	45.28±2.85	2.22±0.19	25.85±1.64	1.71±0.15	0.48±0.13	4.30±.097	10.44±0.62
Intermediate		75	56.53±7.61	15.4±4.44	15.87±1.55	2.13±0.43	0.04±0.02	6.55±0.80	15.87±1.97
Mature		228	40.50±2.60	1.60±0.15	16.95±1.29	1.84±0.17	0.66±0.10	4.74±0.38	14.63±1.12
Temporal effects hypothesis:									
Jun	2006	14	20.86±6.66	0.36±0.20	10.78±4.06	1.50±0.27	1.07±0.71	3.36±1.33	3.71±2.03
	2007	169	19.51±1.40	0.88±0.10	10.18±0.95	1.43±0.14	0.24±0.07	1.54±0.15	5.18±0.37
Jul	2006	14	48.40±23.32	1.60±0.64	16.27±7.88	2.00±1.05	0.20±0.11	20.60±13.23	7.00±2.76
	2007	113	45.48±3.76	2.72±0.25	22.11±2.14	1.50±0.27	0.66±0.20	3.86±0.38	14.42±1.71
Aug	2006	16	81.94±13.39	2.53±0.65	35.24±6.97	4.29±0.95	1.59±0.90	19.29±3.94	18.12±3.23
	2007	193	64.78±3.54	7.63±1.78	28.46±1.58	2.16±0.23	0.50±0.09	5.86±0.41	19.82±1.04

Table 7. Insect abundance (mean dry biomass per night \pm SE) by taxonomic group for key habitat and temporal categories in the Appomattox-Buckingham State Forest, Virginia, U.S.A., 2006-2007.

Appomattox-Buckingham State Forest, Virginia, USA, 1998-2007								
	n	Total insect prey biomass (g)	Coleoptera biomass (g)	Lepidoptera biomass (g)	Diptera biomass (g)	Trichoptera biomass (g)	Other Biomass (g)	
Habitat effects								
hypothesis:								
Dominant								
Vegetation								
Pine	62	6.16±0.67	2.42±0.40	3.09±0.33	0.02±0.01	0.24±0.04	0.38±0.05	
Hardwood	53	6.70±0.67	2.15±0.37	3.98±0.40	0.02±0.01	0.16±0.04	0.39±0.08	
Stand Age								
Young	61	7.53±0.75	2.84±0.46	3.98±0.38	0.03±0.01	0.26±0.04	0.43±0.07	
Intermediate	24	4.31±0.85	1.11±0.22	2.67±0.59	0.01±0.01	0.18±0.06	0.34±0.07	
Mature	30	5.91±0.61	2.15±0.42	3.20±0.40	0.01±0.00	0.11±0.05	0.34±0.08	
Temporal effects								
hypothesis:								
June	2006	31	6.96±1.07	2.70±0.73	3.54±0.47	0.04±0.02	0.30±0.06	0.39±0.10
July	2006	26	4.38±0.96	1.05±0.33	3.03±0.62	0.01±0.00	0.14±0.04	0.15±0.05
	2007	3	3.67±0.84	1.82±0.51	1.76±0.43	0.00±0.00	0.05±0.03	0.03±0.01
August	2006	29	5.92±0.72	1.60±0.25	3.41±0.47	0.01±0.00	0.29±0.07	0.61±0.09
	2007	23	8.94±1.01	4.12±0.66	4.33±0.60	0.01±0.00	0.07±0.01	0.40±0.07

Table 8. Environmental conditions (mean \pm SE) for sampling nights by year and month as reported by the nearest comprehensive weather station to the Appomattox-Buckingham State Forest, Virginia, U.S.A., 2006-2007.

	June		July		August	
	2006 (n = 7)	2007 (n = 28)	2006 (n = 6)	2007 (n = 27)	2006 (n = 6)	2007 (n = 30)
Environmental effects hypothesis:						
Mean Temperature ($^{\circ}\text{C}$)	23.41 \pm 1.07	23.56 \pm 0.56	23.24 \pm 1.38	25.16 \pm 0.43	25.37 \pm 1.53	27.13 \pm 0.44
Maximum temperature ($^{\circ}\text{C}$)	29.68 \pm 0.29	29.60 \pm 0.73	30.93 \pm 0.37	31.49 \pm 0.48	30.19 \pm 0.37	33.75 \pm 0.60
Minimum temperature ($^{\circ}\text{C}$)	16.27 \pm 0.45	17.59 \pm 0.64	17.59 \pm 0.27	18.93 \pm 0.52	17.22 \pm 0.43	20.60 \pm 0.50
Mean humidity (%)	69.00 \pm 3.69	71.28 \pm 1.71	69.00 \pm 1.59	69.75 \pm 1.45	69.00 \pm 2.89	69.32 \pm 1.87
Maximum humidity (%)	93.14 \pm 0.86	93.21 \pm 0.38	94.00 \pm 0.00	92.61 \pm 0.68	94.17 \pm 1.42	92.77 \pm 0.56
Minimum humidity (%)	40.43 \pm 6.50	44.55 \pm 2.59	40.17 \pm 3.04	43.46 \pm 1.80	39.50 \pm 5.06	42.35 \pm 2.60
Barometric pressure (hPa)	1018.00 \pm 0.87	1015.90 \pm 1.06	1019.83 \pm 1.72	1016.50 \pm 0.65	1017.00 \pm 0.73	1016.55 \pm 0.58
Hours of moon light	3.91 \pm 0.49	4.41 \pm 0.38	5.74 \pm 0.78	5.04 \pm 0.47	4.36 \pm 0.98	5.33 \pm 0.57
Fraction of moon	0.38 \pm 0.12	0.51 \pm 0.07	0.70 \pm 0.13	0.55 \pm 0.07	0.32 \pm 0.16	0.51 \pm 0.07

Fig. 1. The location of the Appomattox-Buckingham State Forest in the Southern Appalachian Piedmont Ecoregion of Virginia.



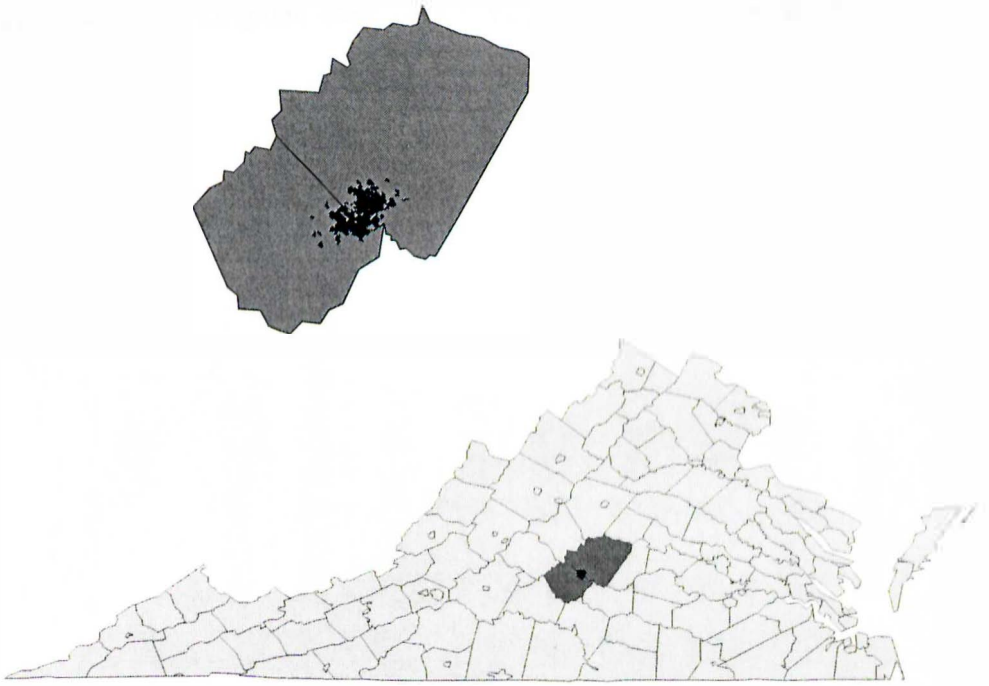


Fig. 2. Mean total bat passes per hour (\pm SE) in relation to dominant vegetation type in the Appomattox-Buckingham State Forest, Virginia, U.S.A., 2006-2007.



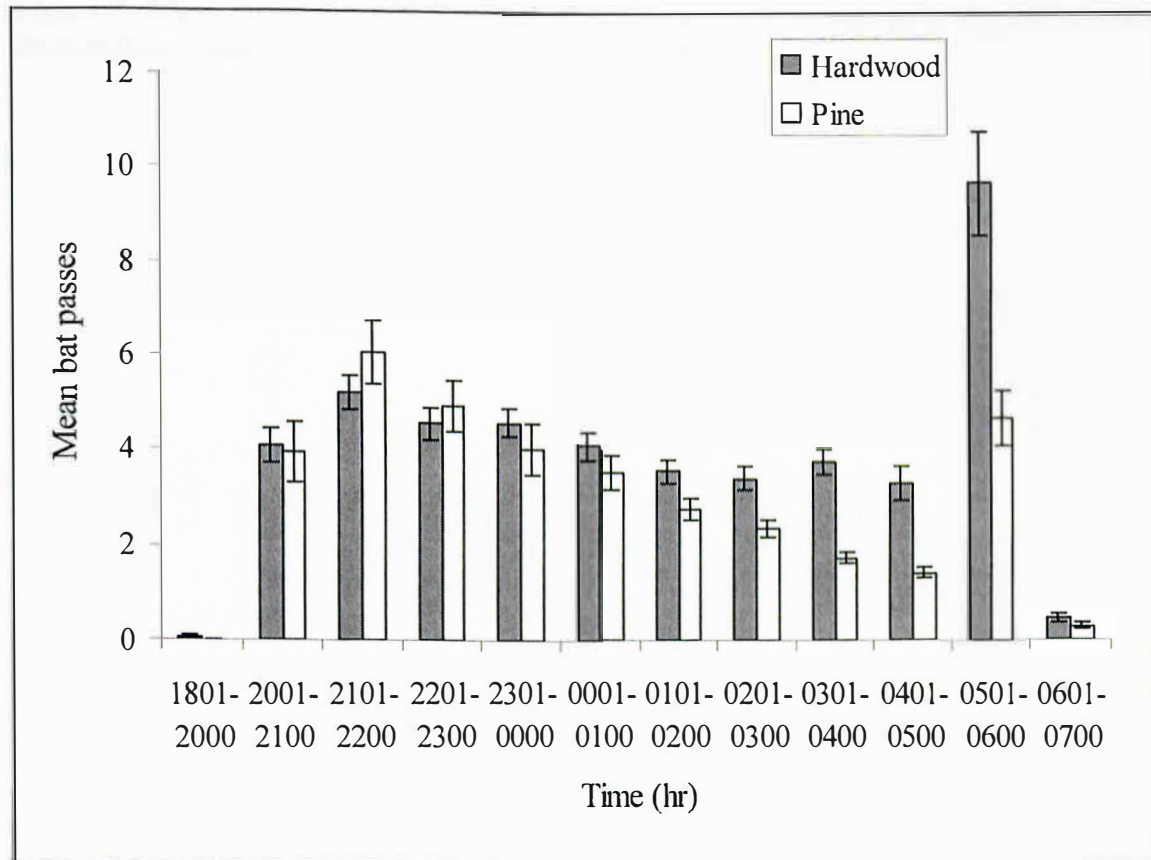


Figure 3. Mean total bat passes per hour (\pm SE) in relation to stand age in the Appomattox-Buckingham State Forest, Virginia, U.S.A., 2006-2007.



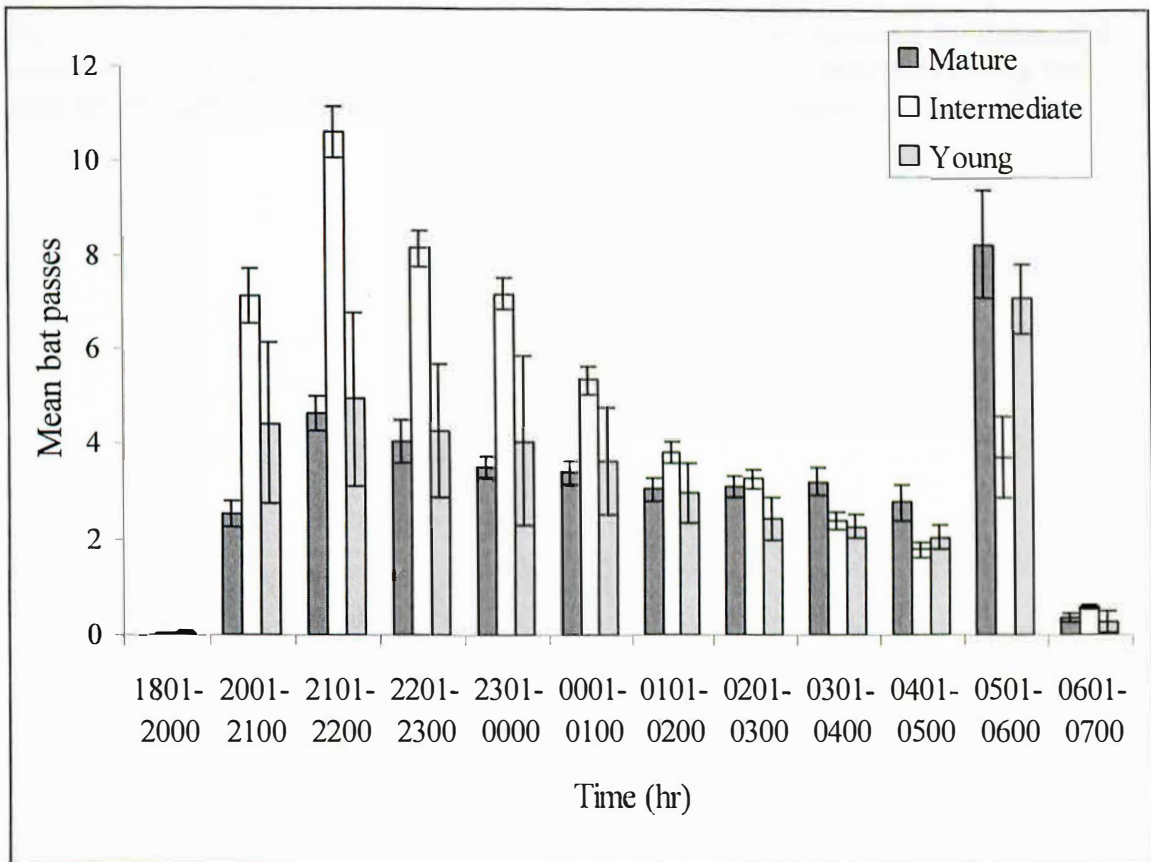


Fig. 4. Conceptual model for interactions among habitat characteristics, environmental conditions, prey abundance, and bat activity. It illustrates the interactions among the multiple research hypotheses: habitat effects, environmental effects, and prey effects.



