Short Communication

Indirect impacts of invaders: A case study of the Pacific sheath-tailed bat (Emballonura semicaudata rotensis)

Jessica Nicole Welch *, James A. Fordyce, Daniel S. Simberloff

Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN, USA

ABSTRACT

Although many indirect consequences of biological invasions are plausible, few studies test hypotheses for management of threatened taxa. A case study of the endangered Pacific sheath-tailed bat (Emballonura semicaudata rotensis) illustrates the importance of investigating indirect effects of invasion on species of conservation concern. We hypothesized that two invaders, feral goats and Lantana camara, would indirectly affect the bat by decreasing availability of suitable resources. Specifically, that microclimate and bat prey abundances in lantana shrub differ from native forest habitat, and that preferential browsing by goats structures forests to be less suitable for bats. Our results suggest that bats avoid lantana shrub. However, we found no evidence that preferential goat browsing influenced bat activity. Our research implies that the impact of lantana on the persistence of the bat has been underestimated and that it is unclear how goats alter bat habitat aside from reducing understory vegetation. Future managers should prioritize efforts that restore native forest and reforest areas currently dominated by lantana. We urge conservation scientists to evaluate indirect effects of invasive species and publish findings that elucidate the consequences for native populations.

© 2016 Published by Elsevier Ltd.

1. Introduction

Global conservation for bats is needed: 15% of species are listed as extinct or threatened, 17% do not have a threat status owing to insufficient data, and over half have unknown population trends (IUCN, 2015). Moreover, bats are an oddity among mammals in that roughly a quarter of species are island endemics (Jones et al., 2009), making them important members of island communities. Given uncertainty regarding population viability and their significant contribution to island diversity, research on threats to bats is a priority for conservation (Mickleburgh et al., 2002).

Endangerment and extinction occur disproportionately on islands, in part owing to island systems vulnerability to invaders (Gimeno et al., 2006). Biological invasion can have profound ecological and socio-economic impacts of isolated ecosystems (reviewed in Reaser et al., 2007). Studies on how biological invasions affect bats have focused on direct interactions, such as predation and epidemiology of introduced pathogens (e.g., Fritts and Rodda, 1993; Rodriguez-Duran et al., 2010). Few have evaluated indirect effects — how interactions between coexisting species are affected by another species (Strauss, 1991) — on bats.

The Pacific sheath-tailed bat (Emballonura semicaudata) is a small insectivore designated “endangered” because its geographic area is <5000 km² and highly fragmented (Bonaccorso and Allison, 2008). Emballonura semicaudata rotensis is a subspecies formerly distributed across limestone islands of Guam and the Commonwealth of the Northern Mariana Islands (CNMI) but now present only on the uninhabited island of Aguiguan (Wiles et al., 2011). The estimated 500 individuals of E. s. rotensis are commonly detected in forests and roost primarily in three caves (Wiles et al., 2011). Consequently, E. s. rotensis is highly vulnerable to stochastic demographic and environmental events.

Unconfirmed threats to E. s. rotensis include invasive species (Berger et al., 2005). Shrub covers at least 20% of Aguiguan (150 ha) and is dominated by lantana (Lantana camara) (Amidon, 2009), a “top 100” invasive species (IUCN, 2001). Many studies have shown that lantana can greatly alter native community structure (see review by Sharma et al., 2005), though its impacts on Aguiguan remain unstudied. Feral goats (Capra hircus) were introduced to Aguiguan during the mid-1800s (Butler, 1992), and their density has reached over 200 individuals per square kilometer (Esselstyn et al., 2002), earning Aguiguan the nickname “Goat Island”. The detrimental effects of goats on Aguiguan’s native species are largely anecdotal.

Here, we consider the conservation of E. s. rotensis to illustrate indirect impacts of invasion. We hypothesized that goat browsing and lantana spread indirectly impact E. s. rotensis by altering habitat structure and prey abundances. To evaluate our hypotheses, we ask: (1) Do bats behave differently in lantana shrub than in native forest, and what
factors account for this pattern? and (2) Does native understory cover indicate goat browsing, and is bat activity related to the structural complexity of native forest?

2. Methods

2.1. Study system

We conducted this study on Aguiguan, CNMI, (14°51’N, 145°33’E) from May 28 to June 14, 2013. The 7.09 km² island consists of three concentric limestone plateaus (Fig. 2). Native limestone forest occurs primarily along the smaller terraces of the island and on steep slopes. The dominant native tree species are *Pisonia grandis*, *Cynometra ramiflora*, and *Guamia mariannae* (Esselstyn et al., 2002). Exotic grasses, *Jatropha gossypiifolia*, and *Chromolaena odorata* seedlings are interspersed with lantana across portions of the shrub habitat (hereafter, lantana shrub). Before the 1930s Aguiguan was covered mostly in native forest, but lantana shrub is now extensive on the central plateau of the island where vegetation was cleared during Japanese occupation (Butler, 1992). We performed all statistical analyses in the R statistical computing environment (v3.0.3, R Development Core Team). The supplemental materials provide details of our study design.

2.2. Indirect effects of lantana

If lantana shrub provides an unfavorable microclimate for *E. s. rotensis*, lantana spread could indirectly affect bats as a consequence of it replacing native forest (Fig. 1). Lantana shrub forms a dense monoculture with no canopy cover and little windbreak. Previous surveys on Aguiguan detected *E. s. rotensis* in forests (Esselstyn et al., 2004; Gorresen et al., 2009), where the microclimate is probably more suitable for a small bat (e.g., Rydell, 1991). Lantana shrub has likely limited the expansion of native forest on Aguiguan because lantana is allelopathic (Gentle and Duggin, 1997), has bird-dispersed seeds (Turner and Downey, 2008), flourishes in disturbed environments (Duggin and Gentle, 1998), and ungulates avoid its unpalatable foliage (Sharma et al., 2005). Moreover, patches of lantana expand within native forest as it has invaded treefall gaps opportunistically (Amidon et al., 2014).

To test if bat activity differed between native forest and lantana shrub, we recorded bat calls using acoustic detectors at six pairs of

![Fig. 1. Hypotheses for the indirect effects of invaders, feral goats and Lantana camara, on Emballonura semicaudata rotensis. Dashed lines signify indirect interactions and solid lines signify direct interactions. The arrow points to the resource user. The red path shows an interaction chain: lantana reduces native forest, which affects insect abundance and composition, which affects bat behavior. The blue path shows another interaction chain: lantana reduces native forest, which affects bat behavior. The green path shows exploitative competition: preferential browsing by goats change the structure of native forest, which affects bat activity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)](image-url)
sites — each pair consisting of a forest and shrub habitat. Sites were monitored for three consecutive nights. We determined bat activity using the acoustic activity index (Miller, 2001), a tally of the number of one-minute recording intervals per night containing two or more consecutive bat call pulses. We compared bat activity between native forest and lantana shrub using a hierarchical Bayesian model where the number of bat calls recorded in each habitat was modeled as being drawn from a binomial distribution described with parameter $p$. We assumed that the binomial parameters characterizing each pair of sites were drawn from a beta distribution that represented island-level activity between the two habitats (Fordyce et al., 2011). To determine which environmental factors correspond with bat habitat use, we recorded the elevation of each site and its distance to the nearest of three caves housing bats as well as nightly weather. We measured on-site temperature at thirty-minute intervals, and we retrieved hourly wind speed (knots) and sky conditions (METAR) for each sampling night from the Saipan International Airport Weather Station, the nearest weather station recording nightly conditions. We calculated Spearman’s rank correlation coefficient to examine the relationship between these environmental factors and bat activity (R package “coin,” Hothorn et al., 2008).

Irrespective of how appropriate lantana shrub microclimate is, lantana spread could also indirectly affect bats if the habitat does not support the bat’s insect prey (Fig. 1). Examination of E. s. rotensis fecal material showed that bats consume high volumes of wasps, moths, and beetles (Valdez et al., 2011). The interactions between lantana and Aguiguan’s native insects have not been examined, but lantana flowers might attract bat prey, especially moths (Sharma et al., 2005). Conversely, processed lantana has been used as a larvicide and insect repellent (Ogendo et al., 2006), so lantana shrub might not support every prey species.

To determine if abundances or composition of nocturnal, flying insects differed between native forests and lantana shrub, we sampled insects synchronically during bat acoustic monitoring using a miniature blacklight trap and an aerial malaise trap with a bottom collector approximately 50 m from each of the acoustic detectors. We identified insects at least to order and calculated abundance and richness for each night. For each sampling night and site, we summed insect abundance by taxonomic order. We used distance-based redundancy analysis to determine if insect composition differed between native forest and lantana shrub (Legendre and Anderson, 1999). We used a hierarchical Bayesian model to compare the abundance of each insect order between native forest and lantana shrub, where insect abundance at each of the paired sites was modeled as being drawn from a binomial distribution with a beta prior (Fordyce et al., 2011). To determine how bat activity corresponds with insect abundance, we calculated Spearman’s rank correlation coefficient for each pair of sites (R package “coin”, Hothorn et al., 2008). To elucidate if intrinsic habitat factors or insect availability drives bat activity, we performed a redundancy analysis to relate bat behavior, as measured by call characteristics (Table A4), to habitat and insect abundance (R package “vegan”, Oksanen et al., 2013).

2.3. Indirect effects of goats

Goats might indirectly affect bats by reducing native forest habitat, because goat browsing can impede regeneration of vegetation (Scowcroft and Hobby, 1987) (Fig. 1). Goat numbers on Aguiguan are reportedly too high to allow seedling recruitment (e.g., Esselstyn et al., 2002; Amidon et al., 2014), although this conclusion is based on circumstantial evidence. To determine if goats are responsible for low understory recruitment on Aguiguan, we counted the number of seedlings <1 m tall within a random 2 m diameter circle at ten locations in Aguiguan forest. For comparison, we counted seedlings in native forests of Tinian, a populated island approximately 8 km NE of Aguiguan that shares a similar history of habitat degradation (Berger et al., 2005). In particular, we sampled in an area of native forest of approximately 0.5 km² that was historically browsed by goats and areas that had no history of goat browsing. We used a generalized linear model with a Poisson distribution to relate forest seedling counts to goat presence.

Goats might also indirectly affect bats through preferential browsing, which can affect habitat structure (Larkin et al., 2012). The proportional abundance of plant species can reflect their relative palatability to herbivores (Parsons et al., 1997), and changes in habitat structure owing to browsers can influence vertebrate species presence (e.g., Plana and Marsden, 2014). On Aguiguan, species of seedlings that appear frequently have been presumed unpalatable to goats (Esselstyn et al., 2002), but measurements of forest structure beyond height and trunk diameter have not been reported. Habitat structure is relevant to managing E. s. rotensis because dense vegetation can hinder bat maneuverability (Miller et al., 2012) and prey detection (Arlettaz et al., 2001). E. s. rotensis wings are long and have above average aspect ratio and low wing loading, which suggests slow hawking in open spaces (Norberg and Rayner, 1987). Therefore, bats might avoid areas within
forests where goat browsing has favored growth of plants that create high structural complexity (hereafter, clutter) (Brigham et al., 1997).

To determine relative preferences of tree vegetation for goats, we performed a cafeteria experiment (i.e., free-choice feeding) on 10 captive goats from the feral population on Aguiguan using leaves of three dominant native forest tree species, *P. grandis*, *C. ramiflora*, and *G. mariannae*. We chose these species because a previous vegetation survey (Esselstyn et al., 2002) suggested that *C. ramiflora* and *G. mariannae* dominate the small tree size classes because goats do not eat them and that other species (e.g., *P. grandis*) have low regeneration because goats eat them. We determined the percentage of each species of leaves remaining at the end of each trial, then coded the percentage as follows: 4 = 75–100%, 3 = 50–75%, 2 = 25–50%, 1 = 0–25%. We used a hierarchical Bayesian model to compare consumption of the three tree species by goats, where the percentage of each tree species leaves remaining after each trial was modeled as a multinomial distribution described with a theta prior (Fordyce et al., 2011).

To determine if habitat structure is related to bat activity, we recorded vegetation characteristics at each native forest site within 15 m of the acoustic detector. In particular, we used measurements of *P. grandis*, *C. ramiflora*, and *G. mariannae* (the three species used in the cafeteria experiment above) to estimate relative amounts of clutter at three-meter height intervals. Because these trees vary in densities and branching heights, we expected that bat activity would reflect clutter amount owing to preferential goat browsing. In particular, we predicted that bat activity would be low at locations with high amounts of *G. mariannae* because we have observed that this species creates high clutter in the forest understory relative to the other two tree species. We calculated Spearman’s rank correlation coefficient to determine the relationship between bat activity and habitat structure (Table A7) (R package “coin”, Hothorn et al., 2008).

3. Results & discussion

3.1. Do bats behave differently in lantana shrub than in native forest, and what factors account for this pattern?

Bats were more active in native forest than lantana shrub (probability of recorded calls in native forest > lantana shrub = 0.993; Table A2; Fig. A1), though bats were not detected at every native forest site (Fig. A2). Considerable differences in bat activity across native forest sites support the hypothesis that within-habitat structure is an important consideration for species management (Sharma et al., 2005). Bats were relatively inactive in lantana shrub when temperature was high (ρ = −0.198, *P* = 0.009; Table A3) and wind was strong (ρ = −0.199, *P* = 0.006). Strong winds likely inhibit bat navigation in lantana shrub, and inactivity during the high temperatures (relative to nightly averages) at dusk and dawn likely indicates retreat into the cover of forest. Given this interpretation, microclimate seems a reason-able explanation for low bat activity in lantana shrub. Contrarily to Gu rresen et al. (2009), we found no strong correlation between bat activity and distance to known roosts (ρ = −0.007, *P* = 0.993). Moreover, elevation was not related to activity (ρ = −0.282, *P* = 0.369), which indicates bats are not limited in their distribution across Aguiguan.

Overall insect abundance was higher in native forest than lantana shrub (P(native forest > lantana shrub) = 0.99; Table A2; Fig. A3), and habitat explained 29% of variation in insect community composition (*F*1,16 = 4.049, *P* = 0.015). Given their variety of insect prey (Valdez et al., 2011), we assume that *E. s. rotensis* will pursue flying insects that are the appropriate size for the bat to handle. Median body length of all insects captured was 4.5 mm (range of 1–16 mm), likely the size of insects consumed by *E. s. rotensis* given its <7 g body weight (Wiles et al., 2011).

There were more dipterans, hymenopterans, and neuropterans in native forest (all P(native forest > lantana shrub) > 0.900, respectively; Table A2), but more isopterans in lantana shrub (P(native forest < lantana shrub) = 0.933). High abundances of hymenopterans and microlepidopterans in native forest, where bats are most active, concur with an earlier study showing that these insects make up a large volume of the bat’s diet (Valdez et al., 2011). Although only a small percentage of their diet consisted of dipterans, it is possible that bats eat a larger volume of these, but soft bodies are not easily located within the bats’ feces (Dickman and Huang, 1988). There was no difference between habitats in beetle numbers though they were frequent in bat fecal pellets. Additional studies on the diet of bats, seasonal variation of insect abundances, and plant-insect interactions will elucidate possible indirect impacts of changes in forestation on bats via declines of tree species important to the bat’s particular phytogenous prey.

We recorded 83 feeding buzzes (i.e., a rapid number of call pulses within a short period that indicates a bat encountering prey; Griffin et al., 1960), 92% of which were in native forest. We found a moderate positive correlation between bat activity and insect abundance (ρ = −0.566, *P* < 0.001). Forty-five percent of variation in bat calls was explained by habitat (*F*1,16 = 15.269, *P* = 0.001; Table A4; Fig. A4) with call duration correlating positively with lantana shrub (Fig. A5), but we failed to detect a relationship between call parameters and insect abundance (R² = 0.08, *F*1,16 = 2.867, *P* = 0.093). We interpret these results to suggest that habitat is a stronger driver of *E. s. rotensis* behavior than is insect abundance. Accordingly, the correlation between bat activity and insect abundance might reflect a corresponding reliance on native forest microclimate (Peng et al., 1992).

3.2. Does native understory cover indicate goat browsing, and is bat activity related to the structural complexity of native forest?

Our results show that the understory of Aguiguan has very few seedlings compared to both historically browsed and unbrowsed native forests on Tinian (X² = 352.38, df = 1, *P* = 0.001; Table A5), which suggests that goats limit regeneration of vegetation on Aguiguan. Although we did not confirm the species of seedlings, previous studies show that most seedlings in Aguiguan’s native forest are *G. mariannae* and *C. ramiflora* (Esselstyn et al., 2002), curiously, *G. mariannae* has very high and *P. grandis* has very low densities in native forest understory across Guam and the CNMI regardless of browsing history (Mueller-Dombois and Fosberg, 1998). Moreover, anecdote and aerial photographs suggest that the perimeter of native forest has not receded despite heavy understory browsing by goats.

Goats strongly preferred *P. grandis* and *C. ramiflora* foliage (low clutter tree species) over that of *G. mariannae* (high clutter tree species) (P(*P. grandis > G. mariannae*) = 0.99, P(*C. ramiflora > G. mariannae*) = 0.997, P(*P. grandis > C. ramiflora*) = 0.76; Table A6). Bat activity correlated negatively with total stem count (ρ = −0.812, *P* = 0.03) and positively with average canopy height (ρ = 0.998, *P* = 0.006), but there was no relation to tree species except for one anomaly (*C. ramiflora* crown volume 3–6 m (ρ = −0.841, *P* = 0.043); Table A7). This is consistent with our hypothesis that bats are more active in less cluttered forests (Gorresen et al., 2009), but not that they are affected by the clutter of particular tree species. The lack of an effect suggests that other processes are the main determinants of habitat structure on Aguiguan, or that there is a complicated interplay between goat browsing and natural disturbance on forest dynamics (e.g., Rojas-Sandoval et al., 2014). Nevertheless, because *E. s. rotensis* forages in spaces with low clutter, processes that reduce availability of open forest decrease the amount of suitable bat foraging habitat.

4. Conclusion

To improve management of endangered species, a first step is to identify and alleviate ongoing threats. Although indirect impacts of invasive species on native populations are plausible in many cases, most proposed consequences of invasion lack supporting research. Our results indicate that indirect impacts of lantana on the population of *E. s.
rotensis has been underestimated. Bats are largely inactive in lantana shrub, where the microclimate is harsh and prey are scarce, making remaining tracts of Aguiguan’s native forest a vital resource. Although goats can be strong drivers of habitat change, it is unlikely that browsing alone will cause native forest to disappear. By contrast, if lantana impedes growth of native trees, the extent of forested habitat on Aguiguan might gradually recede, making lantana spread a concern beyond the context of E. s. rotensis conservation. Because the range of E. s. rotensis is currently limited to Aguiguan, declines of the population’s carrying capacity owing to a lack of suitable resources might lead to demographic and genetic problems associated with small population size (e.g., Shaffer, 1981).

Conservation assessments for E. s. rotensis advise that goats should be eradicated in order to conserve bat habitat (Berger et al., 2005). Still, it is unclear how goats alter Aguiguan’s native forest aside from reducing understory vegetation, because forested habitat remains despite high goat densities over the past 200 years. Aguiguan’s juridictive authority strongly enforces regulations to preserve the goat population, making permanent removal of goats unlikely without substantial evidence of harm to endangered fauna. No management strategies have been implemented for removing or managing lantana on Aguiguan, even though lantana is considered a serious pest in similar environments (Day et al., 2003). We support removal of goats, as this would undoubtedly lead to an increase in native vegetation (e.g., Kessler, 2011), but we insist that lantana should also be managed and subsequent reforestation should be attempted in order to restore E. s. rotensis habitat on Aguiguan.

Though the notion is untested, goats might negatively affect native vegetation and facilitate lantana spread because goats do not browse lantana (“indirect mutualism” in Wootton, 1994). In fact, a study on plant community succession found that lantana persisted longer in cleared plots with subsequent goat browsing than without (Larkin et al., 2012). We recommend long-term goat exclusion plots to characterize the regrowth of vegetation, and to examine if regeneration of native species is possible in lantana shrub if goats are absent. Additionally, wildlife managers should limit disturbances that might favor lantana spread. Multiple invaders within a community can affect the assemblage of native communities and alter interactions among native species (Kuebbing et al., 2013). Investigating interactions between common invasives species, like goats and lantana, will undoubtedly have broad relevance to invasion biology and conservation management.

We have found that indirect effects of an exotic plant and vertebrate herbivore might jeopardize long-term persistence of an endemic, endangered bat. The ubiquity of invasion by feral goats and Lantana camara makes our study relevant to conservation biology worldwide, and adds to the burgeoning topic of indirect effects. More generally, we contend that scientists should more frequently examine indirect effects of invasive species on threatened taxa.

Acknowledgments

We thank the following for their expertise and logistical assistance on this project: Gary McCracken, Tammy Mildenstein, Haldre Rodgers, Ton Castro, Anthony Deleon Gurerro, Commonwealth of the Northern Mariana Islands Department of Fish and Wildlife, Mayor’s Office of Tinian. We thank Zach Marion, St. Thomas LeDoux, and anonymous reviewers for assistance with the manuscript. Funding: This work was supported by Sigma Xi [grant number G20120315161439]; Bat Conservation International [grant number A15-024-001].

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.bioccon.2016.07.004.

References


