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Detection of Spotted Lanternfly (*Lycorma delicatula*) by Bats: A qPCR Approach to Forest Pest Surveillance

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Abstract: Invasive insect pests pose a significant threat to forest ecosystems. Effective pest management relies on detecting these pests, which can be challenging when populations are sparse, newly introduced, or not easily observable. The spotted lanternfly (*Lycorma delicatula* White), a recent invader to North America, has caused extensive damage across the eastern United States since its introduction in 2014. Conventional monitoring methods, such as traps or visual inspections, are limited in their spatial coverage and may not reliably attract or capture target species. In this study, we explored the potential of bat guano as an additional tool for invasive insect detection. We collected guano samples from five bat species across three forested sites in New Jersey, USA, between 2018 and 2022 and used species-specific quantitative PCR (qPCR) to detect spotted lanternfly DNA. Spotted lanternfly DNA was detected in guano from two bat species: big brown bats (*Eptesicus fuscus*) and eastern red bats (*Lasiurus borealis*). Detection probability was strongly influenced by spotted lanternfly phenology, with higher detection rates occurring during the adult life stage. The detection of spotted lanternfly DNA in bat guano demonstrates the feasibility of using guano analysis as a complementary tool for insect pest surveillance. Integrating guano-based monitoring with traditional methods could enhance insect pest detection efforts across diverse forested and agricultural landscapes.

Keywords: chirosurveillance; eDNA; forest health; bat diet; invasive insects; forest pest management; integrated pest management; biodiversity-based ecosystem services

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1. Introduction

Forests are critically important to both people and the environment [1], providing essential ecosystem services, including extraction of raw materials, purification of air and water, climate regulation, and nutrient cycling [2–4]. These services carry an estimated value of USD 16.2 billion annually [5]. Despite their significance, forest ecosystems are also highly vulnerable to environmental changes driven by both direct (e.g., logging and land clearing activities [6]) and indirect (e.g., climate change, wildfires, and air pollution [7]) human-mediated stressors, all of which significantly affect their condition and functioning [8] and their capacity to provide essential ecosystem services [9–11].

Arguably, one of the most significant threats to forest health is the establishment of invasive insect pest populations and the damage they cause [12,13]. Globally, non-native insects cause USD ~70 billion in forest damages, leading to USD 4.2 billion in losses across 20 million hectares annually in the United States alone [14]. These economic costs arise not only from direct losses due to tree mortality and reduced growth, but also from the significant expenses associated with arthropod pest management and forest restoration

activities [15]. Beyond the economic implications, insect infestations weaken trees, increasing their susceptibility to disease, drought, and other environmental stressors [16]. In extreme cases, widespread die-offs can occur, which can significantly alter ecosystem balance, reduce biodiversity, and impair essential forest functions [13,17]. Left unchecked, invasive insect pests can fundamentally reshape forest composition and reduce resilience to other environmental threats [18]. Given these devastating impacts, effective monitoring and management strategies are critical for protecting forest ecosystems.

Detecting invasive insect pests is crucial for effective integrated pest management (IPM) strategies [19]. Early detection significantly enhances pest management outcomes by allowing for rapid intervention to contain pest populations before they reach outbreak levels. Timely detection can potentially decrease damage by up to 50% compared to delayed management efforts [20]. For example, detection of emerald ash borers (*Agrilus planipennis*, Fairmaire) in Michigan, USA, enabled targeted quarantines and removal of infested trees, slowing the rate of spread into neighboring states [21]. Similarly, rapid identification of red imported fire ants (*Solenopsis invicta*, Buren) in Australia allowed for swift mitigation efforts, saving millions of dollars in damages [22]. Detection, however, can be challenging when insect pest populations are sparsely distributed, newly introduced, or not easily observable. Particularly in dense forest environments, insect pest populations may remain undetected for an extended timeframe, as the complexity of forest structure can make early signs of infestations difficult to spot [23]. Low detection probability of emerging insect pest populations promotes establishment, making management strategies much more difficult [19].

Several monitoring techniques are currently employed for detecting invasive insect pests, each with strengths and limitations. Conventional methods, such as sticky traps, blacklight traps, and pheromone traps, are widely used [24–26]. Sticky and blacklight traps are generalist in nature and can capture a wide range of insect species [27]. Their efficacy, however, can vary depending on environmental conditions such as humidity, temperature, and wind, which influence both trap performance and insect behavior [25]. The detection range of conventional traps is also limited by trap placement, with effectiveness declining over larger areas or in locations with dense vegetation [28]. Pheromone traps are highly species-specific, attracting only the target species, which can enhance detection accuracy and reduce bycatch [29]. However, their reliance on species-specific lures can limit applicability, particularly for invasive species whose pheromones have not yet been identified. Additionally, pheromone traps require substantial labor for deployment, maintenance, and inspection, making them resource-intensive, especially in large or remote areas [30]. Molecular methods, such as environmental DNA (eDNA) and quantitative PCR (qPCR) analysis, have emerged as complementary tools and offer sensitivity and detectability without requiring direct capture [31–34]. Molecular techniques can be costly, however, and they require careful validation to ensure accuracy. Regardless of the surveillance approach employed, low insect density in an area can limit the likelihood of successful detection [35]. Further, insects generally may have a low probability of detection if their behavior is cryptic; therefore, an integration of multiple methods into a comprehensive framework would likely enhance overall detection success.

In this context, insectivorous bats may represent a novel addition to insect pest surveillance strategies. Bats naturally forage over extensive geographic ranges (up to 15 km [36]), crossing various habitat types and sampling diverse insect populations [37]. This broad-ranging behavior allows them to track and exploit insect irruptions, thus potentially acting as biological samplers [38–40]. Leveraging bats for surveillance is particularly promising in forested landscapes where conventional trapping may be limited by accessibility or dense

vegetation. Recent advancements in molecular techniques have enabled the analysis of bat guano to identify prey species, including invasive insect pests [36,40–42].

Several studies have demonstrated the utility of bat guano for monitoring insect communities, particularly in agricultural and forested landscapes. For example, molecular analysis of bat guano has been used to track pest outbreaks in agroecosystems, revealing seasonal shifts in prey availability and pest emergence [41–43]. Similarly, studies have detected invasive pests in bat guano earlier than traditional trapping methods, underscoring the potential for bats to serve as an early-warning system for surveillance [43,44]. These findings suggest that bats may provide complementary data to conventional trapping techniques, particularly in environments where insect pests are difficult to survey using traditional methods.

One invasive insect pest of significant concern in the eastern United States is the spotted lanternfly (*Lycorma delicatula*, White), a hemipteran native to Asia that was first detected in Pennsylvania in 2014 [45]. Spotted lanternflies, once hatched in the spring, develop into four instar stages before reaching their adult stage in July [46]. Adults then feed on the phloem of their host plants, causing significant stress and, in many cases, mortality [47]. The feeding behavior of spotted lanternflies disrupts nutrient and water uptake in host trees, leading to wilting, reduced growth, and increased susceptibility to disease and damage from other insects [48]. Its primary host, the tree of heaven (*Ailanthus altissima*, Mil), is itself an invasive species in the region, resulting in the concurrent spread of both invasive insect and host across the United States [47]. Within their invasive range, spotted lanternflies have expanded their host breadth to exploit several other woody species, including several culturally and economically significant plants such as maple trees, iconic across North America and vital to maple syrup production; walnut trees, valued for their use in furniture-making and nut production; hops, essential to beer brewing; grapevines, critical to the wine industry; and various other fruit trees [45,48–50]. Spotted lanternfly induced mortality of host plants can also have cascading effects on forest ecosystems, disrupting wildlife habitats and reducing overall biodiversity [51]. The ecological and economic impacts of spotted lanternflies have been profound, with annual damage to forest and agricultural crops estimated at $200 million in Pennsylvania alone, a figure expected to rise as the insect continues its spread across North America [52,53].

The spotted lanternfly is difficult to monitor due to its cryptic behavior, wide host range, and the ability of its egg masses to blend into surfaces, such as tree bark and rocks [54]. These challenges are further compounded in forested environments because dense vegetation obscures detection, particularly in low-density populations [55]. Innovative and cost-effective strategies that maximize sampling efficiency are therefore essential for timely intervention.

In this study, we aim to evaluate the role of eastern temperate forest bats as an ecological surveillance tool for detecting spotted lanternfly infestations in forest ecosystems. Corresponding with the recent emergence of spotted lanternflies within the region, we collected guano samples from native bat species for four years at three forested sites in New Jersey, USA, and analyzed them using a previously developed species-specific qPCR assay. Our objectives were to (1) assess whether bats consumed spotted lanternflies and, if so, determine (2) the rate at which spotted lanternflies could be detected and (3) which point in the life cycle spotted lanternflies are most readily detected. For the latter two objectives, we constructed an occupancy model to estimate the probability of detecting spotted lanternfly DNA in bat guano among sites, across years, and throughout their life cycle.

2. Materials and Methods

2.1. Study Area and Survey Methods

From May to late August in 2018 through 2022, we conducted bat mist-net surveys on 71 nights, totaling 213 'trap nights' (3 nets/night) at three forested sites in New Jersey, USA (Figure 1). In 2018, we captured bats at Hutcheson Memorial Forest in Franklin Township, Somerset County (hereafter, Hutcheson). Hutcheson is a 202-hectare parcel owned and managed by Rutgers University and consists of old growth oak–hickory forest (one of the last uncut stands of forest in the mid-Atlantic region), abandoned agricultural fields, and early successional forest. In 2019, 2021, and 2022, we captured bats at Morristown National Historical Park—Jockey Hollow Unit, in Morristown, Morris County, (hereafter, Jockey Hollow) and Rutgers University Ecological Preserve, in Piscataway, Middlesex County (hereafter, Rutgers Preserve). The Rutgers Preserve is a 128-hectare property owned by Rutgers University and consists of mature mixed-oak forest, early successional forest, meadows, and wetlands. Jockey Hollow is a 708-hectare property owned by the National Park Service and consists of mature mixed-oak forest, meadows, and wetlands. Due to COVID-19 restrictions on the capture and handling of bats, no sampling occurred in 2020.

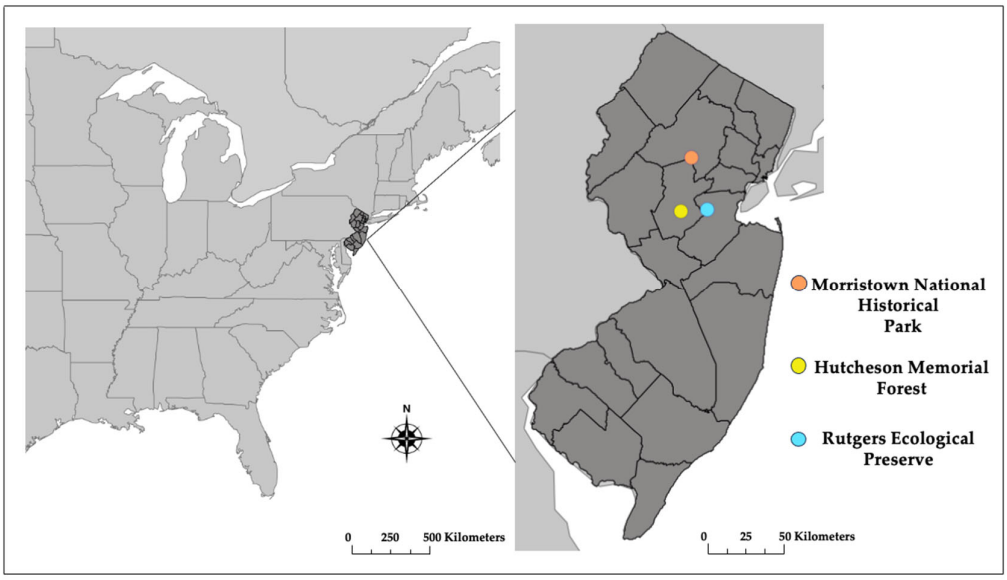

Figure 1. Geographical location of bat survey sites in New Jersey, United States: Hutcheson Memorial Forest in Franklin Township (surveyed in 2018); Morristown National Historical Park in Morristown (surveyed in 2019, 2021, and 2022); and Rutgers Ecological Preserve in Piscataway (surveyed in 2019, 2021, and 2022).

We captured bats on nights when the weather was fair, with temperatures above 10 °C, sustained wind speeds <14.5 km per hour, and chance for precipitation below 30%. On each sampling night, we selected a ~1.5-ha survey location based upon local structural habitat features known to facilitate bat capture [56,57]. In general, survey areas were within close proximity to a water source, and we deployed mist-nets across foraging corridors frequented by bats, such as walking paths and streams. At each survey location, we deployed three triple-high mist-net pole systems (Bat Conservation & Management, Inc. Carlisle, PA, USA), each of which supported three standard two-ply 50 denier nylon nets with a mesh size of 38 mm (Avinet, Inc. Portland, ME, USA) [58]. We operated mist-nets for a 5 h period beginning just prior to the local sunset time, checking nets at 10 min intervals. Upon capture of a bat, we recorded its species and sex. If an individual defecated during these preliminary data collection procedures, we collected a single guano pellet and immediately released the bat. Otherwise, we placed individuals into separate, sterile

cotton cloth holding bags and checked for guano pellets at 5 min intervals. Using flame-sterilized forceps, we transferred each guano pellet into a labeled 1-mL tube containing RNAlater® (Thermo Fisher Scientific, Waltham, MA, USA) ensuring sample stability at room temperature until placement into a −80 °C degree freezer at Rutgers University for long-term storage. Bats were held for a maximum of 30 min between capture and release, and samples were collected under Rutgers IACUC Protocol #PROTO999900205 and all appropriate state and federal permits.

2.2. Laboratory Methods

We extracted DNA from each guano sample using spin column-based Qiagen DNeasy blood and tissue kits (Germantown, MD, USA). We generally followed the manufacturer's protocol, modifying some steps as deemed necessary during the optimization process. The following steps were modified: During the initial extraction step, we removed guano pellets from RNAlater® and placed them into empty 2 mL collection tubes. We added 180 µL of buffer ATL and 20 µL proteinase K to each tube and homogenized guano and reagents using a small pestle. We then vortexed the homogenized mixture for 30 s. To optimize chitinous breakdown and release of DNA from arthropod cells within the guano, we elongated the 56 °C incubation period from 10 min to 24 h. After incubation, we resumed the recommended manufacturer's protocol, with a final elution of 100 µL for higher DNA concentration. We stored DNA extract for up to one week at −20 °C, or at −80 °C if not directly followed by downstream applications.

To determine whether bats consumed spotted lanternflies, we conducted qPCR of each guano sample using a species-specific assay developed by Valentin et al. (2020) [34]. We performed each qPCR reaction in a 96-well plate on an Applied Biosystems 7500 Real-Time PCR system (Applied Biosystems, Life Technologies, Carlsbad, CA, USA), following the published qPCR protocol. Within each qPCR reaction plate, individual wells contained a 20-µL solution consisting of 2 µL of extracted guano DNA, 5.5 µL of denucleated H_2O, 1 µL of each forward and reverse primer, 10 µL of TaqMan Environmental Mastermix 2.0, and 0.5 µL of TaqMan MGB quenched probe. We set thermal cycler parameters at an initial denaturing step of 96 °C for 10 min, followed by 45 cycles of 96 °C for 15 s and annealing and extension at 60 °C for 1 min. We ran samples in triplicate, alongside five serial dilutions from 1/10 to 1/100 k to create a standard curve. In addition, we included negative controls for each laboratory method, consisting of 2 per extraction batch and 1 per qPCR plate for a total of 24 negatives.

2.3. Occupancy Model

To quantify the detection probability of spotted lanternfly DNA in bat guano, we deployed a single-season, single-species occupancy model using the *occMod* function from the RPresence package version 2.13.48 [59]. Occupancy modeling quantifies the probability of species presence while accounting for imperfect detection. Because our objective was to quantify the detection probability of spotted lanternflies in guano given their presence at a site, we only included site-years with at least one spotted lanternfly detection. We recognize that site-years with zero detections could still have spotted lanternflies present but either in small numbers or not yet being preyed upon by native bats. However, including site-years with zero detections would likely falsely penalize the true detection probability when our listed conditions are met. We modeled detection probability (p) as a function of four covariates: pellet count, year, spotted lanternfly phenology, and site. Pellet count represented the number of guano pellets collected on a given survey night and was included to account for sampling effort. Within eDNA studies, it has been shown that increased sampling effort yields higher detection [33,60]. Phenology was recorded as a

binary variable representing the time period in which adults, on average, emerge and are present on the landscape [52]. Because many of the bats in New Jersey are aerial hawking species and consume volant insects, and given that spotted lanternfly larval stages are more sedentary, we expected detection probability to increase when spotted lanternflies were actively flying. In addition, the larger body size of adults relative to larvae may increase the likelihood of bat predation, as larger prey items may be more frequently consumed by bats [61]. Lastly, we included year and site as covariates to account for potential annual or geographic variation in detection probability.

We fit a global model and set occupancy (ψ) as a constant (1), while allowing detection probability (p) to vary with each of the covariates. To identify the best-fit model, we generated a set of 12 candidate models, each representing different combinations of these covariates, including single-variable models and a global model. To evaluate model fit, we applied a bootstrap goodness-of-fit test with 1000 iterations and calculated the overdispersion parameter, $\hat{c} = 1.85$. We adjusted for slight overdispersion and small sample size using the quasi-likelihood AIC (QAICc) [62], ranked models by ΔQAICc, and model-averaged those with ΔQAICc < 4.

To determine if detection probability of spotted lanternfly DNA within bat guano increased annually, we also compared detection probabilities across years using ANOVA. An increase in detection probability over time could relate to growth of spotted lanternfly populations and/or higher rates of predation by bats. In either case, this result would imply that the detection probability of spotted lanternfly in guano is likely to increase as the insect population expands and bats become more accustomed to preying upon them.

3. Results

From 2018 to 2022, we collected 330 guano samples from five species of temperate insectivorous bats. Species representation was highly skewed, with big brown bats (*Eptesicus fuscus*, Palisot de Beauvois) comprising 91.8% (N = 303) of samples. Eastern red bats (*Lasiurus borealis*, Müller) accounted for 5.2% (N = 17) of samples, followed by northern long-eared bats (*Myotis septentrionalis*, Trouessart) at 1.8% (N = 6), silver-haired bats (*Lasionycteris noctivagans*, Le Conte) at 0.9% (N = 3), and a single eastern small-footed bat (*Myotis leibii*, Audubon & Bachman; Figure 2). We detected spotted lanternfly DNA in 10.9% of big brown bat samples (N = 33) and in one eastern red bat sample (N = 1).

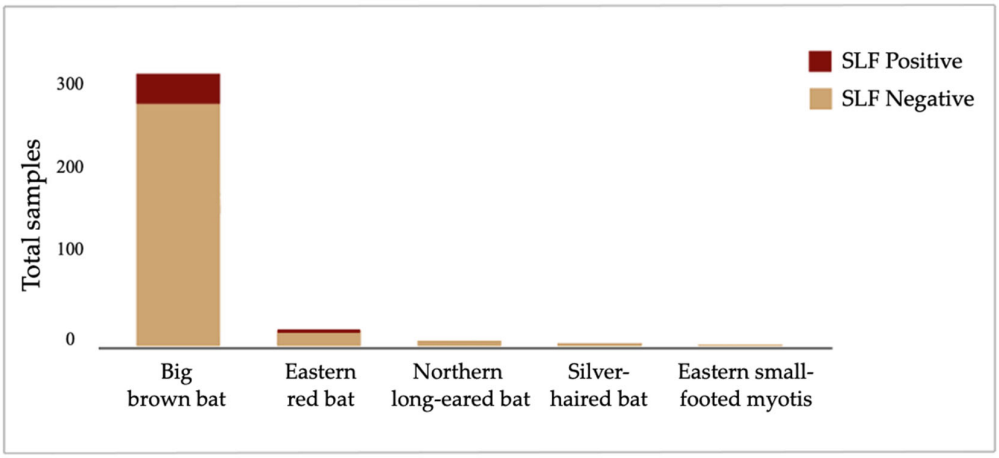

Figure 2. Number of guano pellets collected for each bat species across all sites in New Jersey, United States between 2018 and 2022. Red bars indicate samples which of these samples contained spotted lanternfly (*Lycorma delicatula*) DNA. Tan bars indicate samples that did not contain spotted lanternfly DNA. Note that only the guano of big brown bats and eastern red bats contained spotted lanternfly DNA.

Detection rates for spotted lanternfly DNA in guano varied across sites and years. At Hutcheson, spotted lanternfly DNA was detected in 10.4% of samples in 2018 (5 of 48), with no sampling in subsequent years. At Jockey Hollow, the percent of guano containing spotted lanternfly DNA increased from 25.0% in 2021 (5 of 20) to 26.9% in 2022 (7 of 26). Rutgers Preserve exhibited the highest change in proportions, rising from 12.5% in 2021 (7 of 56) to 29.4% in 2022 (10 of 34). The proportion of positive samples per year overall increased from 10.4% in 2018 (N = 5) to 21% in 2021 (N = 12) and 33% in 2022 (N = 17). The earliest detection of spotted lanternfly DNA in guano occurred in late June and peaked in late July (Figure 3). There were no significant differences in spotted lanternfly detections between males and females (χ^2 = 0.735, df = 1, p = 0.391)

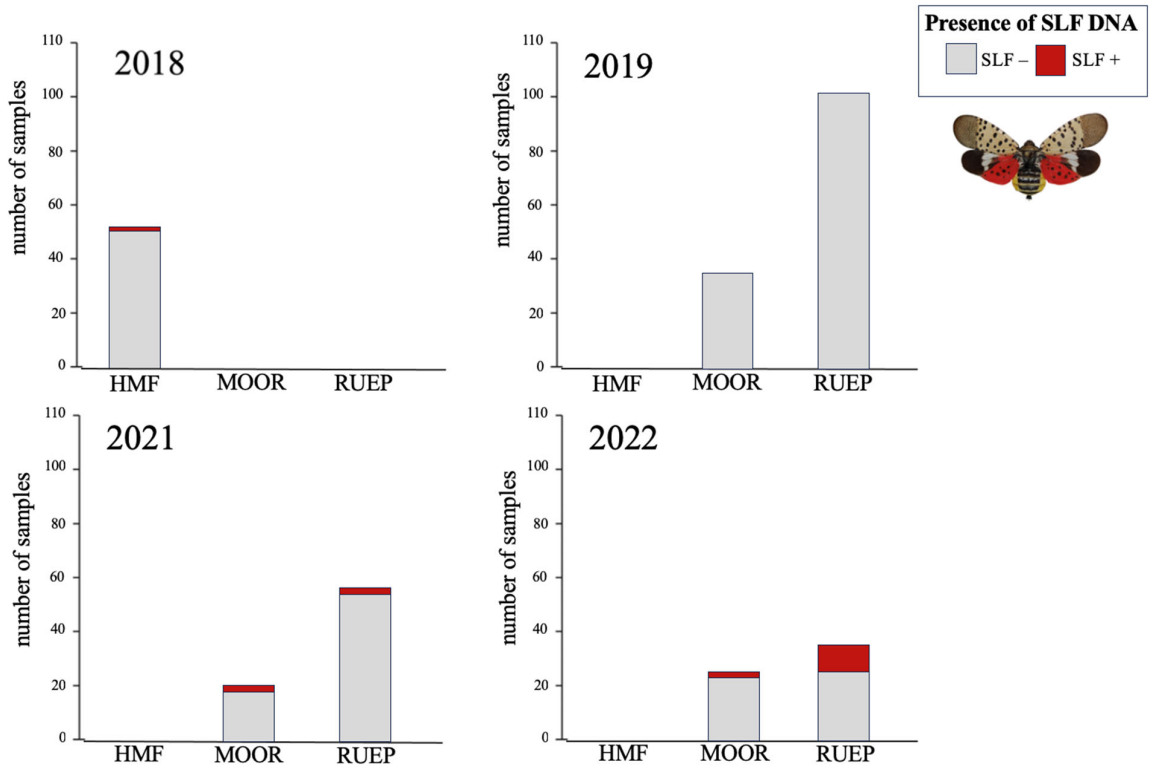

Figure 3. Frequency of occurrence of guano samples in which spotted lanternfly (*Lycorma delicatula*) DNA was detected per site across all years. Spotted lanternfly DNA was detected in (N = 5) samples from sites in New Jersey, United States. Hutcheson Memorial Forest (depicted as HMF), (N = 12) samples from Morristown National Historical Park (depicted as MOOR), and (N = 17) samples from Rutgers University Ecological Preserve (depicted as RUEP). The proportion of positive samples increased from 9% in 2018 (N = 5) to 21% in 2021 (N = 12) and 33% in 2022 (N = 17). We did not detect spotted lanternfly DNA in any samples in 2019. Within the bars of the graph, red represents positive samples, while grey represents samples that are negative for spotted lanternfly detections.

Detectability of Spotted Lanternflies in Bat Guano

Model-averaged beta coefficients from the top models (Table 1) indicated a strong positive effect of phenology (β = 39.83, 95% CI: 13.09–66.56). Detection probability during nymphal stages was low (1.65×10^{-13} to 9.32×10^{-13}) compared to the adult stage, which ranged from 0.58 to 0.76 across site-years. Sampling week 33, corresponding to the adult stage of spotted lanternfly, had the highest frequency of occurrence in pellets containing spotted lanternfly across all samples (Table 2).

Table 1. Top models for predicting detection probabilities of spotted lanternfly (*Lycorma delicatula*) DNA in bat guano. The table includes model name, number of parameters (K), QAICc value, ΔQAICc value, and model weight. Models with ΔQAICc $\leq$ 4 (in bold font) were included in model averaging.

Model	Weight	K	QAICc	ΔQAICc
psi(1)p(Phenology)	**0.349**	**3**	**22.8150**	**0**
psi(1)p(Site + Phenology)	**0.234**	**4**	**23.6176**	**0.8**
psi(1)p(Year + Phenology)	**0.157**	**4**	**24.4169**	**1.6**
psi(1)p(Pellet + Phenology)	**0.127**	**4**	**24.8273**	**2.01**
psi(1)p(Site+Year + Phenology)	**0.077**	**5**	**25.8411**	**3.03**
psi(1)p(Year+Pellet + Phenology)	**0.053**	**5**	**26.5702**	**3.76**
psi(1)p(1)	0	2	31.4944	8.68
psi(1)p(Site)	0	3	32.8820	10.07
psi(1)p(Year)	0	3	32.8874	10.07
psi(1)p(Pellet)	0	3	33.64891	10.83
psi(1)p(Site + Year)	0	4	34.9969	12.18
psi(1)p(Pellet + Year)	0	4	35.0509	12.24

Table 2. Model-averaged effect sizes and 95% confidence intervals for covariates influencing the detection probability of spotted lanternfly (*Lycorma delicatula*) DNA in bat guano. Significant effects in bold type.

Covariate	Effect Size	95% Confidence Interval
Phenology	**39.83**	**[13.09, 66.56]**
Site	0.08	[−0.85, 1.01]
Year	0.14	[−0.46, 0.73]
Number of Pellets	0.02	[−0.10, 0.14]

Modeled detection probabilities across all sites and years, excluding 2019, ranged from 0.32 in 2018 to 0.56 in 2022. An ANOVA comparing detection probabilities across years revealed a significant positive correlation between year and detection probability (estimate = 0.0579, 95% CI [0.0182, 0.0975], p = 0.0189; $F(1, 3)$ = 21.53, R^2 = 0.878). The intercept of the model was estimated at −116.45 (95% CI [−196.63, −36.26], p = 0.0191), indicating that detection probability significantly increased over time (Figure 4).

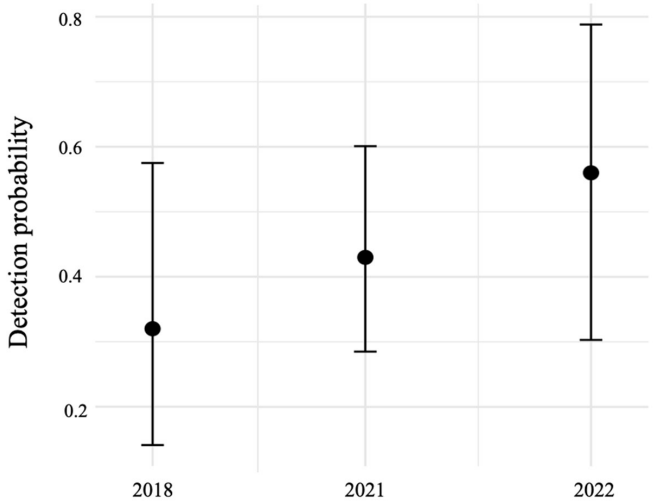

Figure 4. Detection probabilities for spotted lanternfly (*Lycorma delicatula*) in guano samples across all sites in 2018 (0.32 [0.41, 0.575]), 2021 (0.43 [0.285, 0.601]), and 2022 (0.56 [0.303, 0.788]), with error bars representing 95% confidence intervals. Detection probabilities significantly increased over time, as indicated by the positive correlation with year (p = 0.0189).

4. Discussion and Conclusions

Our study confirms that at least two eastern temperate insectivorous bat species prey upon invasive spotted lanternflies, supporting prior research demonstrating that bats opportunistically forage on non-native insects [41,42,44]. Nearly 11% of big brown bat samples contained spotted lanternfly DNA, suggesting that this species recognizes lanternflies as a common dietary item. This result is consistent both with big brown bat skull morphology, which allows for the consumption of large, chitinous insects [43], as well as published literature identifying native planthoppers (e.g., Delphacidae) as a component of big brown bat diets [42]. We also documented spotted lanternfly DNA within a single eastern red bat guano pellet, constituting ~6% of eastern red bat samples. It is possible that eastern red bats occasionally consume spotted lanternfly, but at a lower rate than big brown bats. However, our limited number of eastern red bat captures (N = 17) during this study prevents us from drawing conclusions regarding consumption patterns. Eastern red bats are aerial hawking species that have been documented preying upon medium-sized hemipterans [63,64], so it is plausible that this species consumes spotted lanternfly regularly.

The absence of spotted lanternfly DNA in the guano from eastern small-footed bats, silver-haired bats, and northern long-eared bats is difficult to directly interpret given the low number of samples we were able to collect from these relatively rare species (one, three, and six samples, respectively). It is possible that additional samples would present evidence of spotted lanternfly consumption by any of these three species. However, there are several non-mutually exclusive factors that may make these species less likely to regularly consume spotted lanternflies. First, these bats are smaller than big brown bats and eastern red bats [65] and appear to target smaller insects more commonly [66,67]. Northern long-eared bats have been shown to eat relatively large prey, such as the >40 mm moth family of *Erebidae: Catocala* spp. [61], but the extent to which they target larger prey is not known. Additionally, competition or behavioral interactions with big brown bats during foraging may influence their dietary choices, potentially limiting their consumption of spotted lanternfly when big brown bats are present. Such an interaction has been documented in silver-haired bats, where this species will avoid competition for insects when big brown bats are present in their foraging vicinity [68].

Habitat overlap may also explain the absence of spotted lanternfly DNA in the guano of these three bat species. Spotted lanternflies thrive in forest edge habitats and urban or suburban areas, particularly where its primary host tree is abundant [69]. Individuals typically rest on host trees at heights ranging from ground level to 15 m, often on trunks and higher canopies [70]. While spotted lanternfly adults can fly short distances (~40 m), they lack sustained flight capability [54]. Bats, in contrast, forage across various habitat strata, with species-specific behaviors influencing potential overlap with spotted lanternfly habitats. Most insectivorous bats capture prey in flight using aerial hawking, which may limit their encounters with resting individuals. However, some bat species are known to engage in gleaning, a foraging strategy that involves capturing stationary prey from vegetation, bark, or man-made surfaces [71] Silver-haired bats and eastern small-footed bats tend to forage adjacent to forest edges, suggesting overlap with the preferred habitat of spotted lanternfly [72,73]. However, northern long-eared bats typically forage below the canopy in densely forested areas, which may result in less overlap with spotted lanternfly habitats [74]. Further research and larger sample sizes are needed to evaluate whether habitat use by these bat species aligns with areas where spotted lanternflies are more prevalent.

Spotted lanternflies progress through four nymphal instar stages before reaching their adult stage, with development closely tied to seasonal temperature and host plant availability [70]. Nymphs are typically present from late spring through early summer, while adults generally emerge by early July and remain active until early winter, depending

on temperature [70,75,76]. In our study, 91.2% of positive detections occurred in the late summer between early July and mid-August, suggesting that bats are primarily targeting the adult stage of spotted lanternfly and only infrequently preying upon larval instars, if at all. Spotted lanternfly adults are relatively large hemipterans (~25 mm) with conspicuous coloration and movement [77], and their ability to jump and glide between trees likely makes them accessible prey for both gleaning and aerial hawking bat species. The lack of detections in weeks 34 and 35 (late August) is likely attributable to low sampling effort (only two guano samples obtained across all study years). Big brown bats, however, forage late into the fall [78,79] and likely continue to target spotted lanternfly adults, which remain active into late autumn, often aggregating on host trees where they are accessible to foraging bats. This overlap in activity highlights the potential for bats to play a role in reducing spotted lanternfly populations later in the season.

Despite low detections in guano prior to adult emergence, three positive samples were collected in June (Figure 5). These early detections suggest that bats may occasionally prey upon earlier life stages, or some spotted lanternfly individuals may have emerged as adults earlier in the season. Spotted lanternfly adult emergence is highly variable and influenced by temperature [55], with earlier-than-expected adult emergence potentially influenced by localized heat islands (caused by urbanization or human-altered landscapes) or broader climate trends [80]. Climate change, in particular, is increasingly associated with shifts in insect phenology [80,81]. Warmer temperatures have been shown to accelerate insect development, potentially advancing the transition to adult stages [82]. Changes in precipitation patterns and the length of growing seasons due to climate change may further influence spotted lanternfly development and population dynamics, increasing the variability in adult emergence timing [83]. Alternatively, the late-June detections could be due to bats occasionally preying on late-stage nymphs, particularly the fourth instar, which are larger (12–14 mm) and more conspicuous.

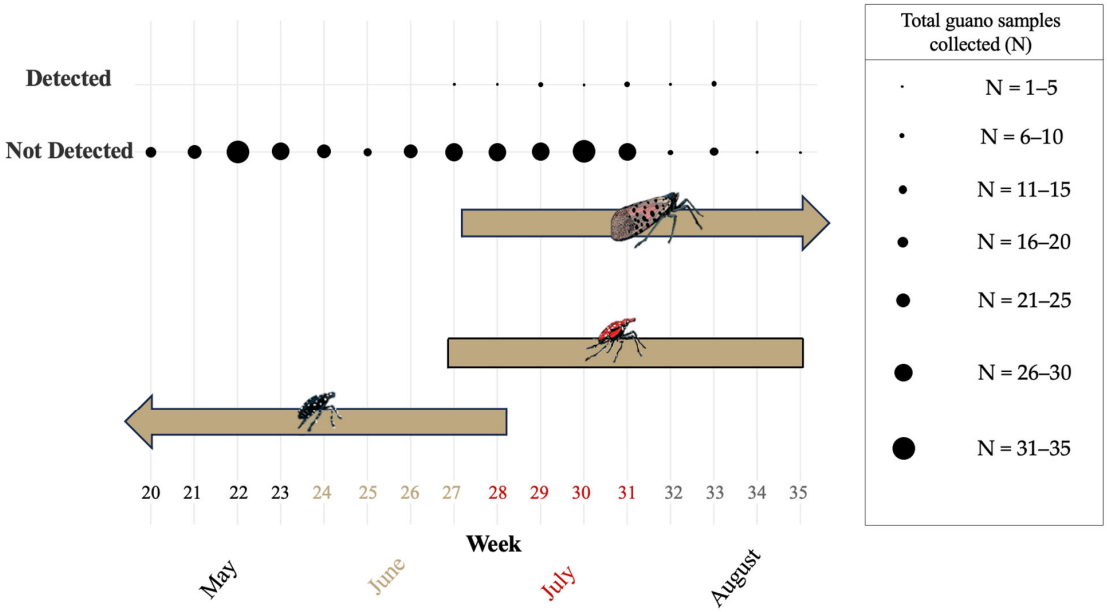

Figure 5. Detection of spotted lanternfly (*Lycorma delicatula*) DNA in weekly bat guano samples collected from 2018 to 2022. Dots represent number of samples collected in each week across the entire study period. Tan bars represent the approximate seasonal phenology of spotted lanternfly life stages. Open-ended arrows indicate that 1st instar nymphs were present prior to the first week of the collection period, or the adults persisted beyond the final collection week. Note: minimal guano sampling occurred during weeks 34 and 35 across years.

Bats adjust their foraging behavior in response to prey availability, tracking fluctuations in insect populations [39,40,84]. Our analysis revealed a significant increase in spotted lanternfly consumption over time, with detection rates correlating with visual detections in New Jersey in 2018 and subsequent population expansion in 2021 and 2022 [77,83]. These results suggest that bats increasingly incorporated spotted lanternflies into their diets as the prey became more abundant and widespread, aligning with previous studies [39,40]. The increasing detection of spotted lanternfly DNA in guano over time suggests that bats may opportunistically exploit this prey species during periods of peak abundance, potentially reducing densities in the landscape, particularly through predation on adults.

Targeting the adult stage of an invasive species can significantly disrupt reproductive cycles and mitigate population growth. For example, removal of adult emerald ash borers and spongy moths through trapping has effectively reduced larval infestations and egg deposition, respectively [21,85]. Spotted lanternflies in New Jersey begin laying eggs in early September and continue through December, overlapping with the active foraging periods of big brown bats and eastern red bats. These species forage in the fall prior to hibernation or migration, aligning their activity with the time when adult spotted lanternflies are most vulnerable to predation during egg-laying [79,86].

Although this evidence of predation alone does not imply impact on spotted lanternfly population growth, bats do exhibit traits that could make them effective top-down regulators of pest species. Their large populations, high metabolism, and ability to alter prey behavior through echolocation can reduce insect reproductive output and density [87–89]. Exclusion studies further demonstrate that bats significantly reduce insect density and herbivory, driving these top-down trophic cascades that are critical for ecosystem health by reducing pest damage [90,91]. With their broad foraging ranges, adaptability to prey availability, and demonstrated effectiveness in controlling other insect pests, bats represent an underutilized but promising natural ally in mitigating the ecological and economic impacts of the spotted lanternfly as it continues to spread across the United States.

The implications of our findings extend beyond understanding bat foraging behavior, offering practical applications for monitoring and managing invasive insects. To capitalize on bat predation as a monitoring tool, guano analysis should be integrated with other surveillance methods (i.e., blacklight traps and visual surveys) to provide complementary data during periods of high pest activity. As molecular tools have advanced, analyzing bat diets through guano has gained traction in ecological research [43,63,83,92]. Techniques like qPCR offer high sensitivity and specificity for detecting target DNA, even at low concentrations [93]. Beyond its technological strengths, guano analysis also has practical advantages. It is less resource-intensive than deploying and maintaining extensive networks of traps, making it a cost-effective and environmentally non-invasive complementary tool [94]. Unlike traditional trapping methods, which may inadvertently capture non-target species [95], guano analysis avoids direct interference with insect populations. This non-invasive approach is particularly advantageous for monitoring cryptic or sparsely distributed pests that are difficult to detect through visual inspections or conventional traps and may help bolster these existing detection methods.

While advantageous, collecting guano from individual bats can be time-consuming and labor-intensive. However, the natural tendency of many bat species to congregate at communal roosting sites provides an efficient alternative. These roosting sites, often easy to locate and revisit, allow researchers to collect large quantities of guano with minimal disturbance. Although individual bats were sampled in this study, big brown bats often exhibit roost site fidelity [96], facilitating repeated guano collection across seasons. This consistency offers valuable opportunities to monitor invasive species like the spotted lanternfly over broad spatial and temporal scales.

Benefits notwithstanding, limitations do exist. First, guano analysis depends on the consumption of target species by bats, which may vary across regions, seasons, and bat species [71]. This reliance introduces uncertainty when target pests are not consistently or preferentially consumed [41]. Additionally, while qPCR of guano is a powerful tool, it can only detect prey that has already been consumed rather than providing real-time pest activity data [34]. This limitation may delay immediate management responses in cases of rapid pest outbreaks. Finally, molecular analyses can be resource-intensive, requiring specialized equipment, expertise, and validation to ensure the reliability of results [97]. These constraints highlight the importance of using guano analysis as a complementary tool, rather than a standalone solution, integrated alongside other established monitoring methods such as trapping and visual surveys.

Future research should optimize species-specific qPCR assays to improve detection sensitivity for invasive insects and ensure consistency across environmental contexts. Expanding sampling across more sites and time points to clarify seasonal trends in bat consumption of spotted lanternflies. Additionally, correlating qPCR detection frequencies with independent population data from conventional trapping could improve the reliability of guano analysis as a tool for estimating relative prey abundance. Metabarcoding offers another avenue for improving guano-based monitoring by detecting a wider range of prey species [92]. While qPCR is highly specific, metabarcoding could identify co-occurring invasive species and ecologically important taxa [98]. Integrating these methods may enhance pest surveillance by providing both targeted and broader ecological insights.

Collaborative research efforts could further expand guano-based monitoring by integrating it into larger pest surveillance networks. Pairing guano analysis with remote sensing of habitat use and spotted lanternfly host tree distribution could help identify hotspots of bat–pest interactions. Additionally, partnerships with forest managers and pest control agencies could refine monitoring protocols that leverage bats' natural foraging behaviors to support management strategies.

As invasive insect threats continue to grow with climate change and habitat alteration [99,100], future studies should assess how the environmental variability influences both pests and bat populations. Investigating the effects of temperature, precipitation, and land use changes on spotted lanternfly phenology and bat foraging behaviors could refine guano-based monitoring strategies. Addressing these research gaps will help maximize the ecological and economic benefits of integrating molecular techniques into pest management frameworks.

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Data Availability Statement: Raw data associated with this paper are stored within Rutgers Libraries Data Portal, which maintains all Rutgers-associated datasets. These data are freely available through the portal. Molecular data are available in processed form upon request.

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