Big bats binge bad bugs: Variation in crop pest consumption by common bat species

Morgan J. Hughes [a], Elizabeth C. Braun de Torrez [a,b], Holly K. Ober [c,*]

[a] Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, Gainesville, FL 32611, USA
[b] Florida Fish and Wildlife Conservation Commission, 1105 SW Williston Road, Gainesville, FL 32601, USA
[c] Department of Wildlife Ecology and Conservation, University of Florida, 155 Research Rd, Quincy, FL 32351, USA

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ABSTRACT

As generalist predators, insectivorous bats exploit fluctuations in prey distribution and abundance. A more nuanced understanding of the influence of bats on arthropod pests requires documentation of the pest species bats consume and of the conditions associated with variation in rates of pest consumption. Here, we used high-throughput metabarcoding of DNA extracted from bat feces to investigate diets of 180 bats representing three Vespertilionidae species common to the southeastern US, a region dominated by agriculture and pine plantations. We detected 23 species of agricultural pests in bat diets, including pests responsible for severe economic damage, such as *Helicoverpa zea, Spodoptera frugiperda, Chloridea virescens* and *Chrysodeixis includens*. Incidence of pest consumption was high: 61% of all bats had consumed at least one agricultural pest species, with each bat consuming an average of 1.7 pest species. The likelihood of consumption of pests to row crops and the average size of pests consumed varied by bat species, with a large foliage-roosting species (*Lasiurus seminolus*) consuming a greater variety of pest species and pest species larger in size than smaller crevice, cavity, and cave roosting bat species (*Nycticeus humeralis, Myotis austroriparius*). Likelihood of pest consumption also varied among sampling periods (season) and among bats of different sizes (as reflected by wing length and mass). Overall, likelihood of pest consumption was higher in the late summer season than during spring or early summer, and higher among larger bats than smaller bats. Bat characteristics and seasonality were generally more effective than geographic features and weather conditions in predicting pest consumption patterns. Strategies for enhancing pest consumption services by bats in agroecosystems should strive to maintain and enhance diverse bat populations on a landscape scale by protecting and augmenting roost structures appropriate for each species. Our finding of widespread pest consumption by bats contributes to mounting evidence worldwide of the important role bats play in agricultural systems and highlights the value of incorporating bat conservation into integrated pest management programs globally.

1. Introduction

Arthropod pests have widespread impacts on production of agricultural commodities ranging from food and fiber to timber and livestock (Steelman, 1976; Wang et al., 2008; Dukes et al., 2009; Tabashnik, 2010). Worldwide, arthropods can destroy 25–50% of agricultural crops, representing a threat to productivity and food stability (Pimentel et al., 1978, 1991). Control costs can exceed $10 billion per year in direct pesticide costs in addition to the estimated $12 billion in societal and environmental damages (Pimentel, 2009).

Bats are capable of providing valuable pest suppression services, given their unique ecological role as volant and nocturnal consumers of arthropods (Williams-Guillén et al., 2008; Riccucci and Benedetto, 2018). The value of these services has been estimated as high as $53 billion per year in the United States (Maine and Boyles, 2015). This estimate is conservative because it doesn't take into account indirect effects such as bat reduction of insects that transmit fungi to crops, or reduction in crop damage due to avoidance of crop fields where bats are present by tympanate moths capable of hearing bat echolocation calls (common agricultural pests) (Agee, 1969; Huang et al., 2003).

The impact of pest consumption by bats varies considerably over space and time due to differences in bat foraging capabilities and

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* Corresponding author.
E-mail address: holly.ober@ufl.edu (H.K. Ober).

arthropod habitat use (Belwood and Fenton, 1976; Salinas-Ramos et al., 2015; Braun de Torrez et al., 2019). Previous studies have demonstrated a close spatiotemporal match between abundance of emergent arthropod pests and both bat activity and diet (Lee and McCracken, 2005; Charbonnier et al., 2014). Additionally, experimental studies have demonstrated an increase in crop damage following the exclusion of bats from agricultural systems (Maine and Boyles, 2015). Landscape-scale, multi-taxon studies that evaluate pest consumption across a broad range of land uses are needed to develop effective recommendations for enhancing integrated pest management strategies involving bats (Williams-Guillén et al., 2016).

Due to their high mobility, insectivorous bats can adjust their foraging behavior to maximize encounters with suitable prey (Cryan et al., 2012; McCracken et al., 2012). Characteristics of individual bats, such as flight capabilities, echolocation attributes, metabolic/nutritional needs, and bite strength determine which arthropods will be encountered, pursued, captured and consumed by a particular bat (Aldridge and Rautenbach, 1987; Sedlock et al., 2014). These characteristics vary not only across bat species but also within, due to factors such as age and reproductive condition (Norberg and Rayner, 1987; Barclay, 1989; Hughes et al., 1995; Denzinger and Schnitzler, 2013). Individuals with morphological attributes that confer greater maneuverability can utilize areas with more obstructions and pursue more evasive prey than those with less maneuverability (Mendez et al., 2017; Magalhães de Oliveira et al., 2020). Individuals with stronger jaw morphology can consume harder prey more efficiently than those with gracile jaw morphology (Freeman, 1981), which may influence pest consumption given that many of the most economically damaging agricultural pests are soft bodied lepidopterans (Suckling et al., 2017). Finally, bats with larger gape width (associated with larger body size) can consume larger prey more efficiently, which may influence pest consumption given that some of the most economically important pests (*Helicoverpa zea* and *Spodoptera exigua)* are large (Tomassini et al., 2014; Montezano, et al., 2018; Invasive Species Compendium, 2020).

Geographic characteristics at various spatial scales may influence which arthropod pests are consumed by bats due to the impact of landscape features on arthropod community composition and bat foraging activity (Williams-Guillén et al., 2016; Russo et al., 2018, Barberi et al., 2010). For example, the activity of bats within agricultural fields is known to be influenced by the surrounding non-crop matrix, so dominant land cover in the area may be relevant to bat consumption of pests to agricultural crops (Kelly et al., 2016; Olimpi and Philpott, 2018). Since many economically important insect pests of row crops use grass species as alternative hosts when crops are not available (Appendix A), acreage of grasses in agroecosystems may influence pest persistence, which may in turn influence the pest consumption services bats provide. Some evidence suggests that pest consumption by bats may decrease as the degree of local agricultural intensification increases (Kalda et al., 2015; Treitler et al., 2016). Therefore, the proportion of a given landscape devoted to heavily managed crops such as pecan, citrus, corn and cotton may be less influential to bat pest consumption patterns than the proportion of the landscape devoted to less intensively managed crops typically grown across smaller acreages such as berries and forage. The latter may be more influential to pest abundance than the widespread, heavily managed crops given their suitability as host species for a variety of arthropod pest species, the lighter pesticide load used to manage these crops, and the increased habitat heterogeneity typical of landscapes where they are grown (Gianessi and Reigner, 2006; Heim et al., 2015; Olimpi and Philpott, 2018).

Temporally variable characteristics may also dictate the prevalence of arthropod pest consumption by bats (Lee and McCracken, 2005). At short time scales, time of night can influence which arthropod species are active at a given site (Beck, 1980). Similarly, weather factors that vary across short time scales, such as temperature and precipitation, can induce nightly fluctuations in arthropod composition at a given site by triggering hatches or migrations (Honek, 1997; Intachat et al., 2001).

Across longer time periods such as seasons, arthropod community composition varies even after accounting for weather, due to arthropod migration patterns and a dietary reliance of arthropods on plants that respond to factors such as day length to determine budding time (Lee and McCracken, 2005). Finally, regional climate influences which arthropod species can persist in a location (Klok et al., 2004).

We conducted a multi-taxon investigation of arthropod consumption by bats across a vast spatial area encompassing a broad range of land uses to better understand factors that influence bat predation on agricultural pests. We used DNA metabarcoding to characterize the diets of three insectivorous bat species common to the southeastern US: Seminole bats (*Lasiurus seminolus*), evening bats (*Nycticeius humeralis*) and southeastern myotis (*Myotis austroriparius*). Because these species are common across one quarter of the US, pest consumption by these species could indicate widespread and substantial impacts on pest populations (Menzel et al., 2000). After documenting which agricultural pests are consumed by these bats, our first objective was to compare pest consumption among the three bat species. We hypothesized that pest consumption across the three bat species would vary predictably according to variation in insect size and hardness, due to differences in bat species size and jaw morphology. We predicted that the largest species, *L. seminolus*, would consume Lepidopteran pests at higher rates due to the adaptation of their gracile jaw morphology to soft-bodied prey, and that they would consume more of the relatively large pests due to their large gape width (Laerm et al., 1999; Barlow et al., 1997; Freeman 1981). We predicted *N. humeralis* would consume the hardest pest species due to their robust jaw morphology (Freeman, 1981). Our second objective was to identify factors other than bat species which were associated with patterns of pest consumption by bats. We hypothesized that pest consumption would vary predictably according to variation in traits of individual bats, environmental conditions, and geographic features. We predicted that bat characteristics and geographic characteristics would be more important than temporally variable characteristics in the rate and diversity of pests consumed, given known relationships between bat and prey characteristics, and the demonstrated influence of landscape features on bat foraging activity (Anthony and Kunz, 1977; Covell, 1984; Honek, 1997; Lee and McCracken, 2005). Identifying factors other than bat species that are associated with pest consumption would enable the prediction of scenarios under which consumption of pests by bats is more likely. An understanding of the factors influencing pest consumption by bats would enable development of more effective strategies to enhance bat pest consumption services in agroecosystems.

2. Materials and methods

2.1. Site selection

We used a stratified semi-random selection approach to locate 36 study sites spread across three study regions in the southeastern US, a region with a high prevalence of agriculture and timber production that is experiencing high rates of land use change (Napton et al., 2010). These three study regions spanned southern Alabama, southern Georgia, and north-central Florida, sampled as part of a larger study (Gottlieb et al., 2017; Ober et al., 2020) (Fig. 1). We placed a grid with 3 km x 3 km cells across each study region and classified land cover within each grid cell by simplifying the USGS EROS National Land Cover Data (US Geological Survey, 2014) land cover types into three categories: Forested, Field, and Other. Next, we used the intersect tool with ratio policy to determine the composition of land cover within each grid cell. To minimize possible confounding effects of urbanization and water resources, we only included grid cells containing > 90% coverage of forests and/or agriculture (Ancillotto et al., 2019). To ensure wide variation in forest cover among cells, we used systematic stratified sampling to select 36 grid cells that were evenly distributed in 12 increments from 0% to 100% forest cover (ESRI, Redlands, California) in
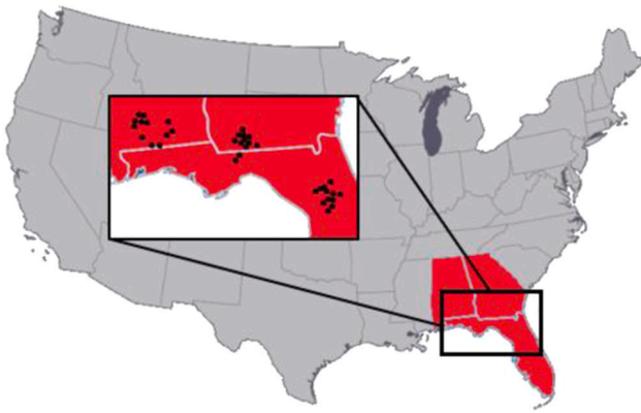
Fig. 1. The states of Alabama, Georgia, and Florida, USA (red), and the location of 36 study sites (black dots) where fecal samples were collected from free-flying bats captured in mist nets for investigation of bat diets in 2018.(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

each study region (ESRI, 2011). We then selected one study site from the three potential sites at each forest cover increment based on access and suitability for capturing bats using criteria from Kunz et al. (2003), ultimately selecting 12 study sites in each of the three study regions, characterized by a range of forest cover.

2.2. Data collection

Between April and August 2018, we sampled each study site 1–4 times during three discrete sampling periods: "early" (April 4 - June 1), "middle" (June 2 - July 20), and "late" (July 22 - August 18). We sampled a similar number of sites within each region during each sampling period. In total we sampled 36 sites across 89 nights, and captured bats at 33 of these sites across 72 nights. Our sampling effort was similar at each site, consisting of 2–5 single-, double-, or triple-high stacked mist nets (Avinet, Inc., Dryden, New York) that were each 4–12 m in length (Carroll et al., 2002; Kunz and Parsons, 2009). Nets were placed along corridors including tree lines (n = 12), unpaved roads within forests (n = 14) and along agricultural field edges (n = 4), and above water sources including irrigation ponds (n = 2), swimming pools (n = 2) and swamps (n = 2). Because the three focal bat species use a variety of structures as roosts (Menzel, et al., 2000), we were not able to quantify availability of potential roost structures for bats at each capture location, or quantify distances to nearest roosts. We opened all nets at sunset and checked them every 10–15 min for five hours following sunset. We placed each captured bat in a disposable paper bag until it defecated, for a maximum of two hours after capture. All bats were released without injury. We collected feces in a sterile vial containing silica desiccant and stored them at −20 °C (Brown et al., 2015). Bat capture and handling followed American Society of Mammalogists guidelines for research on live animals (Sikes et al., 2016), and permits from the University of Florida Institutional Animal Care and Use Committee (no. 201709745) and state wildlife agencies (no. 2018085671868680, 1000719590, LSSC-17–00030).

For each bat we recorded six characteristics in the field: species, sex, age, reproductive condition, mass, and forearm length. Measurements of forearm length were later used along with photographs of the right wing of each bat to estimate wing length using ImageJ software (Schneider et al., 2012). Due to the high correlation between forearm length and wing length, and the known association between wing length and dietary variation, we removed forearm length from subsequent analyses (Magalhães de Oliveira et al., 2020).

To determine if consumption of pests by bats was influenced by prey size or hardness, we calculated the average size and hardness of each

pest consumed. We estimated the average size of each pest species based on the mean sizes reported in the literature (Appendix A). We estimated the hardness of each prey species consumed based on their order, assigning Diptera a hardness value of 1, Lepidoptera a hardness value of 2, and both Hemiptera and Coleoptera a hardness value of 5 (Ghazali and Dzeverin, 2013).

To describe geographic features that could affect prey availability, we used 8 metrics that covered a range of spatial scales. At the small scale (site), we classified each site as dominated by agriculture, hardwood hammock, pinelands, water or open fields based on the dominant land use/land cover within a 50 m radius of the bat capture location. At the intermediate scale (landscape), we classified the landscape surrounding each site as dominated by evergreen forest, deciduous/mixed forest, row crops, open water or scrub/grassland) within a 3 km buffer (National Land Cover Database, 2016). At a larger scale (county), we used 5 metrics to characterize the prevalence of various aspects of agricultural production: the percent of land in the county classified in the USDA census as dedicated to farmland, corn/cotton, fruit/nut/vegetable, berry, and forage production (USDA NASS, 2017). Lastly, we used latitude to reflect the location of each site within the southeastern US.

Finally, we included four temporally variable factors that may influence insect abundance and activity. These were time of night, sampling period (i.e., season), daily precipitation, and daily minimum temperature as determined by National Oceanic and Atmospheric Administration databases at the nearest weather station (Menne et al., 2012).

2.3. Sample processing

After limiting the number of samples (pooled fecal pellets from each individual bat) to ≤3 per species per night to ensure an even geographical distribution of samples, we randomly selected three fecal pellets from each sample. When there were ≤3 pellets or samples, all were used. We extracted DNA from each sample using DNeasy PowerSoil Kit (standard protocol; QIAGEN, Hilden, Germany) with an extended second incubation period at 4 °C for at least one hour (Brown et al., 2015). We then used a customized dual-barcoded two-step polymerase chain reaction (PCR) protocol for amplicon library construction (modified workflow based on the 16S Metagenomic Sequencing Library Preparation protocol from Illumina (Amplicon et al., 2013), and similar to Divoll et al. (2018). The first step amplified insect DNA (~180 bp region of the cytochrome oxidase 1 [CO1] gene) with arthropod-specific primers ("ANML", LCO1490, and CO1–CFMRa) (Jusino et al., 2019) and the second step annealed indices "barcodes" to uniquely identify samples. Purified indexed amplicons were then pooled equimolarly and sequenced on the Illumina MiSeq platform. After sequencing, we identified Operational Taxonomic Units (OTUs) at a 97% clustering threshold (Clare et al., 2016) using the dada2 clustering algorithm on the AMPTK pipeline (Palmer et al., 2018) and identified OTUs to arthropod species using the Biodiversity of Life Database (BOLD; Ratnasingham and Hebert 2007). All samples were run in duplicate or triplicate through the entire protocol to minimize PCR stochasticity, and only OTUs identified in at least 50% of the replicates were kept for subsequent analyses. See Appendix 2 for further details regarding PCR amplicon library construction, sequencing, bioinformatics and assignment of taxonomic identity.

2.4. Data analysis

To characterize pest consumption across all bats, we first categorized each arthropod species consumed by bats as either known to impact agricultural production (pest) or not. We then listed the taxonomic order, primary crop type affected and estimated economic impact for each pest species (Appendix A). Based on the crop affected and economic impact, we subset the pests into three nonexclusive categories hereafter

referred to as pest categories: those that affect row crops, those that affect fruit/nut/vegetable crops, and those of high economic importance (defined as those species with a known impact of >100 million USD annually in the US). Finally, we calculated the total proportion of bats that consumed any agricultural pest and the average number of pest species consumed by each bat.

For all analyses we examined two metrics as response variables that describe the rates and diversity of pest consumption: the likelihood that at least one pest was consumed by a bat and the number of pest species consumed per bat. Both metrics have been used in the literature to describe pest consumption and thus can be compared across studies (Cohen et al., 2020). To compare pest consumption across bat species (Objective 1), we first used a skewness-kurtosis plot from the fitdistrplus package to confirm that the data followed a Binomial and Poisson count distribution for the pest consumption rates and diversity, respectively. We then tested for differences in pest consumption across sampling regions (sampling region as a categorical predictor variable) using a generalized linear model for Binomial/Poisson distributed data in the stats package (Delignette-Muller and Dutang, 2015; R Core Team, 2019). Given that there were no significant differences in pest consumption rates or diversity among the three study regions, we pooled samples across regions for all subsequent analyses. We used a Chi Squared test to examine differences in the likelihood of pest consumption (Binomial distribution) among bat species (bat species as a categorical predictor variable) and a Pairwise Wilcoxon Rank Sum Test to examine differences in the number of pest species consumed (Poisson distribution) among bat species (bat species as a categorical predictor

variable) for each pest category (all agricultural pests, row crop pests, fruit/nut/vegetable crop pests, or economically important pests) (R Core Team, 2019). Finally, we tested for differences in average prey size and hardness among bat species using Analysis of Variance (ANOVA) tests (Gaussian distribution) followed by multiple comparisons tests by means of least significant difference (Mendiburu, 2010; R Core Team, 2019).

To identify which factors best predicted consumption by bats of all pests and pests within each category (Objective 2), we created a suite of 19 single-variable generalized linear models and one null model for each of our two response metrics for each pest category (Shaffer, 1995; R Core Team, 2019)(Appendix C1, C2). We used Akaike's Information Criteria (AIC) to rank the alternate models and determine which factors explained the most variation, and quantified the relative importance of each model using Akaike weights. We reported the models that received substantial empirical support ($\Delta AIC \leq 2.0$).

3. Results

We analyzed fecal samples from 180 individual bats of three species across the southeastern US, *Lasiurus seminolus* [n = 40], *Nycticeius humeralis* [n = 56], and *Myotis austroriparius* [n = 84]. We documented that these bats consumed 23 agricultural pest species across four insect orders (Lepidoptera [n = 11], Hemiptera [n = 7], Coleoptera [n = 3], and Diptera [n = 2]), of which 12 had never previously been documented in bat diets and 16 have high economic impact. These included four notable pest species: *Chloridea virescens*, *Chrysodeixis includens*,
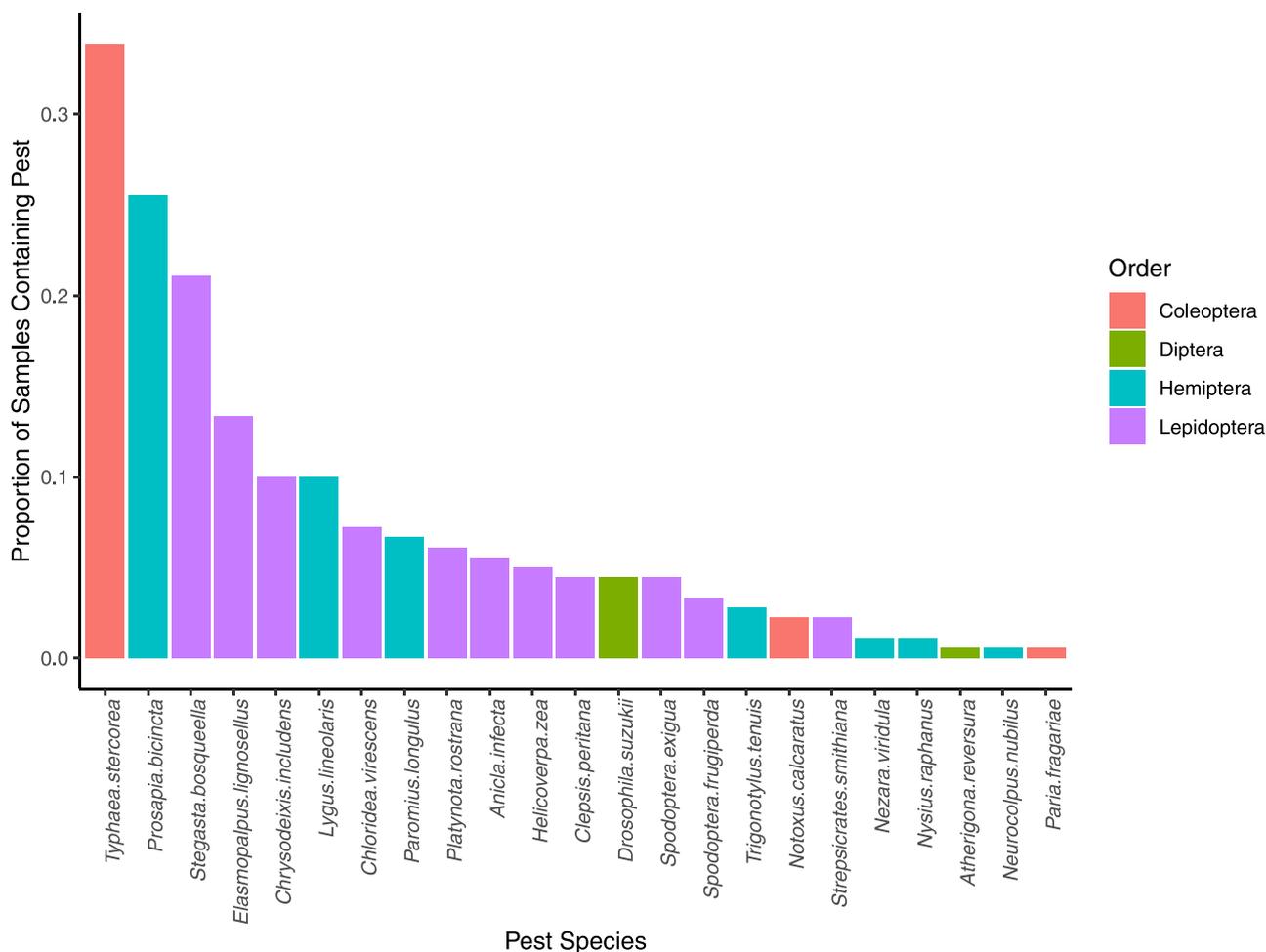

Fig. 2. Proportion of total bats (n = 180 *Lasiurus seminolus*, *Nycticeius humeralis* and *Myotis austroriparius*) that consumed each pest species in Alabama, Georgia, and Florida in 2018. Colors indicate the order of each arthropod pest.

Helicoverpa zea, and *Spodoptera frugiperda* (Fig. 2; Appendix A). Sixty-one percent of bats consumed ≥ 1 pest species, with each individual bat consuming an average of 1.7 pest species.

These 23 pest species consumed by bats primarily affect row crops (n = 12), fruit/nut/vegetable crops (n = 5), pasture/forage grasses (n = 3), vegetable crops (n = 2), and stored grains (n = 1) (Appendix A). The likelihood of a bat consuming a pest was high: 38% of bats consumed at least one pest of row crops, 23% of bats consumed at least one pest of fruit/nut/vegetable crops, and 19% of bats consumed at least one pest of high economic importance.

All three bat species were equally likely to have consumed at least one species of agricultural pest (P = 0.606 ± 0.490) (p = n.s.). However, the number of agricultural pest species consumed differed among bat species, with *L. seminolus* consuming a greater number of agricultural pest species per individual ($\bar{x}$ = 2.55 ± 0.483) than *N. humeralis* ($\bar{x}$ = 1.84 ± 0.478, p = 0.019) and *M. austroriparius* ($\bar{x}$ = 1.25 ± 0.501, p < 0.001) (Fig. 3A).

For pests affecting only row crops, *Lasiurus seminolus* was more likely to have consumed at least one species of pest (P = 0.500 ± 0.506) than *M. austroriparius* (P = 0.273 ± 0.449, p = 0.015) but just as likely as *N. humeralis* (P = 0.464 ± 0.503, p = n.s.). *Lasiurus seminolus* also consumed more species of row crop pests on average ($\bar{x}$ = 1.475 ± 1.921) than *N. humeralis* ($\bar{x}$ = 0.856 ± 1.197, p = 0.005) or *M. austroriparius* ($\bar{x}$ = 0.524 ± 1.047, p < 0.001) (Fig. 3D).

All three bat species were equally likely to have consumed at least one species of pest of fruit/nut/vegetable crops ($\bar{x}$ = 0.233 ± 0.424, p = n.s.), and all three bat species consumed a similar number of pests of fruit/nut/vegetable crops ($\bar{x}$ = 0.256 ± 0.486, p = n.s.) (Fig. 3C). All three bat species were also equally likely to have consumed at least one species of pest of high economic importance ($\bar{x}$ = 0.189 ± 0.393, p = n.s.). However, *L. seminolus* consumed more economically important pest species on average ($\bar{x}$ = 0.525 ± 0.877) than *N. humeralis* ($\bar{x}$ = 0.196 ± 0.519, p = 0.008) or *M. austroriparius* ($\bar{x}$ = 0.167 ± 0.406, p < 0.001) (Fig. 3B).

The pests consumed by *L. seminolus* were on average larger ($\bar{x}$ = 10.86 mm ± 4.55 mm) than those consumed by *N. humeralis* ($\bar{x}$ = 6.92 mm ± 3.94 mm) or *M. austroriparius* ($\bar{x}$ = 8.13 mm ± 4.55 mm) (p = 0.039) (Fig. 3F). The pests consumed by *N. humeralis* ($\bar{x}$ = 2.302 ± 0.91) were on average harder than those consumed by *M. austroriparius* ($\bar{x}$ = 1.743 ± 0.63) (p = 0.004), but not *L. seminolus* ($\bar{x}$ = 2.150 ± 0.79) (Fig. 3E).

Temporal, spatial, and bat characteristics were all associated with variation in the rates and diversity of pest consumption. The model with sampling period (season) was the best single variable model (lowest AIC) for predicting the diversity of agricultural and row crop pest species consumed, and the rates of consumption of agricultural pests. Individual bats consumed fewer crop pest species during the middle sampling period (all agricultural pests: $\bar{x}$ = 1.191 ± 1.739; row crop pests: $\bar{x}$ = 0.426 ± 1.048) than during the late sampling period (all agricultural pests: $\bar{x}$ = 2.426 ± 2.446, p = 0.004; row crop pests: $\bar{x}$ = 1.185 ± 1.459, p = 0.011).

Bat characteristics (species, age, sex, reproductive condition, mass, and wing length) were also associated with the consumption of some categories of pests. The model with bat species received substantial empirical support when predicting the number of agricultural pest species consumed, the number of row crop pest species consumed, and the number of economically important pest species consumed. In addition, the model with bat mass received substantial empirical support and outperformed the model with bat species when predicting the likelihood of consumption of agricultural pests, row crop pests, and economically important pests. Finally, the model with bat wing length received substantial empirical support when predicting the number of economically important pest species consumed and the likelihood of consumption of economically important pests. Both mass and bat wing length had positive relationships with all metrics of pest consumption investigated (Fig. 4).

Geographic factors (site type, landscape type, latitude, and % cover of various crops) were strongly associated only with the consumption of pests that affect fruit/nut/vegetable production. Percent cover of forage on the landscape was the best single variable model for predicting both the rates of consumption and the number species consumed for fruit/nut/vegetable pests while percent cover of fruit/nut/vegetable crops and corn/cotton on the landscape received substantial empirical support when predicting the number of fruit/nut/vegetable pest species
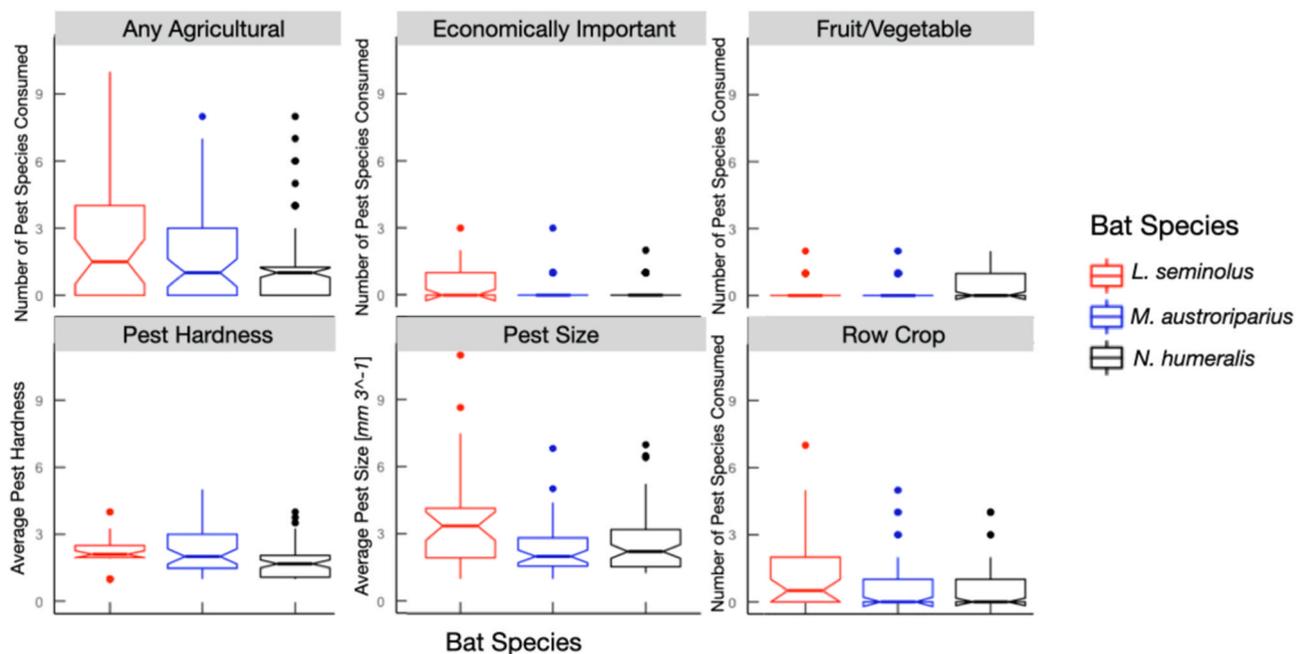

Fig. 3. Comparison of arthropod pests consumed by three common species of bats (*Lasiurus seminolus*, *Nycticeius humeralis*, and *Myotis austroriparius)* captured in Alabama, Georgia, and Florida according to: A) number of pest species affecting any type of agricultural crop, B) number of economically important pest species, C) number of pest species affecting fruit/nut/vegetable crops, D) number of pest species affecting row crops, E) average hardness of pests, and F) average body length of pests. Each boxplot represents the first quartile, median, and third quartile with whiskers indicating the highest and lowest value within 1.5 IQR of the median.
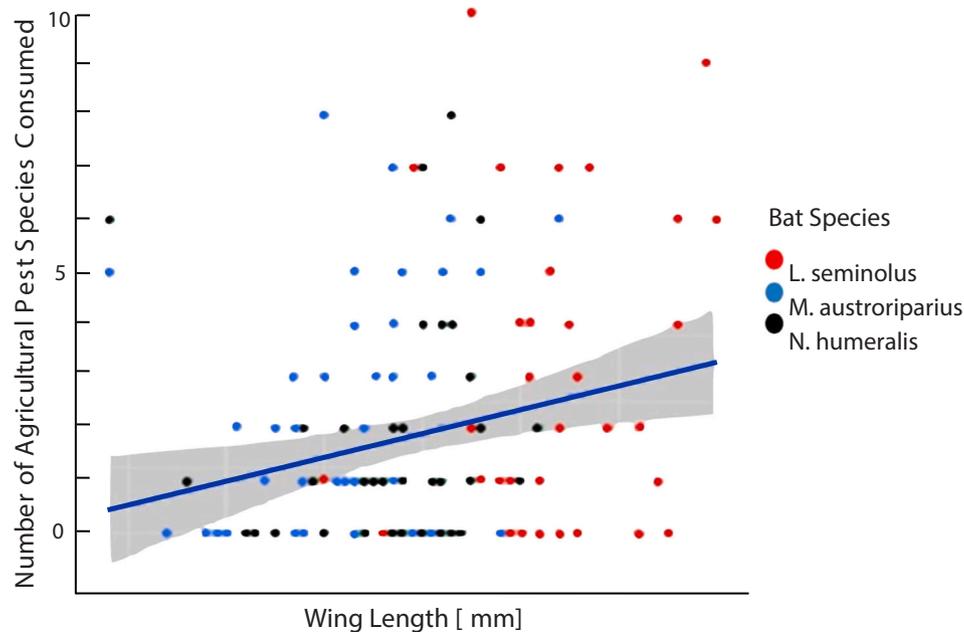
Fig. 4. The relationship between bat wing length (an indication of bat size) and the number of agricultural pest species consumed across three common species of bats (*Lasiurus seminolus*, *Nycticeius humeralis*, and *Myotis austroriparius*) in Alabama, Georgia, and Florida.

consumed.

4. Discussion

We found that the incidence of pest consumption by bats was high, with the majority of individual bats consuming at least one agricultural pest species. We documented that three widespread, common bat species consumed three of the most important crop pests in the US: *Helicoverpa zea* (Lepidoptera: Noctuidae) (Corn earworm), *Spodoptera frugiperda* (Lepidoptera: Noctuidae) (Fall armyworm), and *Chloridea virescens* (Lepidoptera: Noctuidae) (Tobacco budworm). These pests feed on a variety of crops including soybean, cotton, corn, peanut, tobacco, strawberries, and alfalfa (Covell, 1984). The net economic damage attributed to *C. virescens* and *H. zea* is estimated at $1 billion and $350 million annually in the US, respectively (Hardwick, 1965; Blanco, 2012). Given that bats consume adult insects, they prevent both direct damage from depredation of crops in the following larval generation and indirect damage from the transfer of fungal diseases, which is known to commonly occur with *H. zea* (Maine and Boyles, 2015). Further, as the first published investigation of the diet of *M. austroriparius* and *L. seminolus*, and the first dietary study in the southeastern US using DNA metabarcoding, we documented consumption of 12 agricultural pest species that have never been reported in bat diets. These species collectively cause billions of dollars of damage to agricultural crops per year (Appendix A).

Variation in pest consumption across bat species was somewhat consistent with our predictions. We anticipated that *L. seminolus* would consume more lepidopteran pests than *N. humeralis* and *M. austroriparius* due to their jaw morphology and overall large size, which is well-matched to the soft bodies and large size typical of Lepidoptera. This prediction was supported for all agricultural pests, row crop pests, and economically important pests, which are categories dominated by Noctuidae moths, a family previously documented as preferred prey for a closely related bat species, *L. borealis* (Clare et al., 2009). The identified dietary differences between *L. seminolus* and *N. humeralis* are likely not driven by horizontal partitioning of crop fields by foraging bats because previous studies have shown that these two species share similar foraging areas (Carter et al., 2004). It may instead be the case that bat species are partitioning foraging space vertically, or that bat

species are selecting different prey species within the same space. Regardless of the mechanism underlying the observed differences in pest consumption among bat species, the higher rates and diversity of pest consumption by *L. seminolus* suggest a previously unrecognized role of this species in consuming and possibly suppressing agricultural pests.

Despite differences in the rates and diversity of pest consumption among bat species, mass and wing length outperformed bat species in several of our analyses, suggesting that morphological characteristics of bats also influence arthropod pest consumption. Across all individuals, larger bats (as determined by greater mass and wing length) consumed agricultural pest species, pests of row crops, and economically important pests at greater rates than smaller bats. Given that bats of different sizes favor prey of different sizes (Anthony and Kunz, 1977; Charbonnier et al., 2014; Ober and Hayes, 2008), and that crop pest species are slightly larger on average than non-pest species (Aizpurua et al., 2018), crop pests may be more suitable prey for large (>9 g) bats, leading to higher rates of consumption. Sexual dimorphism within bats may explain some of the intra-specific variation as females were larger in all three species ($p < 0.01$) and females have different nutritional requirements when pregnant and lactating which may alter their foraging behavior (Myers, 1978; Mackie and Racey, 2007). The ability of individual bat characteristics to explain rates of prey consumption suggest it may be possible to extrapolate rates of pest consumption to bat species of similar morphology in other regions.

No short-term weather characteristics were associated with likelihood of pest consumption. However, in contrast to our predictions, we found strong evidence for seasonal variation in the rates and diversity of pest consumption, which corresponds to the high degree of seasonality that has been documented in diets of other insectivorous bat species (Clare et al., 2011; Salinas-Ramos et al., 2015). We found that the number of pest species consumed per bat was highest during the latest sampling period (late June through late August) and lowest during the middle sampling period (early June through late July). It is unclear what is driving this temporal pattern. It may be due to seasonal migration of some pest species such as *H. zea* or peaks in abundances for other species corresponding with available plant hosts. Alternatively, it may reflect diet diversification within the bat community resulting from partitioning of foraging space and subsequently prey between adults and juveniles at the time of year juveniles become volant. Relative to adults,

newly volant juvenile bats are more likely to utilize open foraging habitats such as crop fields (Adams, 1969) and to consume softer prey items (Rolseth et al., 1994; Hamilton and Barclay, 1998). (Table 1).

Contrary to our expectations, we found little evidence for a strong relationship between the diversity or frequency of pest consumption and landscape characteristics. The only category of pests strongly influenced by any of the geographic factors we investigated were pests of fruit/nut/vegetable crops. The number of such pest species consumed by bats was associated with forage, fruit/nut/vegetable, and corn/cotton production at the largest spatial scale investigated (county). Twenty-one of the pest species consumed by bats are known to use Poaceae grasses or alfalfa as primary hosts and may use these fields as refuges during winter and following row crop harvests (Appendix A; Wilkinson and Landis, 2005). It should be noted that we investigated only landscape composition and not landscape configuration. Given the tendency of many species of bats to forage along edges and use connecting elements such as tree lines, future research should address the impact of these features on pest consumption (Ancillotto et al., 2021). Structurally complex landscapes display increased biodiversity and arthropod density year-round, which may bolster bat populations by providing stable alternative prey resources and increase the time that pest species are available as prey, increasing overall consumption rates by bats (Kalda et al., 2015; Kelly et al., 2016; Ancillotto et al., 2017; Monck-Whipp et al., 2018; Olimpi and Philpott, 2018; Rodríguez-San Pedro et al., 2018; Weier et al., 2018).

Developing bat-friendly farmscape management is critical to maximizing pest consumption services provided by bats. The species in our study that consumed the greatest number of agriculture pest species, *L. seminolus*, as well as others in the Lasiurus genus, roost in the foliage of trees (Menzel et al., 2000). Therefore, although the common practice of installing artificial bat houses to provide supplemental roosting options may enhance abundance of cavity-roosting bats such as *Nycticeius humeralis* and *Myotis austroriparius* (Long et al., 1998, 2006), it is unlikely to recover all pest suppression lost by agricultural expansion and intensification. In addition to installing bat houses, we recommend other management practices including the protection and establishment of natural roosts (e.g., large trees) (Fuentes-Montemayor et al., 2013, 2017; Russo et al., 2018), reduction of artificial light (Zeale et al., 2018), limited use of pesticides to reduce bioaccumulation, the establishment of connective landscape features that serve as flight corridors (Heim et al., 2015), and the establishment of bat-safe water sources (Korine et al., 2016). Reduction in pesticide application and artificial light may be especially important to bat consumption of crop pests during the late summer and fall as bat consumption of pests appears to peak. To augment roosting opportunities for crop-pest feeding bats, we recommend conservation of forest patches in the matrix surrounding crop fields to maximize patches of suitable roosting habitat with large trees.

5. Conclusions

Our results indicate that common species of bats in the Southeastern US regularly consume a variety of agricultural pests including 12 that have never before been documented in bat diets and 16 that have a substantial economic impact (Appendix A). We provide strong evidence that bats play an important ecological role in agroecosystems throughout the southeastern US. We observed pest consumption in all three species studied but observed the highest rates and diversity of pest consumption in *L. seminolus*, a foliage roosting species common to the region. Both within and across species, we observed the highest rates of pest consumption in larger bats suggesting that management actions should prioritize larger species, especially those with jaw morphology suitable for moth consumption, if the objective is to maximize pest consumption services.

Overall, the ability of individual bat characteristics to explain rates of prey consumption indicate that it may be possible to extrapolate pest consumption patterns to species of similar morphology in other regions.

Table 1
Variables used in analyses to identify factors influential to the consumption of arthropod pests by bats and to determine the relative importance of bat characteristics, geographic features, and temporally variable attributes.

Variable category	Variable name	Variable type	Description
Bat	Sex	Categorical	Male, female
	Age	Categorical	Adult, sub-adult
	Reproductive condition	Categorical	Pregnant, lactating, post-lactating, non-reproductive, scrotal male
	Mass	Continuous	Measured to the nearest 0.1 g
	Wing length	Continuous	Estimated to the nearest 0.1 mm
Geographic	Site type	Categorical	Small scale dominant land use/cover: agriculture, hardwood hammock, pinelands, water, open fields
	Landscape type	Categorical	Intermediate scale dominant land use/cover: evergreen forest, deciduous forest, row crops, open water, scrub/grassland
	Farmland	Continuous	Large scale: % cover of farmland in county
	Berries	Continuous	Large scale: % cover of berry crops in county
	Corn/cotton	Continuous	Large scale: % cover of corn or cotton crops in county
	Fruit/nut/vegetable	Continuous	Large scale: % cover of fruit, nut or vegetable crops in county
	Forage	Continuous	Large scale: % cover of forage crops in county
	Latitude	Continuous	Global scale: northing UTM coordinate
Temporal	Time of night	Continuous	Bat capture time: number of minutes past sunset
	Sampling period	Categorical	Early, middle, late
	Precipitation	Continuous	Rainfall, to nearest mm on day of bat capture
	Minimum temperature	Continuous	Minimum daily temperature on day of bat capture

However, the importance of bats as consumers of pests may vary seasonally depending on factors not measured in this study. We found few associations between fine scale land use and the diversity or rates of pest consumption, indicating that management strategies incorporating bats should consider the large spatial scales across which bats travel. Our finding of widespread pest consumption by bats of various sizes and habitat associations contributes to mounting evidence of the important role of bats in suppressing pest populations worldwide, and highlights the need to incorporate bat conservation into integrated pest management programs across diverse agricultural systems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107414.

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