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10/04/2012 11:56 AM

To: midwestwindhcp@fws.gov
cc:
Subject: Wind Energy and Bats Public Comment

To whom it may concern:

Firstly, I would like to apologize for my tardiness in submitting this comment. While I initially misread the end-date for public comment as being October 11th, I feel very strongly that I ought to voice my support for a strategy to minimize harm to wildlife while supporting renewable energy sources regardless of time frame. As an aspiring biologist, I am aware of many of the challenges faced by policy makers when it comes to reconciling the often conflicting interests of a varied set of stakeholders. I wish all of you at the Fish and Wildlife Service the best as they confront the changing landscape of the 21st century.

I recently flew from Salt Lake City to Pittsburgh with a brief layover in Chicago. It was as we began the descent into Midway Airport that I saw a plethora of wind turbines cozily nestled into an agricultural landscape. While Chicago is renown as "the windy city," many other areas across the interior of the continent have as of yet untapped wind energy potential. As more areas are converted into potential revenue sources, it is important to consider what we might stand to lose if a comprehensive plan to mitigate the negative ecological effects of wind turbines is not established forthright.

I have attached an article by Dr. Justin Boyles which attempts to express the economic benefit of bats in the United States. This estimate extrapolated from the bat population of Texas and cotton industry, placed the value of bats to the agricultural industry is roughly \$22.9 billion annually in reduced pesticide costs. However, they reasoned that the estimate could be over fifty-billion annually. This does not include the recreational values of bats as either as tourist attractions or mosquito abatement. Given the drawn out life history of bats with their low fecundity and longevity, populations are slow to recover. I would suggest that in low wind speed conditions, particularly in agricultural areas where wind farms can be situated, that curtailment is especially important, both to farmers and ultimately consumers in costs, financial and physical from the decreased demand for pesticides.

I'm certain you are aware of the Bats and Wind Energy Cooperative (www.batsandwind.org). Several scholarly publications regarding curtailment options have been published there, including one which compared the operational cost of raising the minimum wind speed operation for turbine rotation and electricity generation. The attached article by Dr. Edward Arnett displayed that this curtailment option significantly reduced nightly bat mortality by as much as 90% but had a marginal cost to the utility of only 1% of their annual income. Another study found that ultrasonic deterrents similarly reduced mortality, though not to as great a degree. As a consumer of electrical energy, I would be willing to pay a marginally more expensive utility bill each month for such a reduction in needless death. One of the reasons why sustainable energy sources such as wind, solar, and geothermal energy are so popular with the public is that they are substantially less detrimental on our environment than carbon-emitting energy sources. While I feel that curtailment at low wind speeds and deterrents should be necessary at all wind farms, I particularly feel they should be enforced where endangered, threatened or migrating species occur.

There exists a plethora of literature published which details the composition of bat communities, established by both acoustic analysis and capture techniques, at sites prior to wind farm construction. I see this as a positive trend which should be continued, perhaps even mandatory. The importance of daily, standardized searching procedures for bat and bird carcasses below wind turbines cannot be emphasized enough. While we know that flying animals are killed by these machines, we cannot truly understand the full impact without daily searches which can provide species, age, and local weather information which might better help us to fully understand the impact. These searches should be daily during the summer months when peak activity occurs to prevent underestimation due to decomposition, scavengers, or human error. The data gained from such surveys should be shared so that scientists may better understand population-level effects and inform policy decisions.

I have also included an articles about the importance of bats to ecosystem function, but I am sure the Fish and Wildlife Service is well aware of the vital importance played by these amazing creatures with unfortunate publicity.

Thank you for listening,

Derek Allen



Boyles et al. 2011_ Bats Economic Importance.pdf



Kunz et al. 2011_ Bat Ecosystem Services.pdf



Arnett et al. 2011 Altering turbine speed.pdf



Deterrent 2009-2010 Field Study Final Report wind.pdf

Altering turbine speed reduces bat mortality at wind-energy facilities

Edward B Arnett^{1*}, Manuela MP Huso², Michael R Schirmacher¹, and John P Hayes³

Wind-turbine operations are associated with bat mortality worldwide; minimizing these fatalities is critically important to both bat conservation and public acceptance of wind-energy development. We tested the effectiveness of raising wind-turbine cut-in speed – defined as the lowest wind speed at which turbines generate power to the utility system, thereby reducing turbine operation during periods of low wind speeds – to decrease bat mortality at the Casselman Wind Project in Somerset County, Pennsylvania, over a 2-year period. Observed bat mortality at fully operational turbines was, on average, 5.4 and 3.6 times greater than mortality associated with curtailed (ie non-operating) turbines in 2008 and 2009, respectively. Relatively small changes to wind-turbine operation resulted in nightly reductions in bat mortality, ranging from 44% to 93%, with marginal annual power loss ($\leq 1\%$ of total annual output). Our findings suggest that increasing turbine cut-in speeds at wind facilities in areas of conservation concern during times when active bats may be at particular risk from turbines could mitigate this detrimental aspect of wind-energy generation.

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Wind-energy development is rapidly increasing worldwide, owing to concerns about climate change and the increasing financial costs of and long-term environmental impacts from fossil-fuel use (Pasqualetti *et al.* 2004; Arnett *et al.* 2007). Although wind-generated electricity is renewable and generally considered environmentally “clean”, extensive fatalities of bats have been recorded at wind facilities worldwide (Dürr and Bach 2004; Kunz *et al.* 2007; Arnett *et al.* 2008; Figure 1). Because of the distinctive life-history traits of bats, their populations are sensitive to changes in mortality rates and tend to make slow recoveries following declines (Barclay and Harder 2003).

Turbine-related fatalities raise concern about potential impacts on bat populations at a time when many species of bats are known – or suspected – to be in decline (Racey and Entwistle 2003; Winhold *et al.* 2008) and continued development of wind energy is planned (Kunz *et al.* 2007; EIA 2010).

Previous research suggests that more bat fatalities occur during relatively low-wind periods in summer and fall months (Arnett *et al.* 2008). Bats restrict their flight activity during periods of rain, low temperatures, and strong winds (Eckert 1982; Erickson and West 2002). Studies at proposed and operating wind facilities have also documented lower bat activity during high (usually $>6.0 \text{ m s}^{-1}$) wind speeds (Reynolds 2006; Horn *et al.* 2008). Non-spinning turbine blades and turbine towers do not kill bats (Horn *et al.* 2008) and shutting down turbines during low-wind (usually <6.0

m s^{-1}) periods in summer and fall has been hypothesized as a means for reducing bat fatalities (Kunz *et al.* 2007; Arnett *et al.* 2008). Raising turbine cut-in speed (ie the lowest wind speed at which turbines generate power to the utility system) above the manufactured cut-in speed (usually $3.5\text{--}4.0 \text{ m s}^{-1}$ on modern turbines) renders turbines non-operational until the higher cut-in speed is reached and turbines then begin to spin and produce power. Thus, raising turbine cut-in speed during low-wind periods should reduce bat kills. Indeed, results from the only published study on the subject indicate that increasing turbine cut-in speed to 5.5 m s^{-1} reduced bat mortality by nearly 60% as compared with normally operating turbines (Baerwald *et al.* 2009).

We studied how increasing turbine cut-in speed affects bat fatalities at wind turbines. Our objectives were (1) to determine if rates of bat fatality differed between fully operational turbines and turbines with cut-in speeds of 5.0 m s^{-1} and 6.5 m s^{-1} , and (2) to quantify the economic costs of different curtailment programs and timeframes. We predicted that bat fatalities would be (1) significantly higher at fully operational turbines as compared with observed mortality associated with both cut-in speed treatments and (2) significantly lower at turbines with a cut-in speed of 6.5 m s^{-1} as compared with that at turbines with 5.0 m s^{-1} , because increasing cut-in speed reduces operating time to generate power.

■ Study area

The study was conducted at the Casselman Wind Project ($39^{\circ} 51' 22.41'' \text{ N}$, $79^{\circ} 08' 32.22'' \text{ W}$ to $39^{\circ} 51' 08.58'' \text{ N}$, $79^{\circ} 06' 18.60'' \text{ W}$) in Somerset County near Rockwood, Pennsylvania. This facility lies within the Appalachian mixed mesophytic forest ecoregion that encompasses moist broadleaf forests of the Appalachian Mountains (Brown and Brown 1972; Strausbaugh and Core 1978). Elevations

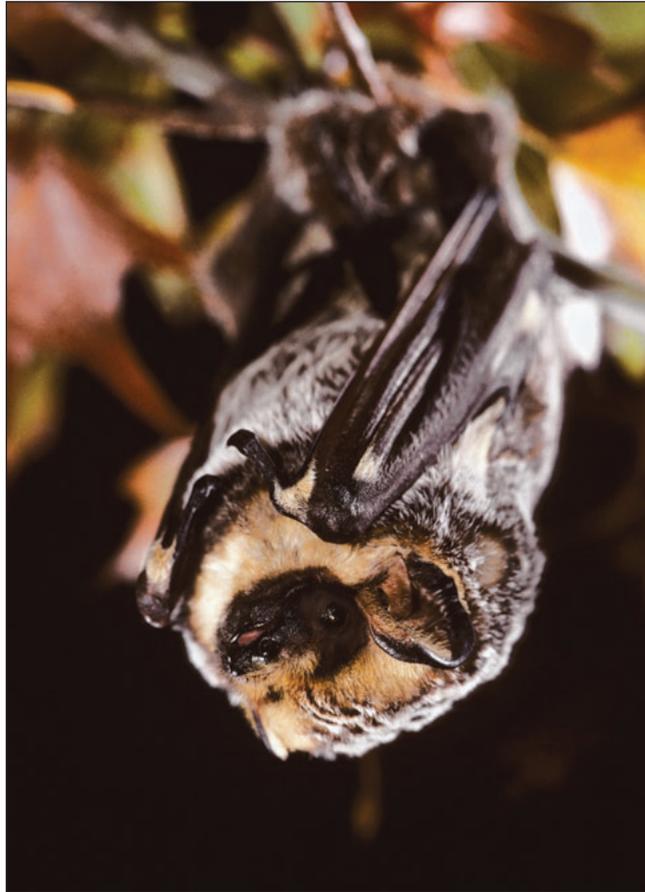
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Beyond the Frontier: Listen to Ed Arnett discussing this research on Frontiers' monthly podcast, at www.frontiersinecology.org.



MD Tuttle/Bat Conservation International

Figure 1. Wind facilities on forested ridges in the eastern US are associated with large numbers of bat deaths, especially migratory foliage-roosting species like the hoary bat (*Lasiurus cinereus*).

range from 732–854 m. Twenty-three General Electric SLE 1.5-megawatt (MW) turbines – each with a rotor diameter of 77 m, rotor-swept-area of 4657 m², hub height of 80 m, variable rotor speeds from 12–20 revolutions per minute, and a cut-in speed of 3.5 m s⁻¹ – are situated at the facility in two “strings”; the western string consists of 15 turbines, sited on land predominated by forest, whereas the eastern string comprises eight turbines in open grassland that was reclaimed after strip mining. In a study conducted simultaneously at this site, searches for bat carcasses indicated no difference in bat fatality rates between the two strings of turbines (Arnett *et al.* 2009). Migratory foliage-roosting bats – including hoary bats (*Lasiurus cinereus*), silver-haired bats (*Lasionycteris noctivagans*), and eastern red bats (*Lasiurus borealis*) – were the species killed most frequently at this site, representing 75% of all bat fatalities recorded (Arnett *et al.* 2009). Tri-colored bat (*Perimyotis subflavus*), big brown bat (*Eptesicus fuscus*), and little brown bat (*Myotis lucifugus*) fatalities also occurred, but in smaller numbers (Arnett *et al.* 2009).

■ Methods

We included 12 of the 23 turbines at the Casselman site – eight on the western string and four on the eastern string

– and defined three turbine treatments: (1) fully operational, (2) cut-in speed at 5.0 m s⁻¹ (C5), and (3) cut-in speed at 6.5 m s⁻¹ (C6). We used a randomized block design (Hurlbert 1984) with “turbine” as the blocking factor and “night within turbine” as the sampling unit for treatment. Randomization was constrained so that on each night of sampling, each of the three treatments was assigned to four turbines, at least one of which was on the eastern string. Full balance of the design (ie each turbine assigned each treatment for an equal number of nights) was therefore achieved after 15 nights. The entire randomization process was repeated five times, for a total of 75 nights annually, resulting in each treatment occurring on 25 nights within each block (turbine) each year.

We found little nightly variation in wind speed among turbines and assumed wind speeds were similar at all turbines at any given time. The turbines used in our study generally do not rotate at wind speeds <3.5 m s⁻¹ and “feather” (ie turbine blades are pitched parallel with the wind direction and only spin at very low rotation rates if at all; Figure 2). Thus, application of treatments was dependent on ambient wind speed and treatments could have changed throughout the night. When wind speeds were <3.5 or >6.5 m s⁻¹, all turbines were in the same operational condition and no curtailment treatments were in effect for those times; treatments were in effect only when wind speeds were between 3.5 and 6.5 m s⁻¹. Evidence of bat mortality (presence of bat carcasses) was observed the day after treatments had been implemented, but it was impossible to determine the precise time of night and under exactly what wind speed fatalities occurred. Our design accounted for this effect by maintaining balance (four replicates of each treatment on each night) and reassigning treatments randomly to turbines each night. Treatment-related mortality was measured as the sum of all individual carcasses of bats estimated to have been killed during the previous night (referred to here as “fresh” carcasses) observed along transects near a given turbine (see below) after a particular treatment assignment, thereby evenly distributing the effect of varying wind speed within a night and among nights across all turbines and treatments in the study.

We delineated rectangular plots 126 m east–west by 120 m north–south (60 m from the turbine mast in each cardinal direction; 15 120 m² total area) centered on each turbine sampled; this area represented the maximum possible search area (Arnett *et al.* 2009, 2010). We established transects at 6-m spacing within each plot, and observers searched 3 m on each side of the transect line; thus, the maximum plot in the east–west direction could be up to 126 m wide. We did not attempt to locate fatalities in low visibility habitats (eg forest, dense grass); also, because the area cleared of forest within plots and the amount of dense vegetation in cleared areas varied among turbines, we did not search the entire maximum possible area surrounding most turbines. We used Global Positioning System (GPS) technology to estimate total

area searched and area of each habitat within each turbine plot (Arnett *et al.* 2009, 2010).

Daily searches were conducted at turbines from 27 July to 9 October 2008, and from 26 July to 8 October 2009, coinciding with when most (usually >80% of) bats are killed at wind facilities (Arnett *et al.* 2008). The study was intentionally established as a “blind” test, and searchers were unaware of turbine treatment assignments throughout the study’s duration. On each day, visual searches commenced at sunrise and all study areas were searched within 8 hours (Figure 3). When a dead bat was found, observers placed a flag near the carcass and continued searching. Upon completion of searching, observers returned to each flagged carcass and recorded information on species, sex and age (where possible), turbine number, distance from turbine, azimuth from turbine, surrounding habitat characteristics, and estimated time of death (eg ≤ 1 day, 2 days; Figure 3). Carcasses were then removed from the plot.

The experimental unit was the set of 25 nights that received a particular cut-in treatment for each turbine. The total number of fresh carcasses found after each treatment at each turbine was modeled as a Poisson random variable; we fitted these data to a Generalized Linear Mixed Model using PROC GLIMMIX in SAS v 9.2 (SAS Institute 2008), and used the amount of searchable area as a means of standardizing predictions to reflect expected values when 100% of the area was searched (McCullagh and Nelder 1992). The block effect was negligible and results were almost identical when data were fit to a simple log-linear model. We tested whether treatment means differed from one another using an *F* test and tested linear contrasts of means with a single degree-of-freedom chi-square test, corresponding (respectively) to an *F* test and a single degree-of-freedom contrast *t* test in a General Linear Model analysis of variance context.

■ Results

Between 27 July and 9 October 2008, 32 fresh carcasses of bats were observed near turbines. At least one fresh carcass was found near each turbine, and 10 of the 12 turbines had at least one fatality during a fully operational night. There was no evidence that fatalities occurred disproportionately at some turbines, and fatalities were well distributed among all turbines (Arnett *et al.* 2010). We found three fatalities at turbines curtailed when the preceding night’s wind speeds were $< 5.0 \text{ m s}^{-1}$ (C5), six at turbines curtailed when the preceding night’s wind speeds were $< 6.5 \text{ m s}^{-1}$ (C6), and 23 at fully operational turbines. Mean bat fatalities per turbine over 25 nights was 0.27 (95% confidence interval [CI]: 0.07, 1.05) for those with a 5.0 m s^{-1} cut-in speed, 0.53 (95% CI: 0.20, 1.42) for those with a 6.5 m s^{-1} cut-in speed, and 2.04 (95% CI: 1.19, 3.51) for fully operational turbines (Figure 4a). There was strong evidence that the number of fatalities over 25 nights differed among turbine treatments ($F_{2,33} =$



Figure 2. A wind turbine shown in a “feathered” position during the curtailment experiment at the Casselman Wind Project in Somerset County, south-central Pennsylvania.

7.36, $P = 0.004$). We found no difference between the number of fatalities for C5 and C6 turbines ($\chi_1^2 = 0.68$, $P = 0.41$). Mean total fatalities at fully operational turbines were 5.4 times greater than those at curtailed turbines (C5 and C6 combined; $\chi_1^2 = 14.11$, $P = 0.0005$, 95% CI: 2.08, 14.11). In other words, in 2008, we found that 82% (95% CI: 52–93%) fewer fatalities occurred when turbines were curtailed as compared with when turbines were fully operational.

Likewise, between 26 July and 8 October 2009, 39 fresh carcasses were observed near turbines. Similar to 2008, we found at least one fresh carcass near each turbine each night, and 11 of the 12 turbines had at least one fatality during a fully operational night; again, this indicates that fatalities were well distributed among turbines (Arnett *et al.* 2010). We found eight fatalities at turbines curtailed when the preceding night’s wind speeds were $< 5.0 \text{ m s}^{-1}$ (C5), six at turbines curtailed when the preceding night’s wind speeds were $< 6.5 \text{ m s}^{-1}$ (C6), and 25 at fully operational turbines. Mean bat fatalities per turbine over 25 nights was 0.73 (95% CI: 0.34, 1.56) for those with a 5.0 m s^{-1} cut-in speed, 0.55 (95% CI: 0.23, 1.31) for those with a 6.5 m s^{-1} cut-in speed, and 2.29 (95% CI: 1.46, 3.58) for fully operational turbines (Figure 4b). Again, there was strong evidence that the number of fatalities



Figure 3. A field biologist records data on bat fatalities. (Inset) A little brown bat (*Myotis lucifugus*) carcass found beneath a wind turbine.

over 25 nights differed among turbine treatments in 2009 ($F_{2,33} = 6.94$, $P = 0.005$). There was no difference between the number of fatalities for C5 and C6 turbines ($\chi_1^2 = 0.24$, $P = 0.616$). Mean total fatalities at fully operational turbines were 3.6 times greater than those at curtailed turbines (C5 and C6 combined; $\chi_1^2 = 12.93$, $P = 0.0003$, 95% CI: 1.79, 7.26). In other words, in 2009, we found that 72% (95% CI: 44–86%) fewer fatalities occurred when turbines were curtailed in comparison with the number of fatalities when turbines were fully operational.

Financial costs of curtailment

Lost power output – attributable to the treatments applied during the experiment – was equivalent to approximately 2% of the total projected output for the 12 turbines during the 75-days-per-year we studied. Hypothetically, if the treatments had been applied to all 23 turbines at this facility for the duration of the study (one-half hour before sunset to one-half hour after sunrise for 75 days), the 5.0 m s⁻¹ curtailment used would have resulted in 3% lost power output during the study period, but only 0.3% of total annual power output. If the 6.5 m s⁻¹ curtailment were applied to all 23 turbines during

the study period, lost output would have been 11% of total output for the period and 1% of total annual output. In addition to decreased revenue from lost power, the company also incurred minor costs for staff time to set up processes and controls and to implement curtailment treatments.

Discussion

Our findings were consistent with our prediction that bat fatalities would be significantly reduced by changing turbine cut-in speed and reducing operational hours during low-wind periods, and corroborate the results of a previous study (Baerwald *et al.* 2009). Both studies suggest that bat fatalities may be reduced by at least 44% when turbine cut-in speed is raised to 5.0 m s⁻¹. However, the actual conservation and population-level consequences of reducing fatalities by changing turbine cut-in speed remain unclear, owing to a dearth of information on bat populations – especially for migratory foliage-roosting bats (O'Shea *et al.* 2003; Cryan and Brown 2007). Without a better understanding of population size, demographics, and impacts of fatalities on bat population viability, it is not possible to determine the influences of any single source of mortality or of mitigation strategies on bat populations. It is thought that cumulative impacts of wind-energy development on bat populations can be expected (Kunz *et al.* 2007; Risser *et al.* 2007), in part because bats have low reproductive rates and are slow to recover from population declines (Barclay and Harder 2003). But until adequate demographic information on bat populations is obtained, the context and impact of wind-turbine-related fatalities and reductions in those fatalities remain uncertain.

Increased bat activity (Reynolds 2006; Horn *et al.* 2008) and fatalities (Arnett *et al.* 2008) at wind-power facilities have been related to low wind speed and weather conditions typical of passing storm fronts, but causal mechanisms underlying this relationship remain unclear. Bats may simply be migrating at higher altitudes – ie above turbine rotors – during high-wind periods, when observed fatalities are low. Alternatively, migration may be less efficient for bats in strong wind conditions, decreasing migratory movements by these species during such periods (Baerwald *et al.* 2009). Arrivals of hoary bats on Southeast Farallon Island off the coast of California during the fall migration were related to periods of low wind speed, dark phases of the Moon, and low barometric pressure, supporting the hypothesis that the timing of migration events is predictable (Cryan and Brown 2007). Low barometric pressure can coincide with the passage of cold fronts that may be exploited by migrating birds and bats (Cryan and Brown 2007). Regional climate patterns, as well as local weather conditions, can be used to predict the foraging and migratory activity of bats (Erickson and West 2002). On a local scale, strong winds can influence the abundance and activity of insects, which in turn

influence the activity of insectivorous bats; such bats are known to reduce foraging activity during periods of rain, low temperatures, and strong winds (Eckert 1982; Erickson and West 2002). Episodic hatchings of insects that are likely associated with “favorable” weather and flight conditions may periodically increase local bat activity (Hayes 1997; Erickson and West 2002). More studies are needed to elucidate these patterns, as well as migration behavior, across regions to develop robust predictive models of environmental conditions preceding fatality events and for predicting when turbine curtailment will be most effective in reducing bat fatalities.

Our study design differs from that of Baerwald *et al.* (2009) in part because we were able to change allocation of treatments each night. By reassigning our treatments among turbines each night, we minimized the potential influence that turbine location might have had on mortality within the project. Additionally, any differences in searchable area among turbines were contained in the turbine blocking factor. Our comparison among treatments was within turbines, so we were able to use a simple count of fresh carcasses, unadjusted for observation bias, but using searchable area as an offset (McCullagh and Nelder 1992). The almost even distribution of fatalities among turbines indicates that there was no strong distinction in fatality among turbines, so detected effects can be reasonably attributed to the treatments. Our design is powerful, but it assumes correct determination of carcasses as “fresh” by field observers. We do not believe our misclassification rate was high (Arnett *et al.* 2009), nor did we have reason to believe the probability of misclassifying a carcass as fresh was associated with treatments, because observers were unaware of the treatment allocation scheme. Thus, errors in classification of fresh carcasses should be equal among turbines and treatments and should not have influenced results of our study. Moreover, we compared bat fatalities at 12 experimental turbines to those at 10 fully operational turbines at the Casselman facility that were sampled during the same time period for a different study (see Arnett *et al.* 2010). We estimated bat fatalities per turbine (ie all carcasses found and corrected for field bias) to be 1.48–5.09 times greater ($\bar{x} = 2.57$) in 2008 and 1.23–2.58 times greater ($\bar{x} = 1.80$) in 2009 at the fully operational turbines than at the experimental turbines (Arnett *et al.* 2010). These findings provide further support for our contention that reducing operational hours during low-wind periods reduces bat fatalities.

Numerous factors influence power loss – and thus financial costs – of raising cut-in speed of wind turbines to reduce bat fatalities. These factors include type and size of wind turbines, market or contract prices of power, electricity purchase agreements and associated fines for violating delivery of power, variation in temporal consistency, and speed and duration of wind across different sites. Estimated power loss during our experiment was considerably different from that reported by Baerwald

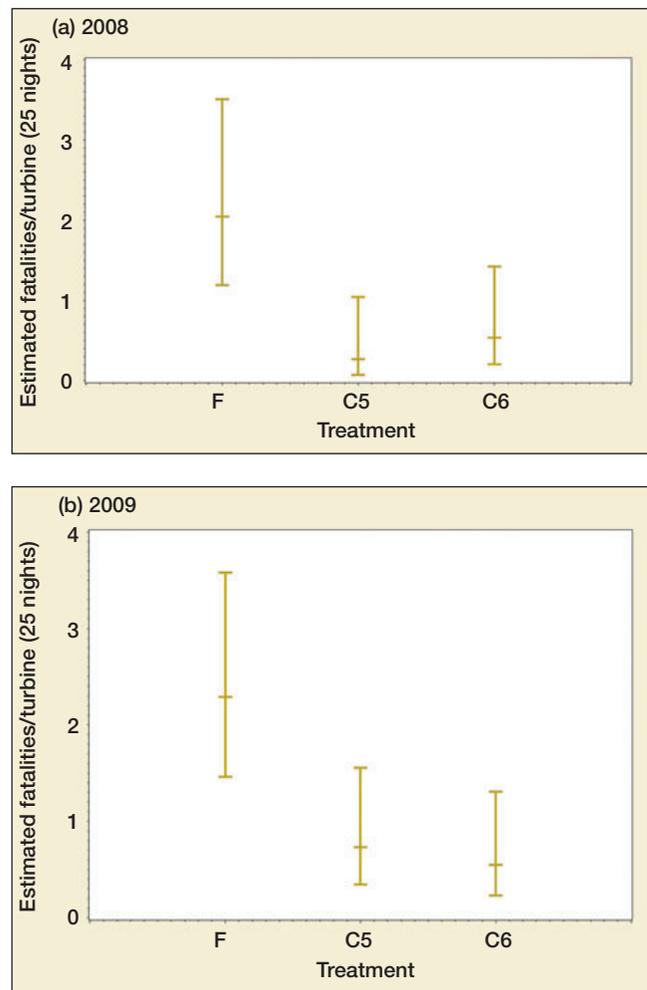


Figure 4. Estimated number of fresh carcasses of bats per turbine, and 95% confidence intervals, over 25 nights for each of three treatments: cut-in speed at 5.0 m s^{-1} (C5), cut-in speed at 6.5 m s^{-1} (C6), and fully operational (F, no change to cut-in speed) for 12 turbines at the Casselman Wind Project in Somerset County, Pennsylvania; (a) 27 July to 9 October 2008 and (b) 26 July to 8 October 2009.

et al. (2009), primarily because they projected estimated losses only for a 30-day period and for just the 15 turbines used in their experiment, whereas we projected power loss for a 75-day period and for all 23 turbines at the site, not just for our treatment turbines. Also, technological limitations of turbines studied by Baerwald *et al.* (2009) forced them to change cut-in speed for the entire duration of the study. Lost power production resulting from our experimental treatments was markedly low when considering total annual productivity, but power loss was three times higher for the 6.5 m s^{-1} change in cut-in speed as compared with the 5.0 m s^{-1} treatment. This difference in power loss reflects the cubic effect of wind speed on power production (Albadi and El-Saadany 2009). Contrary to our prediction, we found no difference in bat fatalities between the 5.0 m s^{-1} and 6.5 m s^{-1} treatments during either year of the study, and curtailment at 5.0 m s^{-1} proved to be far more cost-effective. However, we

found little differentiation in the amount of time different cut-in speed treatments were in effect (WebFigure1), which may explain in part why we found no difference in bat fatalities between the two treatments.

Our study is the first to randomly allocate different cut-in speeds on a nightly basis and to evaluate multiple cut-in speeds. We demonstrated reductions in average nightly bat fatality ranging from 44–93%, with marginal annual power loss. Our findings suggest that increasing cut-in speeds at other wind facilities during summer and fall months will reduce bat fatalities. Additional studies evaluating changes in turbine cut-in speed among different sizes and types of turbines, wind regimes, habitat types, and species of bats (eg Brazilian free-tailed bats, *Tadarida brasiliensis*) would be useful in assessing the general effectiveness of this mitigation strategy. Developing a broader understanding of the demographics and population viability of bats is fundamental in fully evaluating the implications of conservation strategies at wind facilities, but these data are unlikely to be available for most species of bats in the immediate future. We contend that wind operators should implement curtailment measures at turbine sites characterized by high or moderately high numbers of bat fatalities and that such sites warrant mitigation efforts even in the absence of bat population data.

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AGRICULTURE

Economic Importance of Bats in Agriculture

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White-nose syndrome and the increased development of wind-power facilities are threatening populations of insectivorous bats in North America. Bats are voracious predators of nocturnal insects, including many crop and forest pests. We present here analyses suggesting that loss of bats in North America could lead to agricultural losses estimated at more than \$3.7 billion/year. Urgent efforts are needed to educate the public and policy-makers about the ecological and economic importance of insectivorous bats and to provide practical conservation solutions.

Infectious Disease and Wind Turbines

Insectivorous bats suppress populations of nocturnal insects (1, 2), but bats in North America are under severe pressure from two major new threats. White-nose syndrome (WNS) is an emerging infectious disease affecting populations of hibernating cave-dwelling bats throughout eastern North America (3). WNS is likely caused by a newly discovered fungus (*Geomyces destruct-*

tans). This fungus infects the skin of bats while they hibernate and is thought to trigger fatal alterations in behavior and/or physiology (e.g., premature depletion of energy reserves) (3, 4). Since February 2006, when WNS was first observed on bats in upstate New York, *G. destructans* has spread west of the Appalachian Mountains and into Canada. To date, over one million bats have probably died, and winter colony declines in the most affected region exceed 70% (5). Populations of at least one species (little brown bat, *Myotis lucifugus*) have declined so precipitously that regional extirpation and extinction are expected (5).

At the same time, bats of several migratory tree-dwelling species are being killed in unprecedented numbers at wind turbines across the continent (6, 7). Why these species are particularly susceptible to wind turbines remains a mystery, and several types of attraction have been hypothesized (6). There are no continental-scale monitoring programs for assessing wildlife fatalities at wind turbines, so the number of bats killed across the entire United States is difficult to assess. However, by 2020 an estimated 33,000 to 111,000 bats will be killed annually by wind turbines in the Mid-Atlantic Highlands alone (7). Obviously, mortality from these two factors is substantial and will likely have long-term cumulative impacts on both aquatic and terrestrial ecosystems (5, 7). Because of these combined threats, sudden and simultaneous

Insectivorous bat populations, adversely impacted by white-nose syndrome and wind turbines, may be worth billions of dollars to North American agriculture.

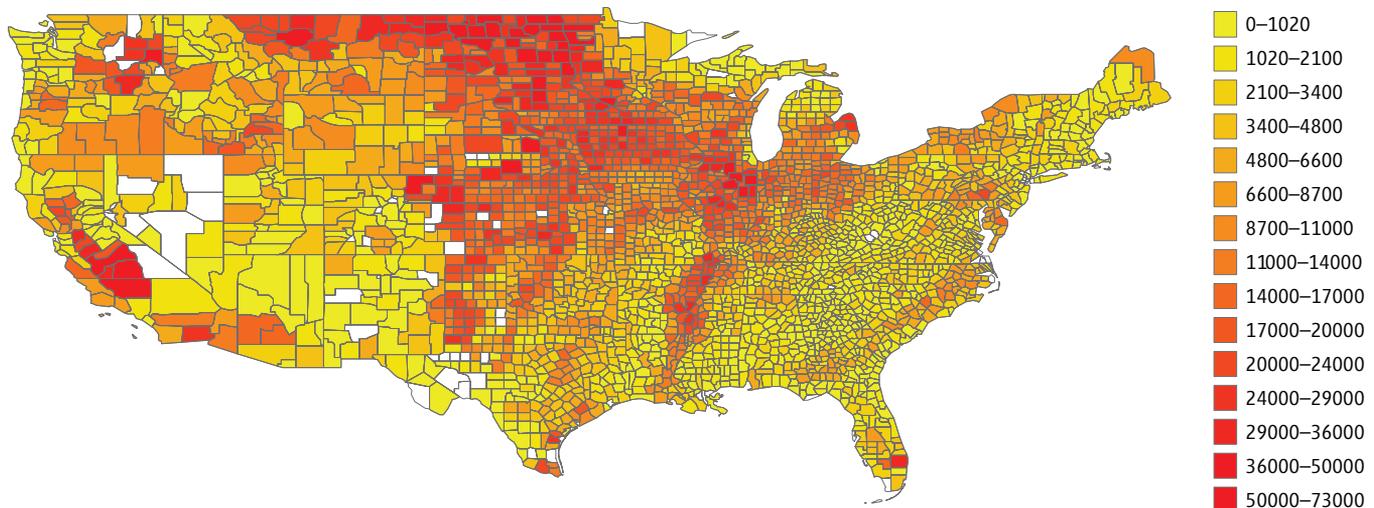
population declines are being witnessed in assemblages of temperate-zone insectivorous bats on a scale rivaled by few recorded events affecting mammals.

Economic Impact

Although much of the public and some policy-makers may view the precipitous decline of bats in North America as only of academic interest, the economic consequences of losing so many bats could be substantial. For example, a single colony of 150 big brown bats (*Eptesicus fuscus*) in Indiana has been estimated to eat nearly 1.3 million pest insects each year, possibly contributing to the disruption of population cycles of agricultural pests (8). Other estimates suggest that a single little brown bat can consume 4 to 8 g of insects each night during the active season (9, 10), and when extrapolated to the one million bats estimated to have died from WNS, between 660 and 1320 metric tons of insects are no longer being consumed each year in WNS-affected areas (11).

Estimating the economic importance of bats in agricultural systems is challenging, but published estimates of the value of pest suppression services provided by bats ranges

The worth of insectivorous bats. Estimated annual value of insectivorous bats in the agricultural industry at the county level. Values ($\times \$1000$ per county) assume bats have an avoided-cost value of $\sim \$74$ /acre of cropland (12). (See SOM for details.)



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from about \$12 to \$173/acre (with a most likely scenario of \$74/acre) in a cotton-dominated agricultural landscape in south-central Texas (12). Here, we extrapolate these estimates to the entire United States as a first assessment of how much the disappearance of bats could cost the agricultural industry [see Supporting Online Material (SOM)].

Assuming values obtained from the cotton-dominated agroecosystem in Texas, and the number of acres of harvested cropland across the continental United States in 2007 (13), we estimate the value of bats to the agricultural industry is roughly \$22.9 billion/year. If we assume values at the extremes of the probable range (12), the value of bats may be as low as \$3.7 billion/year and as high as \$53 billion/year. These estimates include the reduced costs of pesticide applications that are not needed to suppress the insects consumed by bats (12). However, they do not include the “downstream” impacts of pesticides on ecosystems, which can be substantial (14), or other secondary effects of predation, such as reducing the potential for evolved resistance of insects to pesticides and genetically modified crops (15). Moreover, bats can exert top-down suppression of forest insects (1, 2), but our estimated values do not include the benefit of bats that suppress insects in forest ecosystems because economic data on pest-control services provided by bats in forests are lacking. Even if our estimates are halved or quartered, they clearly show how bats have enormous potential to influence the economics of agriculture and forestry.

Although adverse impacts of WNS on bat populations have occurred relatively rapidly, impacts of wind energy development appear to pose a more chronic, long-term concern. WNS has caused rapid and massive declines of hibernating bats in the northeastern United States, where this disease has persisted for at least 4 years (5). Thus, the coming growing season may be the first in which the adverse effects of this disease will become noticeable. Because of regional differences in crop production, the agricultural value of bats in the U.S. Northeast may be comparatively small relative to much of the United States (see the figure) (SOM). However, evidence of the fungus associated with WNS was recently detected in the Midwest and Great Plains, where the estimates of the value of bats to agriculture are substantial (see the figure). Additionally, because this region has the highest onshore wind capacity in North America, increased development of wind energy facilities and associated bat fatalities in this region can be expected (16). Thus, if mortality of bats associated with WNS and

wind turbines continues unabated, we can expect noticeable economic losses to North American agriculture in the next 4 to 5 years.

Policy

A recently stated goal of the United Nations Environment Programme is to demonstrate the value of biodiversity to policy-makers and the public (17). In keeping with this goal, we hope that the scale of our estimates and the importance of addressing this issue will resonate both with the general public and policy-makers. Bats provide substantial ecosystem services worldwide, and their benefits to human economies are not limited to North America. For example, pioneering research in tropical ecosystems shows the importance of plant-visiting bats in the pollination of valuable fruit crops (18, 19). Although the economic impacts of mass mortality of bats associated with WNS appear to be confined, at present, to North America, wind turbines are also causing bat fatalities in Europe (20), and the potential for WNS to spread to other parts of the world is unknown.

We suggest that a wait-and-see approach to the issue of widespread declines of bat populations is not an option because the life histories of these flying, nocturnal mammals—characterized by long generation times and low reproductive rates—mean that population recovery is unlikely for decades or even centuries, if at all. Currently there are no adequately validated or generally applicable methods for substantially reducing the impacts of WNS or wind turbines on bat populations. To date, management actions to restrict the spread of WNS have been directed primarily toward limiting anthropogenic spread (e.g., cave and mine closures and fungal decontamination protocols) (21). Other proactive solutions for understanding and ameliorating the effects of WNS include developing improved diagnostics to detect early-stage infections and fungal distribution in the environment; defining disease mechanisms; investigating the potential for biological or chemical control of the fungus; and increasing disease resistance through habitat modification, such as creation of artificial or modified hibernacula that are less conducive to disease development and transmission (11, 22). Other approaches, such as culling of infected bats have been widely discussed and dismissed as viable options for control (23). New research also shows that altering wind turbine operations during high-risk periods for bats significantly reduces fatalities (24, 25). Specific action on these issues will benefit from scientific research carefully aimed at providing practical conservation solutions for bats in the face

of new threats and at assessing their economic and ecological importance. We as scientists should also make concerted efforts to develop and use more effective methods for educating the public and policy-makers about the ecosystem services provided by bats.

Bats are among the most overlooked, yet economically important, nondomesticated animals in North America, and their conservation is important for the integrity of ecosystems and in the best interest of both national and international economies. In our opinion, solutions that will reduce the population impacts of WNS and reduce the mortality from wind-energy facilities are possible in the next few years, but identifying, substantiating, and applying solutions will only be fueled in a substantive manner by increased and widespread awareness of the benefits of insectivorous bats among the public, policy-makers, and scientists.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/332/6025/42/DC1

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Evaluating the effectiveness of an ultrasonic acoustic deterrent for reducing bat fatalities at wind turbines

Final Report



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Bats and Wind Energy Cooperative**

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EXECUTIVE SUMMARY

We implemented a 2-year study to test the effectiveness of an ultrasonic acoustic deterrent for reducing bat fatalities at wind turbines at the Iberdrola Renewables Locust Ridge I and II Wind Farms located in Columbia and Schuylkill Counties, Pennsylvania. We randomly selected a set of control and treatment turbines that were searched daily in summer and fall 2009 and 2010 and estimates of fatality, adjusted for searcher efficiency, carcass persistence, and habitat and area adjustment, were compared between the two sets of turbines.

In the first year (2009), we randomly selected 10 turbines that were fitted with deterrent devices and 15 control turbines and searched each turbine daily for carcasses from 15 August to 10 October 2009. We did not assess inherent differences between sets of turbines in 2009. In 2010, we attempted to account for potential inherent differences between turbine sets and modified the design to reflect a Before-After Control-Impact (BACI) design. The same sets of turbines were monitored for a period of time prior to implementation of the deterrent treatment (1 May to 26 July 2010), then again during the deterrent implementation period (31 July through 9 October 2010). This design allowed for incorporating initial inherent differences between the two experimental treatment sets prior to implementation of the treatment as a reference for interpreting any differences detected during implementation of the treatment.

In 2009, we estimated 60% higher fatality (95% CI: 26%, 104%) per control turbine than per Deterrent turbine, or conversely, we estimated 21–51% fewer bats were killed per Deterrent turbine than per control turbine during this period. Without accounting for inherent differences, we estimated 18–62% fewer bats were killed per Deterrent turbine than per control turbine in 2010. However, there was marginal evidence that the ratio of control:Deterrent fatalities was greater during the treatment period than in the pre-treatment period; about 10% in the fatality rate between the two sets. Thus, when accounting for this inherent difference, between 2% more and 64% fewer bats were killed per Deterrent turbine relative to control turbines in 2010 after accounting for inherent turbine differences prior to treatment implementation.

We also determined species-specific response to deterrents for those species with adequate sample sizes. We estimated that twice as many hoary bats were killed per control turbine than Deterrent turbine, and nearly twice as many silver-haired bats in 2009. In 2010, although we estimated nearly twice as many hoary bats and nearly 4 times as many silver-haired bats killed per control turbine than at Deterrent turbines during the treatment period, these only represented an approximate 20% increase in fatality relative to the pre-treatment period for these species when accounting for inherent differences between turbine sets.

This study, and previous experiments with earlier prototypes, revealed that broadband ultrasound broadcasts may reduce bat fatalities by affect behavior of bats by discouraging them from approaching the sound source. Yet, the effectiveness of ultrasonic deterrents as a means to prevent bat fatalities at wind turbines is limited by the distance and area that ultrasound can be broadcast; ultra sound attenuates quickly and is heavily influenced by humidity. Humid conditions (nightly average of ~80%) contributed to limited affected airspace during our study. Also, we only deployed 8 deterrent devices on each turbine and did not cover the maximum amount of possible airspace bats could encounter. Also, during both years of the study water

leakage caused some deterrents to malfunction and not all deterrents were operational at all times during the study period. Thus, we contend that our findings may represent a more conservative estimate of the potential reduction achievable through application of the deterrent we tested. However, we caution that we do not yet have a deterrent device ready for operational deployment at wind facilities. With further experimentation and modifications, this type of deterrent method may prove successful and broadly applicable for protecting bats from harmful encounters with wind turbine blades. We anticipate further research and development of acoustic deterrent devices in 2011 and a new field test of the effectiveness of the new prototype in 2013. Future research and development and field studies should attempt to optimize both placement and number of devices on each turbine that would affect the greatest amount of airspace in the rotor-swept area to estimate potential maximum effectiveness of this tool to reduce bat fatalities. Future efforts also must evaluate the cost-effectiveness of deterrents in relation to different curtailment strategies to allow a cost-benefit analysis for mitigating bat fatalities.



Deterrent devices attached to the nacelle of a wind turbine at the Locust Ridge Wind Farm in Pennsylvania (E.B. Arnett, Bat Conservation International)

INTRODUCTION

As wind energy production has steadily increased worldwide, bat fatalities have been reported at wind facilities throughout North America (Johnson 2005, Kunz et al 2007, Arnett et al. 2008, Baerwald and Barclay 2009) and Europe (e.g., Durr and Bach 2004, Brinkman et al. 2006, Rydell et al. 2010) in a wide range of landscapes. Fatality rates observed at large commercial wind facilities on forested ridges in the eastern U.S. have ranged from 20.8–69.6 bats/turbine/year (Arnett et al. 2008), but new reports from the upper Midwest indicate relatively high fatalities at some facilities in this region (e.g., Gruver et al. 2009). Assuming 1) an average of ~12 bats killed per megawatt (MW) of installed capacity, assumed to be per year (Arnett et al. 2008); 2) the current installed capacity in the U.S. (36,698 MW as of September 2010; U.S. Department of Energy 2011) and Canada (4,008 MW as of December 2010; CANWEA 2010) totaling 40,706 MW; and 3) that reported fatality rates are representative and remained constant, the projected average number of bat fatalities in 2010 could have been more than 488,000 bats. Given these fatality rates, the accelerating growth of the wind industry (EIA 2010), and suspected and known population declines in many bat species (Racey and Entwistle 2003, Winhold et al. 2008, Frick et al. 2010), it is imperative to develop and evaluate solutions that can reduce the number of future bat fatalities.

Prior studies have demonstrated that a substantial portion of bat fatalities consistently occur during relatively low-wind conditions over a relatively short period of time during the summer-fall bat migration period (Arnett et al. 2008). Curtailment of turbine operations under these conditions and during this period has been proposed as a possible means of reducing impacts to bats (Kunz et al. 2007, Arnett et al. 2008, Cryan and Barclay 2009). Indeed, recent results from the only two published studies in Canada (Baerwald et al. 2009) and the U.S. (Arnett et al. 2011) indicate that changing turbine “cut-in speed” (i.e., wind speed at which wind-generated electricity enters the power grid) from the manufactured speed (usually 3.5–4.0 m/s for modern turbines) to between 5.0 and 6.5 m/s resulted in at least a 50% reduction in bat fatalities (and as high as 93%; Arnett et al. 2011) compared to normally operating turbines. While costs of lost power from curtailment can be factored into the economics and financing and power purchase agreements of new projects, altering turbine operations even on a partial, limited-term basis potentially poses operational and financial difficulties for existing projects, so there is considerable interest in developing other solutions to reduce bat fatalities that do not involve turbine shutdowns. Also, changing turbine cut-in speed may not be effective in other regions that experience bat fatalities although this strategy may ultimately prove sufficiently feasible and economical for reducing bat fatalities. Thus, research on alternative mitigation strategies and their associated costs are warranted.

Studies in Scotland suggest that bat activity may be deterred by electromagnetic signals from small, portable radar units. Nicholls and Racey (2009) reported that bat activity and foraging effort per unit time were significantly reduced during experimental trials when their radar antenna was fixed to produce a unidirectional signal that maximized exposure of foraging bats to their radar beam. The effectiveness of radar as a potential deterrent has not been tested at an operating wind facility to determine if bat fatalities could be significantly reduced by these means. Moreover, the effective range of electromagnetic signals as well as the number of radar units needed to affect the most airspace near individual turbines would need to be determined to

fully evaluate effectiveness and to allow some cost-benefit analysis relative to other potential deterrents or curtailment (Baerwald et al. 2009, Arnett et al. 2011).

Echolocating bats produce high frequency vocal signals and perceive their surroundings by listening to the features of the echoes reflecting from targets in the path of the sound beam (Griffin 1958). Thus, bats that use echolocation depend heavily on auditory function for orientation, prey capture, communication, and obstacle avoidance. Bats of some species avoid certain territorial social calls emitted by conspecifics (e.g., Barlow and Jones 1997) and are deterred by “clicks” emitted by noxious moths (e.g., Hristov and Conner 2005). Because echolocating bats depend upon sensitive ultrasonic hearing, broadcasting ultrasound from wind turbines may disrupt or “jam” their perception of echoes and serve as a deterrent (Spanjer 2006, Szewczak and Arnett 2006). Such masking of echo perception, or simply broadcasting high intensity sounds at a frequency range to which bats are most sensitive, could create an uncomfortable or disorienting airspace that bats may prefer to avoid.

Few studies have investigated the influence of ultrasound broadcast on bat behavior and activity, particularly in the field. Griffin et al. (1963) showed that broadband random ultrasonic noise could mask bat echolocation somewhat but not completely. Mackey and Barclay (1989) concluded that ultrasound broadcasts reduced bat activity and attributed the reduction to greater difficulty in the bats hearing the echoes of insects and thus reduced feeding efficiency. Spanjer (2006) tested the response of big brown bats (*Eptesicus fuscus*) to a prototype eight speaker deterrent device emitting broadband white noise at frequencies ranging from 12.5–112.5 kHz in the laboratory and found that during non-feeding trials, bats landed in a quadrant containing the device significantly less when it was broadcasting broadband noise. Spanjer (2006) also reported that during feeding trials, bats never successfully captured a tethered mealworm when the device broadcasted sound but captured mealworms near the device in about 1/3 of trials when it was silent. Szewczak and Arnett (2006, 2007) tested the same acoustic deterrent in the field and found that when placed by the edge of a small pond, where nightly bat activity was consistent, nightly activity decreased significantly on nights when the deterrent was activated. Horn et al. (2007) tested the effectiveness of a larger, more powerful version of this deterrent device in reducing nightly bat activity and found mixed results; in one experiment bat activity was significantly reduced with deterrents while the other showed no difference in activity levels between treated and untreated turbines.

The goals of this study were to improve the deterrent devices previously tested to maximize capability to broadcast ultrasonic emissions from the nacelle of wind turbines and to test their effectiveness on reducing bat fatalities. The objectives of this study were 1) to conduct carcass searches and field bias trials (searcher efficiency and carcass removal; following Arnett et al. 2009, 2010) to determine rate of bat fatality at turbines; and 2) compare bat fatality rates at turbines treated with the deterrent to untreated turbines.

Figure 1. Location of the Locust Ridge Wind Farm Project and its 64 turbines in Columbia and Schuylkill Counties, east-central Pennsylvania.



File Path: Z:\Projects\PA\LocustRidge\MapDocuments\Misc\Turbine Layout.mxd. Date: October 14, 2008 2:10:53 PM

STUDY AREA

The Locust Ridge Wind Project is located near the towns of Shenandoah, Mahanoy City, and Brandonville in Columbia and Schuylkill Counties, Pennsylvania (Figure 1) and consists of two facilities. The Locust Ridge I (LRI) Wind Farm has 13 Gamesa G87 2.0 MW turbines, each on 80 m monopoles with a rotor diameter of 87 m and a swept area of 5,945 m². There were 51 Gamesa G83 2.0 MW turbines, each on 80 m monopoles with a rotor diameter of 83 m and a swept area of rotor-swept area of 5,411 m², at the Locust Ridge II (LRII) Wind Farm. LR II comprised four strings of turbines, including A (n = 5), B (n = 12), C (n = 9), and D (n = 25; Figure 1) strings. The facilities lie within the Appalachian mixed mesophytic forests ecoregion and the moist broadleaf forests that cover the plateaus and rolling hills west of the Appalachian Mountains (Brown and Brown 1972, Strausbaugh and Core 1978). All strings are located on a moderately deciduous forest ridge with evergreen species interspersed. The vegetation surrounding the facility consists of dense thickets of scrub oak (*Quercus berberidifolia*) interspersed with chestnut oak (*Quercus prinus*) and gray birch (*Betula populifolia*) and mature hardwood forests of red oak (*Quercus rubra*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*) and scrub oak, with witch-hazel (*Hamamelis virginiana*) and sassafras (*Sassafras albidum*).

METHODS

Turbine Selection and Deterrent Installation

We randomly selected 15 of the 51 turbines located at LR II to be searched as part of a separate study to determine post-construction fatality rates and to meet permitting requirements of the Pennsylvania Game Commission's (PGC) voluntary agreement for wind energy (PGC 2007). These 15 turbines formed our reference (herein referred to as "control") turbines for comparing with Deterrent turbines. In 2009, unforeseen mechanical and safety issues arose at the LR II site and most of these turbines had to be excluded from our potential treatment group due to potential safety hazards. Thus, we included the 13 turbines at LRI as well as the remaining available turbines at LR II (n = 36 remaining available turbines) when randomly selecting our 10 turbines to be fitted with deterrent devices; 3 turbines were randomly selected from the 13 available at the LRI site and 7 of 36 available at LR II. We did not assess whether there were any potential inherent differences between the two types of turbines, and assumed that there were no confounding differences in our findings.

The deterrent devices used in this study consisted of a waterproof box (~45 x 45 cm, ~0.9 kg) that housed 16 transducers (Figure 2) that emitted continuous broadband ultrasound from 20 to 100 kHz (manufactured by Deaton Engineering, Georgetown, Texas; see Appendix 1 for select specifications). The transducers in these units had an optimum transmission level at their resonant frequency of 50 kHz transmission and reduced transmit levels at higher and lower frequencies over a broadband range of 20–100kHz (see Appendix 1). This frequency range overlaps with the dominant frequency range of all bats known in the study area. Three factors influence the predicted effective transmitted power at a given distance: the original transmitted power (sound pressure level; SPL), attenuation with distance due to the wave front spreading

Figure 2. Photos depicting the acoustic deterrent device, its installation, and approximate location on turbines at the Locust Ridge I and II Wind Farms in Pennsylvania.



A deterrent device used in this study (E. Arnett, Bat Conservation International).

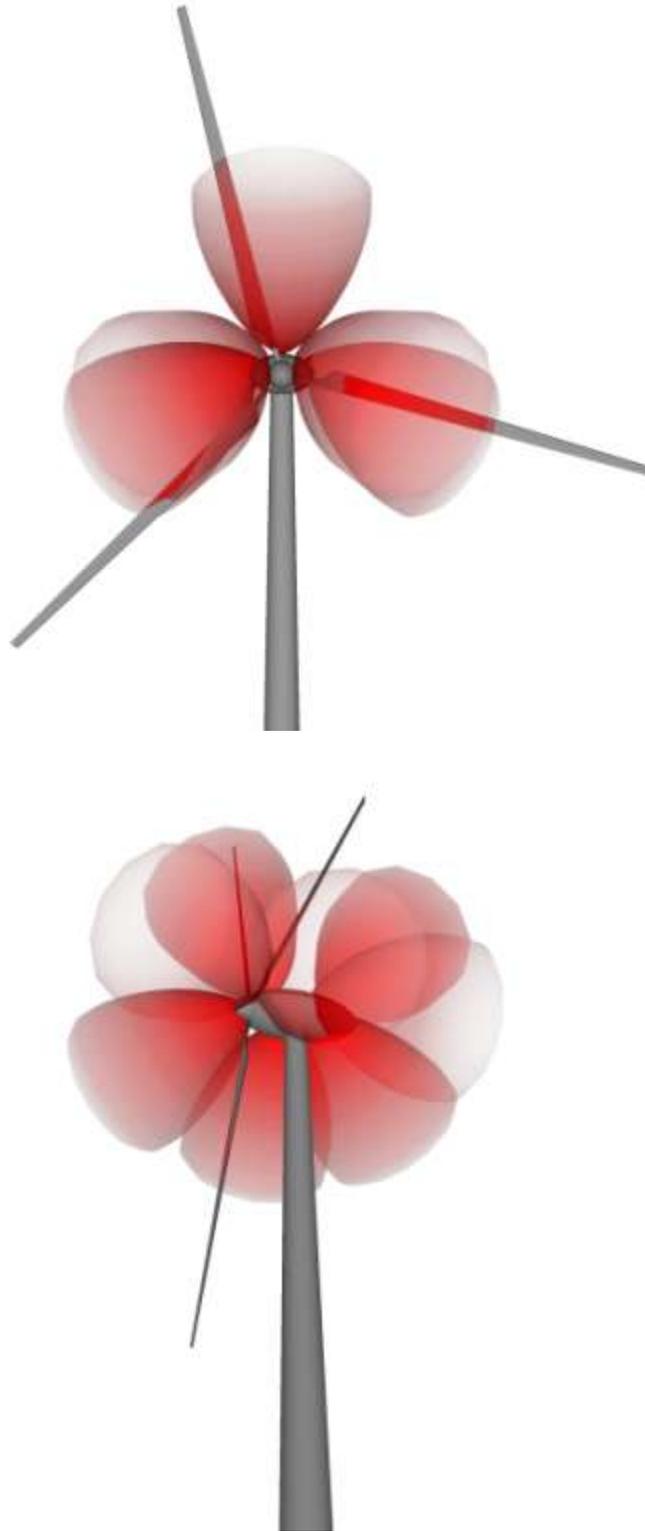


Attaching devices to a safety rail on the top of the turbine nacelle (M. Baker, Bat Conservation International).



A wind turbine with six deterrent devices shown (3 mounted on each side of the nacelle; M. Baker, Bat Conservation International).

Figure 3. Depiction of acoustic deterrent placement on the nacelle of turbines and ultrasonic broadcast volume from devices (broadcast volume approximation of data from Senscorp beam pattern data, Appendix 1c).



(inversely proportional to the square of the distance, frequency independent), and the attenuation (absorption) in air of the sound wave (dependent on frequency, humidity and distance; see Appendix 1 for select specifications and estimated range of transmission under three different levels of humidity and assuming constant temperature and air pressure).

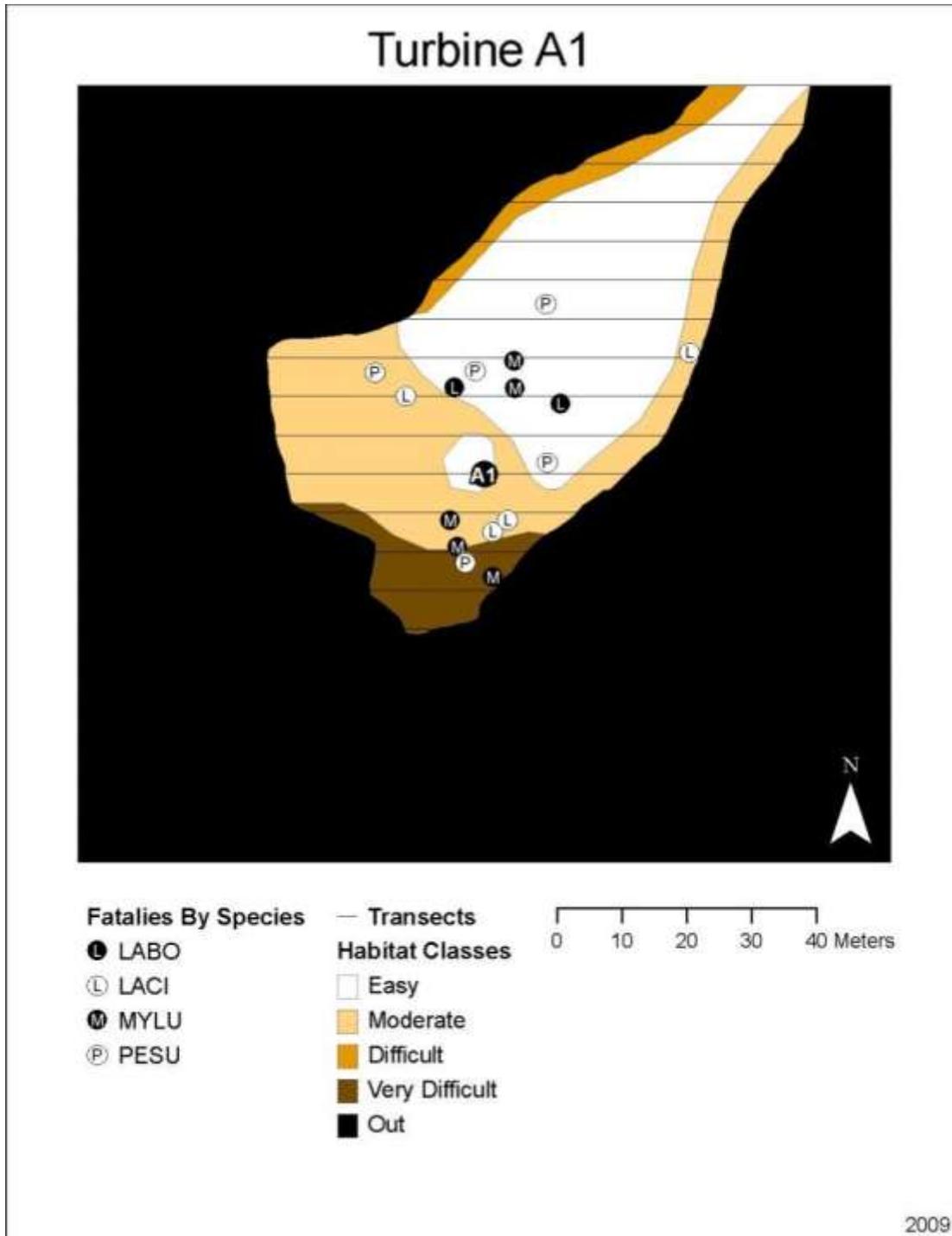
We used the following estimation to base the target signal level of the experimental deterrent: A typical bat emits calls at about 110 dB sound pressure level (SPL) at 10 cm (Surlykke and Kalko 2008). During search phase flight a typical North American species of bat emits about 12 calls per second, each about 5 milliseconds in duration (Fenton 2003, Parsons and Szewczak 2009). Given the speed of sound at 340 m/sec and duration of an open air call, the bat's own call will theoretically mask echoes returning from objects within about 1.5 m (i.e., the bat cannot hear early return echoes while vocalizing). An echo from a target about 1.5 m away will return about 45 dB less than the original 110 dB signal, or at about 65 dB. The bat's next call would mask echoes returning from about 25 m away. By this first order estimation, a bat would theoretically perceive information from returning echoes with amplitudes of ≤ 65 dB over a range from about 1.5–25 m. Thus, we estimated that a broadband signal of ≥ 65 dB would begin jamming or masking most bat's echo perception from targets beyond about a 1.5 m range.

We attached 8 individual deterrent devices to the nacelle of each of 10 sample turbines. Three devices on each side of the nacelle were pointed downward with one aimed into the rotor-swept area, one parallel with the monopole, and one aimed toward the back of the nacelle (Figures 2 and 3). Additionally, two devices were aimed at reflector plates; one that projected emissions into the upper part of the rotor-swept area, and one toward the rear of the nacelle (Figures 2 and 3). All devices connected to control boxes that were powered from outlets located in the nacelle and each was set on a timer to operate from ½ hour before sunset to ½ hour after sunrise each night of the study.

Delineation of Carcass Search Plots and Habitat Mapping

We delineated a rectangular plot 126 m north-south by 120 m east-west (60 m radius from the turbine mast in any direction; 15,120 m² total area) centered on each turbine sampled; this area represents the maximum possible search area for this study [see Figure 4 for an example]. Transects were set 6 m apart within each plot and in an east-west direction, due to the topography and layout of turbines at this facility (Figure 4). However, dense vegetation and the area cleared of forest at this facility was highly varied and, thus, we eliminated unsearchable habitat (e.g., forest) and usually did not search the entire possible maximum area. We used a Trimble global positioning system (GPS) to map the actual area searched at each turbine (see Figure 4 for an example). The density-weighted area searched was used to standardize results and adjust fatality estimates (see methods). The habitat visibility classes within each plot were also mapped using a GPS unit. We recorded the percent ground cover, height of ground cover (low [<10 cm], medium [11–50 cm], high [>50 cm]), type of habitat (vegetation, brush pile, boulder, etc), and the presence of extreme slope and collapsed these habitat characteristics into visibility classes that reflect their combined influence on carcass detectability (following PGC 2007; see Appendix 2).

Figure 4. Sample search plot at a wind turbine depicting the maximum plot size of 126 m north-south and 120 m east-west, transect lines (searched 3 m on each side), unsearchable area (black), and area encompassed by easy (white), moderate (light tan), difficult (dark tan), and very difficult (brown) visibility habitat.



Fatality Searches

We conducted daily searches at 15 control turbines (A1, A3, A5, B1, B4, B7, B9, B12, C3, C5, C7, C9, D4, D12, D25) and 10 Deterrent turbines (T1, T5, T10, A2, B3, B6, B11, C1, C6, D21) from 15 August to 10 October 2009 and 1 May to 26 July and 31 July to 9 October 2010. Each searcher completed 5–7 turbine plots each day during the study. Searchers walked at a rate of approximately 10–20 m/min. along each transect searching out to 3 m on each side for fatalities. Searches were abandoned only if severe or otherwise unsafe weather (e.g., heavy rain, lightning) conditions were present and searches were resumed that day if weather conditions permitted. Searches commenced at sunrise and all turbines were searched within 8 hr after sunrise.

We recorded date, start time, end time, observer, and weather data for each search at turbines. When a dead bat or bird was found, the searcher placed a flag near the carcass and continued the search. After searching the entire plot, the searcher returned to each carcass and recorded information on date, time found, species, sex and age (where possible), observer name, identification number of carcass, turbine number, perpendicular distance from the transect line to the carcass, distance from turbine, azimuth from turbine, habitat surrounding carcass, condition of carcass (entire, partial, scavenged), and estimated time of death (e.g., ≤ 1 day, 2 days, etc.). A field crew leader confirmed all species identifications at the end of each day. Disposable nitrile gloves were used to handle all carcasses to reduce possible human scent bias for carcasses later used in scavenger removal trials. Each carcass was placed into a separate plastic bag and labeled. Fresh carcasses, those determined to have been killed the night immediately before a search, were redistributed at random points on the same day for searcher efficiency and scavenging trials. Following PGC's protocol, all downed bats were euthanized, even if no physical injury was observed due to the possibility of barotraumas, following acceptable methods suggested by the American Society for Mammalogists (Gannon et al. 2007); because sedation or anesthesia was not used in our study, we employed cervical dislocation.

Field Bias Trials

Searcher efficiency and removal of carcasses by scavengers was quantified to adjust estimates of total bat and bird fatalities for detection bias. We conducted bias trials throughout the entire study period and searchers were never aware which turbines were used or the number of carcasses placed beneath those turbines during trials. Prior to the study's inception, we generated a list of random turbine numbers and random azimuths and distances (m) from turbines for placement of each bat used in bias trials.

We used only fresh killed bats for searcher efficiency and carcass removal trials during the study. At the end of each day's search, a field crew leader gathered all carcasses from searchers and then redistributed fresh bats at predetermined random points within any given turbine plot's searchable area. Data recorded for each trial carcass prior to placement included date of placement, species, turbine number, distance and direction from turbine, and visibility class surrounding the carcass. We attempted to distribute trial bats equally among the different visibility classes throughout the study period and succeeded in distributing roughly one-third of all trial bats in each visibility class (easy, moderate, and difficult [difficult and very difficult

were combined]). We attempted to avoid “over-seeding” any one turbine with carcasses by placing no more than 4 carcasses at any one time at a given turbine. Because we used fresh bats for searcher efficiency trials and carcass removal trials simultaneously, we did not mark bats with tape or some other previously used methods (e.g., Kerns et al. 2005) that could impart human or other scents on trial bat carcasses. Rather, we used trial bat placement details (i.e. azimuth, distance, sex, species) and signatures from hair and tissue samples (i.e. hair removed between the scapulae and wing punches) to distinguish them from other fatalities landing nearby. Each trial bat was left in place and checked daily by the field crew leader or a searcher not involved with the bias trials at turbines where carcasses were placed. Thus, trial bats were available to be found by searchers on consecutive days during daily searches unless removed by a scavenger. We recorded the day that each bat was found by a searcher, at which time the carcass remained in the scavenger removal trial. If, however, a scavenger removed a carcass before detection it was removed from the searcher efficiency trial and used only in the removal data set. When a bat carcass was found, the searcher determined if a bias trial carcass had been found by looking for markings described above and contacting the crew leader to determine if the location (direction and distance) matched any possible trial bats. All trial bats were left in place for the carcass removal trial. Carcasses were left in place until removed by a scavenger or they decayed and disintegrated to a point beyond recognition. Carcass condition was recorded daily up to 20 days, as present and observable (1) or missing or no longer observable (0).

Statistical Methods

Carcass persistence/removal. Estimates of the probability that a bat carcass was not removed in the interval between searches were used to adjust carcass counts for removal bias. Removal included scavenging, wind or water, or decomposition beyond recognition. In most fatality monitoring efforts, it is assumed that carcass removal occurs at a constant rate that is not dependent on the time since death; this simplifying assumption allows us to estimate fatality when search intervals exceed one day. The length of time a carcass remains on the study area before it is removed is typically modeled as an exponentially distributed random variable. The probability that a carcass is not removed during an interval of length I can be approximated as the average probability of persisting given its death might have occurred at any time during the interval:

$$\hat{r}_{jk} = \hat{t}_{jk} * (1 - \exp(-I_{ij} / \hat{t}_{jk})) / I_{ij}$$

\hat{r}_{jk} is the estimated probability that a carcass in the k^{th} visibility class that died during the interval preceding the j^{th} search will not be removed by scavengers;

\hat{t}_{jk} is the estimated average persistence time of a carcass in the k^{th} visibility class that died during the interval preceding the j^{th} search;

I_{ij} is the length of the effective interval preceding the j^{th} search at the i^{th} turbine;

NOTE: k^{th} visibility class can be expanded to any combination of factors that have been modeled as affecting a carcass’s persistence time or probability of detection (e.g. size, season, etc.).

Data from 351 and 408 bat carcasses in 2009 and 2010, respectively, were used in our analysis, with carcass persistence time modeled as a function of visibility class. We fit carcass persistence/removal data for bats to an interval-censored parametric failure time model, with carcass persistence time modeled as a function of size and/or visibility class. We used a relatively liberal alpha of 0.15 to identify factors (e.g., carcass size, visibility classes) that influence bias parameter values (i.e., searcher efficiency and carcass persistence) for removal of bat carcasses.

Searcher efficiency. Estimates of the probability that an observer will visually detect a carcass during a search were used to adjust carcass counts for observer bias. Failure of an observer to detect a carcass on the search plot may be due to its size, color, or time since death, as well as conditions in its immediate vicinity (e.g., vegetation density, shade). In most fatality monitoring efforts, because we cannot measure time since death, it is assumed that a carcass' observability is constant over the period of study, which it likely is not. In this study, searches were conducted daily and carcass persistence times were long, providing an opportunity for a searcher to detect a carcass that was missed on a previous search. The estimator proposed by Huso (2010) and applied in this study assumes that a carcass missed on a previous search will not be observed on a subsequent search, i.e. there are inherent environmental conditions that make the carcass unobservable like heavy foliage, terrain, etc. If this assumption is not met, it can lead to overestimates of fatality. Other estimators assume that a carcass missed on a previous search has the same probability of being observed as it had on the first search, i.e. there is nothing inherent in the environment surrounding the carcass that makes it unobservable, missing it is purely a chance event and that if the carcass is not removed by predators and enough searches are conducted, it will eventually be observed. If this assumption is not met, it can lead to underestimates of fatality. It is likely that neither assumption is appropriate in all cases.

Searcher efficiency trial carcasses were placed on search plots and monitored for 20 days. The day on which a bat carcass was either observed or removed by a scavenger was noted. In these trial data, if a carcass had not been found within the first 8 searches it had essentially no chance of being found. This lends empirical support to the idea that there are some environmental conditions surrounding the carcass that determine its probability of being found. However, several carcasses missed on the first search were found on subsequent searches, lending support to the idea that at least for some carcasses, the probability of missing them is purely a chance event. To allow for some possibility of observing a carcass once having missed it, the set of trial carcasses comprised those found or still observable but not found within the first 8 searches. After accounting for carcasses removed before a searcher had the chance of observing them, we fit data from 139 (2009) and 169 (2010) bat carcasses to a logistic regression model, with odds of observing a carcass given that it persisted, modeled as a function of visibility class. Again, we used a relatively liberal alpha of 0.15 to determine if a significant effect among visibility classes existed. Because we found no bats in the Very Difficult visibility class, SE was not modeled for this class.

Density of carcasses and proportion of area surveyed. Density of carcasses is known to diminish with increasing distance from the turbine (e.g., Kerns et al. 2005), so a simple adjustment to fatality based on area surveyed would likely lead to overestimates, because

unsearched areas tend to be farthest from turbines where carcass density is lowest. The calculated function (see below) relating density to distance from a turbine was used to weight each square meter in the plot. The density-weighted fraction of each plot that was actually searched was used as an area adjustment to per-turbine fatality estimates rather than using a simple proportion.

The density of bat carcasses (number of carcasses/m²) was modeled as a function of distance (m) from the turbine. Because searcher efficiency and visibility class are confounded with distance, only fresh bat carcasses found in Easy visibility class were used for this analysis and all non-incident data from all searched turbines were used, yielding a total of 172 fresh bat carcasses. We assumed that the carcass persistence time and searcher efficiency would be equal for all carcasses within this class and would not change as a function of distance from the turbine. We also assumed that no bat carcasses killed by turbine blades would fall > 200 m from the turbine. Carcasses were “binned” into 2 m rings (Figure 5) extending from the turbine edge out to the theoretical maximum plot distance. We determined the total area among all search plots that was in the Easy visibility class (m²) in each ring and calculated carcass density (number of carcasses/m²) in each ring. Density was modeled as a conditional cubic polynomial function of distance (dist):

$$\text{If distance} \leq 50\text{m, then density} = \exp(-1.77328 + 0.0346454 * \text{dist} - 0.00271076 * \text{dist}^2 + 0.0000229885 * \text{dist}^3) - 0.01, \text{ else density} = 0.009363847 * \exp(-0.05 * (\text{distance} - 50))$$

Relative density was derived by dividing the predicted density of each m² unit by the total predicted density within 200 m of a turbine, providing a density-weight for each m² unit. The density weighted area (DWA) of a plot was calculated as the sum of the density weights for all m² units within the searchable area. If no portion of a designated plot was unsearchable, the density weight for the plot would be 1.

The physical area surveyed within a plot differed among turbines and ranged from 20–47% of the delineated theoretical maximum search plot, with an average of 31% whereas the weighted density area of plots averaged 62% (range: 44–78%). In addition, using this density weight, we estimated 7.2% of the carcasses killed at a turbine would be found beyond the boundaries of the designated search plot.

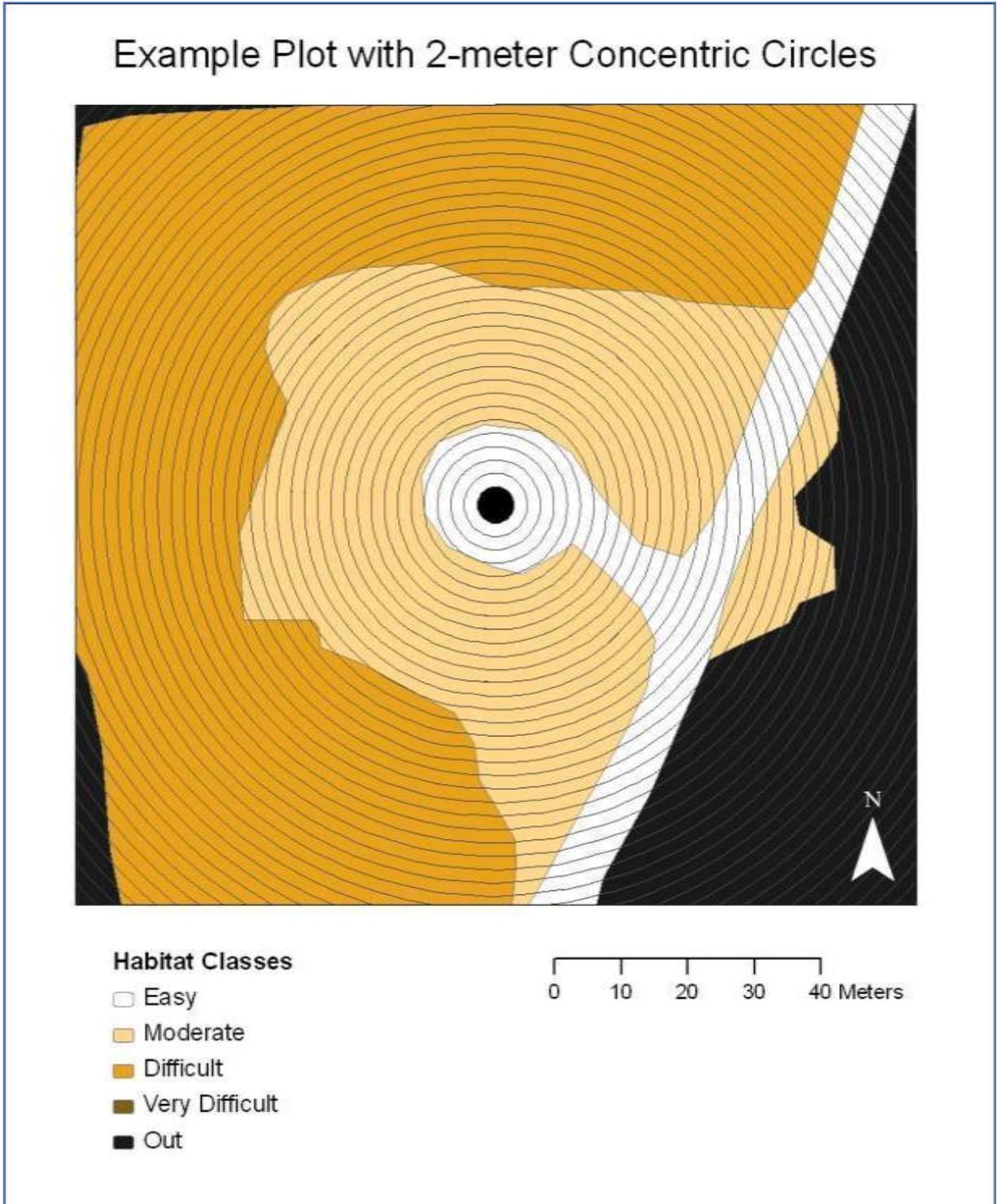
Fatality estimates. We adjusted the number of bat fatalities found by searchers by estimates of searcher efficiency and by the proportion of carcasses expected to persist unscavenged during each interval using the following equation:

$$\hat{f}_{ijk} = \frac{c_{ijk}}{\hat{a}_i * \hat{p}_{jk} * \hat{r}_{jk} * \hat{e}_{jk}}$$

where:

\hat{f}_{ijk} is the estimated fatality in the k^{th} visibility class that occurred at the i^{th} turbine during the j^{th} search;

Figure 5. Hypothetical carcass search plot for a wind turbine illustrating 2 m rings extending from the turbine edge out to the theoretical maximum plot distance and a depiction of “easy” searchable area (shaded area within line drawing) in the plot, used to develop weights for adjusting fatalities.



c_{ijk} is the observed number of carcasses in the k^{th} visibility class at the i^{th} turbine during the j^{th} search;

\hat{a}_i is the density-weighted proportion of the area of the i^{th} turbine that was searched;

\hat{p}_{jk} is the estimated probability that a carcass in the k^{th} visibility class that is on the ground during the j^{th} search will actually be seen by the observer;

\hat{r}_j is the probability than an individual bird or bat that died during the interval preceding the j^{th} search will not be removed by scavengers; and

\hat{e}_{jk} is the effective interval adjustment (i.e., the ratio of the length of time before 99% of carcasses can be expected to be removed to the search interval) associated with a carcass in the k^{th} visibility class that died during the interval preceding the j^{th} search.

The value for \hat{p}_{jk} was estimated through searcher efficiency trials with estimates given above; \hat{r}_j is a function of the average carcass persistence rate and the length of the interval preceding the j^{th} search; and \hat{r}_j , \hat{e}_j and \hat{p}_{jk} are assumed not to differ among turbines, but differ with search interval (j) and visibility class (k).

The estimated annual per turbine fatality for bats and birds was calculated using a newly derived estimator (Huso 2010; herein referred to as the MH estimator). The equation for the MH estimator for this study is:

$$\hat{f} = \frac{\sum_{i=1}^{10} \sum_{j=1}^{n_i} \sum_{k=1}^3 \hat{f}_{ijk}}{10}$$

where n_i is the number of searches carried out at turbine i , $i = 1, \dots, 10$, and \hat{f}_{ijk} is defined above. The per turbine estimate and confidence limits were multiplied by 64, the total number of turbines, and divided by 0.9279 to adjust for actual density-weighted area searched to give total annual fatality estimates (Cochran 1977). This estimate assumes that no fatalities occurred during the winter, i.e. prior to April and after November. No closed form solution is yet available for the variance of this estimator, so 95% confidence intervals of this estimate were calculated by bootstrapping (Manly 1997). Searcher efficiency was estimated from a bootstrap sample (with replacement) of searcher efficiency data, carcass persistence estimated from a bootstrap sample of carcass persistence data, and these values were applied to the carcass data from a bootstrap sample of turbines to estimate average fatality per turbine. This process was repeated 1000 times. The 2.5th and 97.5th quantiles from the 1,000 bootstrapped estimates formed the 95% confidence limits of the estimated fatality.

Comparison between treatment and control turbines. In 2009, we compared average fatality at control with Deterrent turbines for all bats and for each species using one-way analysis

of variance with each turbine as the experimental unit and \log_e transformed estimated total fatalities as the response. In 2010, estimated average bat fatality per turbine at control and Deterrent turbines, during the treatment phase and the period immediately preceding it (pre-treatment phase) was analyzed in a Before-After, Control-Impact design (BACI; Hurlbert 1984, Hewitt et al. 2001) using ANOVA repeated measures with the turbine as the experimental unit, repeatedly measured twice. In both years, the fatality data were log transformed to satisfy assumptions of normality and homogeneity of variance (Steele et al. 1997).

RESULTS

In 2009, we searched 15 control turbines and 10 Deterrent turbines each day between 15 August and 10 October. We found 194 carcasses (135 at control, 59 at Deterrent) of 6 species (Table 2). Two carcasses were not identifiable to species. During the pre-treatment period between 1 May and 26 July 2010, we searched 15 control turbines daily for all but 2 days (16 May and 2 June) and 10 Deterrent turbines daily for all but 4 days (9, 20, 24, 25 July 2010) due to heavy rain, or facility maintenance. During the treatment period between 1 August and 15 October, we searched 15 control turbines daily for all but 4 days (26 August; 22, 29, 30 September 2010) and 10 Deterrent turbines daily for all but 3 days (19 August; 9, 30 September 2010) due to heavy rain or facility maintenance. During the pre-treatment period from 1 May to 26 July 2010, we found 59 carcasses comprising 6 species of bats (37 at control, 22 at Deterrent). During the treatment period, we found 223 carcasses comprising 6 species of bats (162 at control, 61 at Deterrent; Table 3). Fatalities were found at all 25 turbines searched and time required to search each plot ranged from 12–100 minutes in both years of the study.

Fatality Estimates in 2009

A total of 278 trial carcasses were used to estimate searcher efficiency in this study. One hundred thirty-nine of the 145 (96%) carcasses in the Easy class that persisted >7 days were found by searchers, while 105 of the 123 (85%) carcasses in the Moderate class that persisted long enough to be observed were found. Eight of 10 (80%) carcasses in the Difficult class were found. A logistic regression model of the odds of detection given persistence as a function of visibility classes was fit to the data and there was strong evidence of a difference in searcher efficiency among the visibility classes ($\chi^2 = 10.32, p < 0.006$).

Data from 351 scavenger removal trial carcasses were fit to an interval-censored parametric failure time model. Average carcass persistence time was found to be strongly related to visibility classes ($\chi^2 = 6.58, p = 0.037$). Average persistence time was estimated to be 9.4 days (95% CI: 7.7, 11.7 days), 13.9 days (95% CI: 10.8, 18.3 days) and 8.7 days (95% CI: Deterrent 4.6, 16.1 days) in Easy, Moderate and Difficult visibility classes respectively. Estimates of the probability of a bat carcass persisting for 1 day (r) were 0.948 (95% CI: 0.938, 0.958), 0.964 (95% CI: 0.955, 0.973) and 0.942 (95% CI: 0.900, 0.970), respectively.

The average per-turbine fatality rate at Deterrent turbines was significantly less than at control turbines ($F_{1,23} = 14.7, p = 0.0009$). We estimated an average of 11.6 bats (95% CI: 9.4, 14.1) were killed per turbine at Deterrent turbines during this period, compared to 18.4 bats (95%

Table 2. Number of bats by species and age/sex class found under turbines at the Locust Ridge Wind Project, Columbia and Schuylkill Counties, Pennsylvania, 1 April–15 November 2009.

2009						
	Adult male	Adult female	Juvenile male	Juvenile female	Unknown	Total
Control						
Big brown	3	-	2	3	2	10
Eastern red	6	2	1	-	4	13
Hoary	11	8	2	3	6	30
Little brown	12	2	6	2	2	24
Silver-haired	12	8	3	2	1	26
Tri-colored	12	2	8	5	4	31
Unknown	-	-	-	-	1	1
Sub-total	<i>56</i>	<i>22</i>	<i>22</i>	<i>15</i>	<i>20</i>	135
Deterrent						
Big brown	1	-	2	-	1	4
Eastern red	2	3	1	2	1	9
Hoary	6	1	-	1	2	10
Little brown	9	2	1	-	1	13
Silver-haired	1	1	-	1	5	8
Tri-colored	3	2	2	4	2	13
Unknown	-	-	-	-	2	2
Sub-total	<i>22</i>	<i>9</i>	<i>6</i>	<i>8</i>	<i>14</i>	59
Total	78	31	28	23	34	194

Table 3. Number of bats by species and age/sex class found under turbines at the Locust Ridge Wind Project, Columbia and Schuylkill Counties, Pennsylvania, 1 May–26 July (Pre-experiment phase) and 31 July–9 October (experiment phase) 2010.

2010 Pre-treatment period (1 May–26 July)						
	Adult male	Adult female	Juvenile male	Juvenile female	Unknown	Total
Control						
Big brown	5	1	-	-	2	8
Eastern red	4	7	-	-	-	11
Hoary	6	4	-	-	1	11
Little brown	1	2	-	-	-	3
Silver-haired	1	1	-	-	-	2
Tri-colored	2	-	-	-	-	2
Unknown	-	-	-	-	-	-
Sub-total	<i>19</i>	<i>15</i>	-	-	3	37
Deterrent						
Big brown	5	1	-	-	-	6
Eastern red	6	1	-	-	-	7
Hoary	4	1	-	1	1	7
Little brown	-	-	-	-	-	-
Silver-haired	-	-	-	-	-	-
Tri-colored	2	-	-	-	-	2
Unknown	-	-	-	-	-	-
Sub-total	<i>17</i>	<i>3</i>	-	<i>1</i>	<i>1</i>	22
Total	36	18	0	1	4	59

Table 3. - Continued.

2010 Treatment period (31 July–9 August)						
	Adult male	Adult female	Juvenile male	Juvenile female	Unknown	Total
Control						
Big brown	2	4	2	1	-	9
Eastern red	28	19	-	-	3	50
Hoary	32	10	4	4	11	61
Little brown	6	-	-	-	-	6
Silver-haired	9	10	-	-	1	20
Tri-colored	8	2	1	1	4	16
Unknown	-	-	-	-	-	-
Sub-total	85	45	7	6	19	162
Deterrent						
Big brown	1	-	-	-	-	1
Eastern red	9	10	-	-	3	22
Hoary	11	6	-	2	3	22
Little brown	1	1	-	-	1	3
Silver-haired	1	1	1	-	2	5
Tri-colored	2	2	1	-	3	8
Unknown	-	-	-	-	-	-
Sub-total	25	20	2	2	12	61
Total	110	65	9	8	31	223

CI: 16.0, 21.3) killed per turbine at control turbines (Figure 6). We estimated 60% higher fatality (95% CI: 26%, 104%) per control turbine than per Deterrent turbine from 15 August to 10 October 2009, or conversely, 21–51% estimated fewer bats were killed per Deterrent turbine than per PGC turbine during this period.

Table 4 presents estimated bat fatalities (mean and 95% confidence intervals) for each species of bat killed per turbine, adjusted for searcher efficiency, carcass removal, and area, at control and Deterrent turbines in 2009. We estimated twice as many hoary bats ($\bar{x} = 2.09$, 95% CI = 1.18, 4.04) killed per control turbine than Deterrent turbine, and nearly twice as many silver-haired bats ($\bar{x} = 1.88$, 95% CI = 0.92, 5.14), although the estimated effect was not significant for this species (Table 5). Results for other species were highly variable with no statistically significant difference between turbine groups.

Fatality Estimates in 2010

A total of 169 bat carcasses were used to estimate searcher efficiency in this study. Eighty three of 86 (97%) carcasses in the Easy class that persisted >7 days were found by searchers, while 59 of 70 (84%) carcasses in the Moderate class that persisted long enough to be observed were found. Eight of 13 (62%) carcasses in the Difficult class were found. Because no fatalities were found in the Very Difficult class, we removed the 6 bats placed in this class from our analysis. A logistic regression model of the odds of detection given persistence was fit to the visibility classes and there was strong evidence of a difference in searcher efficiency among the visibility classes ($\chi^2 = 14.59$, $p < 0.007$).

Data from 408 scavenger removal trial carcasses were fit to an interval-censored parametric failure time model. Average carcass persistence time was found not to be related to visibility class ($\chi^2 = 0.56$, $p = 0.907$), but there was moderate evidence that average persistence time was longer before the treatment period than during the treatment period ($\chi^2 = 4.27$, $p = 0.12$). Average persistence time was estimated to be 7.8 days (95% CI: 6.4, 9.6 days) prior to implementation of the treatments and 6.2 days (95% CI: 5.4, 7.1 days) during the implementation of the treatments. This slight difference in average persistence time had little effect on the probability of a carcass persisting through the search interval. The estimated probability of a bat carcass persisting for 1 day (r) was 0.939 (95% CI: 0.926, 0.950) prior to the treatment period and 0.923 (95% CI: 0.912, 0.933) during the treatment period.

Bat fatality data from the pre-treatment period were used to evaluate if there were inherent difference between control and Deterrent turbines. We used a BACI design to determine whether the ratio of average per-turbine fatality at control turbines ($n = 15$) to Deterrent turbines ($n = 10$) during implementation of the deterrents was significantly greater than it was in the period immediately preceding implementation of the treatments. There was marginal evidence that the ratio of control:Deterrent fatalities was greater during the treatment period than in the pre-treatment period ($F_{1,23} = 3.9$, $p = 0.061$). During the pre-treatment period, prior to implementation of the deterrents, fatality per control turbine was estimated to be 1.09 times greater than per Deterrent turbine (95% CI: 0.74–1.61). While this was not statistically significant, it represented an initial inherent difference of about 10% in the fatality rate between the two sets.

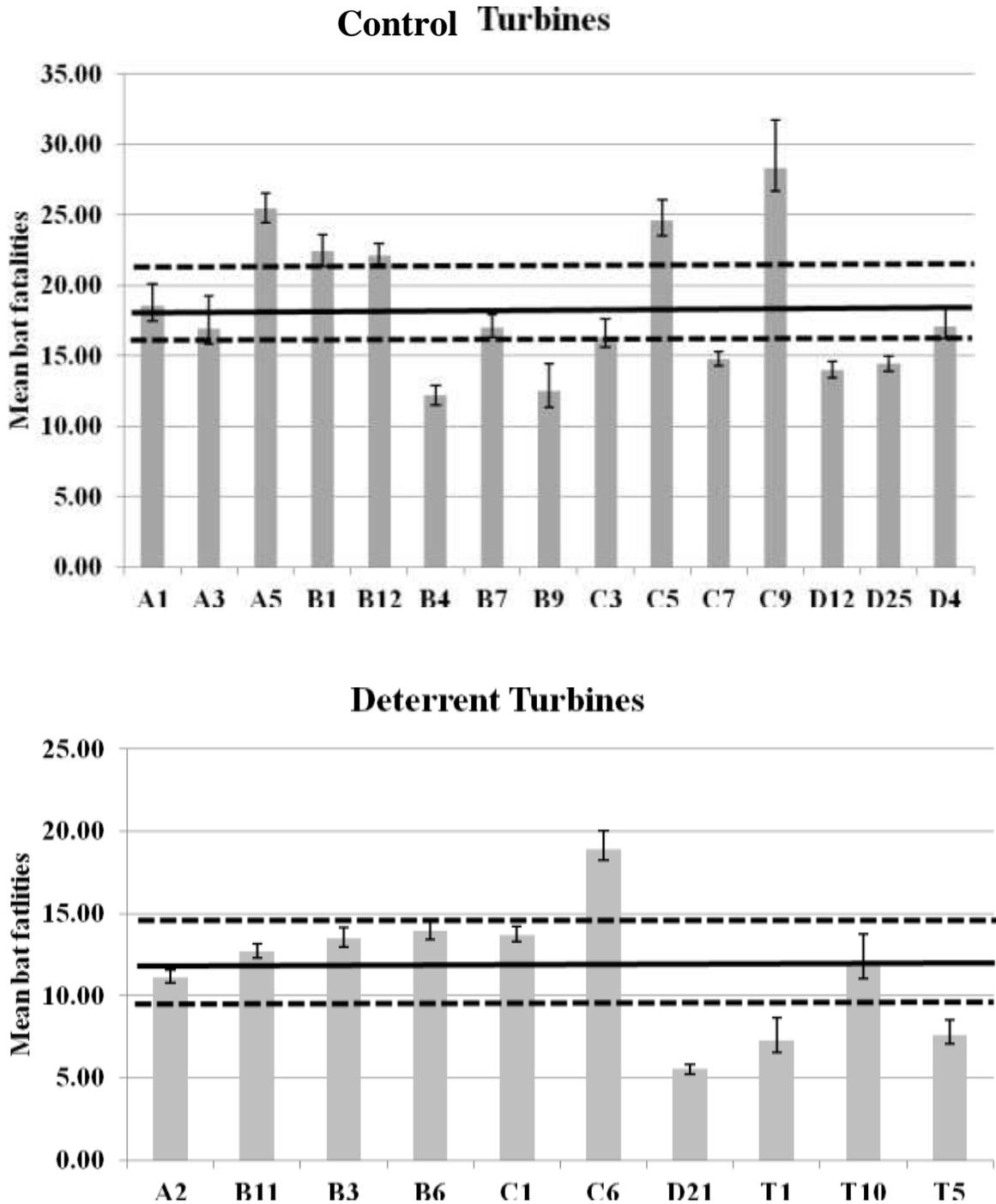
Table 4. Number of each species found (N) and the estimated bat fatalities/turbine (mean and 95% confidence intervals [CI]) for each species of bat per turbine, adjusted for searcher efficiency, carcass removal, and area, at control and Deterrent turbines at the Locust Ridge Wind Project in Columbia and Schuylkill Counties, Pennsylvania, 15 August–10 October 2009.

<i>Species</i>	<u>Control Turbines</u>				<u>Deterrent Turbines</u>			
	N	Mean	Lower 95% CI	Upper 95% CI	N	Mean	Lower 95% CI	Upper 95% CI
Big brown bat	10	1.34	0.35	2.59	4	0.78	0.20	1.36
Eastern red bat	13	1.81	0.95	2.83	9	1.73	0.73	2.73
Hoary bat	30	4.14	3.13	5.19	10	1.98	1.12	3.22
Little brown bat	24	3.36	2.14	5.05	13	2.66	1.57	3.82
Silver-haired bat	26	3.51	2.08	4.98	9	1.85	0.75	3.27
Tri-colored bat	31	4.15	2.36	6.20	13	2.47	1.29	3.99
Unknown bat	1	0.12	0.10	0.48	1	0.17	0.16	0.51

Table 5. Ratio between bat fatalities per control turbine relative to Deterrent turbines (mean and 95% confidence intervals [CI]) for each species of bat from the Locust Ridge Wind Project in Columbia and Schuylkill Counties, Pennsylvania, 15 August–10 October 2009. Confidence intervals that do not include 1.0 are considered statistically significant (*).

<i>Species</i>	Mean Ratio Control:Deterrent	Lower 95% CI	Upper 95% CI
Big brown bat	1.74	0.41	6.13
Eastern red bat	1.06	0.44	2.75
Hoary bat*	2.09	1.18	4.04
Little brown bat	1.27	0.71	2.36
Silver-haired bat	1.88	0.92	5.14
Tri-colored bat	1.68	0.80	3.58
Unknown bat	0.12	0.00	2.28

Figure 6. Mean estimated bat fatalities/turbine (\pm 95% confidence intervals) for all species of bat, adjusted for searcher efficiency, carcass removal, and area, for each control and Deterrent turbine in relation to overall mean (solid line; 95% confidence intervals dashed lines) for each group at the Locust Ridge Wind Project in Columbia and Schuylkill Counties, Pennsylvania, 15 August–10 October 2009.



During the treatment period, we estimated an average of 12.8 bats (95% CI: 9.5, 17.2) were killed per turbine at Deterrent turbines compared to 22.9 bats (95% CI: 18.0, 29.3) killed per turbine at control turbines (Figure 7). Bat fatalities per control turbine was estimated to be 1.8 times greater than per Deterrent turbine (95% CI: 1.22–2.64); in other words, 18–62% fewer bats killed per Deterrent turbines relative to control turbines during the treatment. As stated above, however, fatality per control turbine was estimated to be 1.09 times greater than per Deterrent turbine (95% CI: 0.74–1.61) prior to implementation of the treatment. Thus, the ratio of fatality per control turbine relative to Deterrent turbines after implementing the treatment was estimated to be 1.64 times greater than the pre-treatment period ratio (95% CI: 0.98, 2.76). In other words, between 2% more and 64% fewer bats were killed per Deterrent turbine relative to control turbines after accounting for inherent turbine differences prior to treatment implementation.

Estimated bat fatalities (mean and 95% confidence intervals) for each species of bat killed per turbine, adjusted for searcher efficiency, carcass removal, and area, at control and Deterrent turbines in 2010 are presented in Table 6. In 2010, we were able to compare the fatality rates during treatment with what was occurring at the same locations pre-treatment. Prior to implementation of the deterrents, we estimated 1.47 times as many hoary bats (95% CI = 0.39, 3.42) and 1.32 times as many silver-haired bats (95% CI = 0.47, 3.27) killed per control turbine than Deterrent turbine. So although we estimated nearly twice as many hoary bats (\bar{x} = 1.88, 95% CI = 1.19, 2.82) and nearly 4 times as many silver-haired bats (\bar{x} = 3.78, 95% CI = 1.12, 12.82; Table 7) killed per control turbine than Deterrent turbine during the treatment period, these represented only about a 20% increase in fatality relative to the pre-treatment period. High variation among turbines, small numbers of carcasses found and frequent zero-counts of these and other species at each turbine prevented formal statistical tests of these ratios using the BACI design.

DISCUSSION

Previous research has indicated difficulty to mask or “jam” bats' echolocation except under specific conditions (e.g., Griffin et al. 1963, Møhl and Surlykke 1989). Indeed, bats can actually adjust their echolocation under jamming conditions (e.g., Ulanovsky et al. 2004, Gillam and McCracken 2007). Bats are, however, likely “uncomfortable” when broadband ultrasound is present because it forces them to shift their call frequencies to avoid overlap, which in turn will lead to suboptimal use of echolocation or they may not echolocate at all (Griffin 1958, Ulanovsky et al. 2004).

In contrast to previously tested acoustic “repellers” (Hurley and Fenton 1980), the device we have developed shows some promise for deterring bats from the surrounding airspace near wind turbines. This study represents the first field test of a deterrent device to reduce bat fatalities at wind turbines by comparing fatalities at treated and untreated turbines. Our findings generally corroborate with previous conclusions that a regime of presumably uncomfortable or disorienting ultrasound can deter bats from occupying such a treated airspace (Spanjer 2006, Szewczak and Arnett 2006, 2007, Horn et al. 2007). While the response we observed (~18–62%

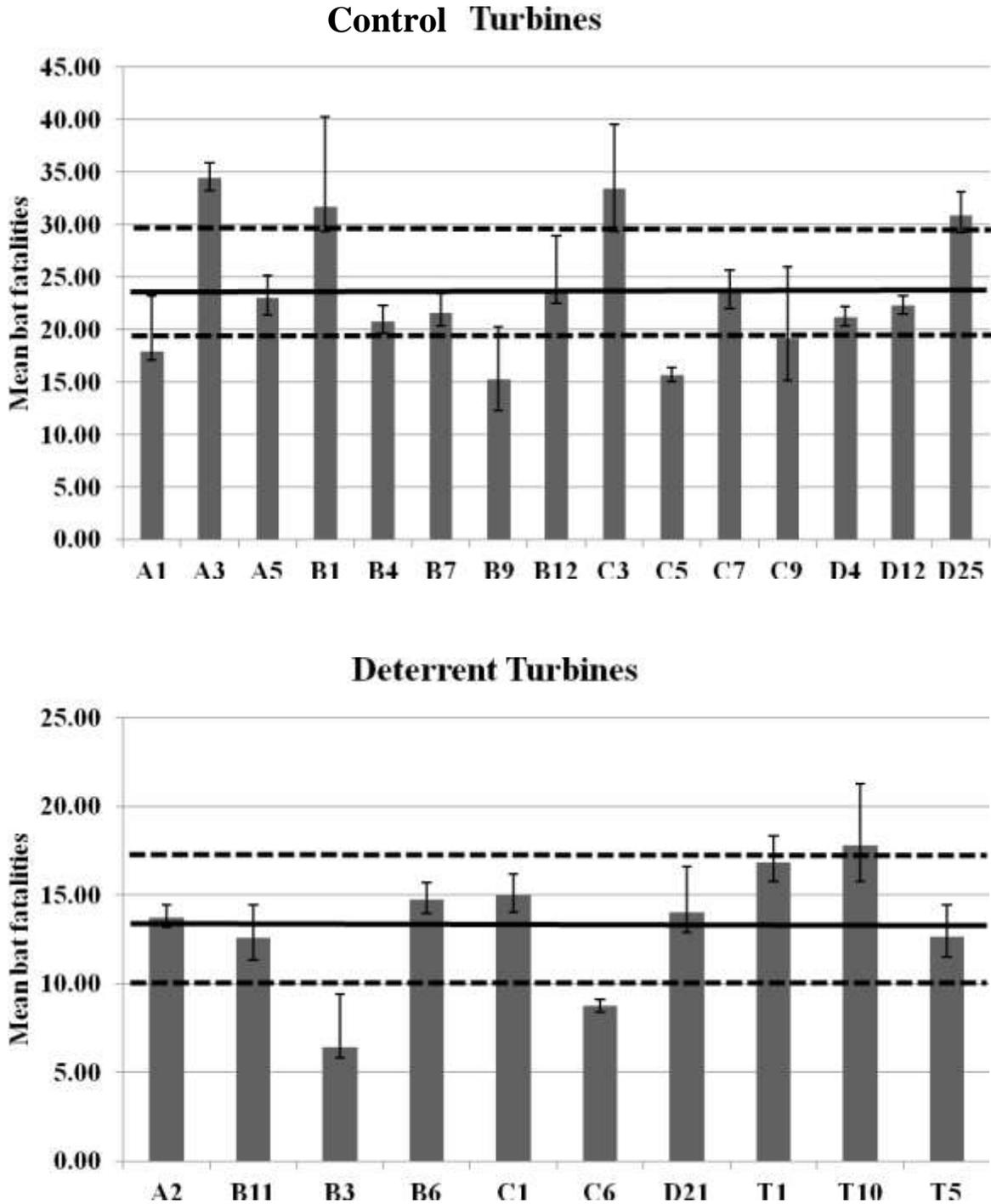
Table 6. Estimated bat fatalities/turbine (mean and 95% confidence intervals [CI]) for each species of bat per turbine, adjusted for searcher efficiency, carcass removal, and area, at control and Deterrent turbines at the Locust Ridge Wind Project in Columbia and Schuylkill Counties, Pennsylvania, 31 July–9 October 2010.

<i>Species</i>	<u>Control Turbines</u>				<u>Deterrent Turbines</u>			
	N	Mean	Lower 95% CI	Upper 95% CI	N	Mean	Lower 95% CI	Upper 95% CI
Big brown bat	9	1.19	0.39	2.12	2	0.38	0.23	0.85
Eastern red bat	50	7.16	5.32	9.27	22	4.77	2.70	6.92
Hoary bat	61	9.12	7.08	11.70	22	5.02	3.37	7.31
Little brown bat	6	0.87	0.39	1.38	3	0.65	0.20	1.27
Silver-haired bat	20	2.87	1.48	4.47	5	1.00	0.18	2.03
Tri-colored bat	16	2.32	1.37	3.38	8	1.55	0.91	2.23

Table 7. Ratio between bat fatalities per control turbine relative to deterrent turbines (mean and 95% confidence intervals [CI]) for each species of bat from the Locust Ridge Wind Project in Columbia and Schuylkill Counties, Pennsylvania, 31 July–9 October 2010. Confidence intervals that do not include 1.0 are considered statistically significant (*).

<i>Species</i>	Mean Ratio		
	Control:Deterrent	Lower 95% CI	Upper 95% CI
Big brown bat	3.72	0.70	7.87
Eastern red bat	1.59	0.93	2.78
Hoary bat*	1.88	1.19	2.82
Little brown bat	1.72	0.43	5.22
Silver-haired bat*	3.78	1.12	12.82
Tri-colored bat	1.59	0.84	2.96

Figure 7. Mean estimated bat fatalities (\pm 95% confidence intervals) for all species of bat, adjusted for searcher efficiency, carcass removal, and area, for each control and Deterrent turbine in relation to overall mean (solid line; 95% confidence intervals dashed lines) for each group at the Locust Ridge Wind Project in Columbia and Schuylkill Counties, Pennsylvania, 31 July–9 October 2010.



reduction in fatality) generally falls within the range of variation among turbines we studied in 2009, nothing in the statistical evaluation of the data suggested that our random selection of the 10 treatment turbines somehow skewed the mortality rates among the turbines we chose. We acknowledge that 3 of our Deterrent turbines had to be located on the Locust Ridge I portion of the facility where no control turbines were selected. While this could have influenced the results, we noted in 2009 that two of these three turbines (T1 and T5) had fewer mean fatalities relative to the overall mean for deterrent turbines (Figure 6), while in 2010, the mean fatalities of all three of these turbines were generally equal to or greater than the overall mean for deterrents. Fatalities at other turbines in both the control and Deterrent set also varied from one year to the next and we do not believe data from the three turbines from Locust Ridge I biased our findings. In 2010, we examined potential inherent difference between the two sets of turbines and our findings suggested only a minor difference existed in fatalities between control and Deterrent turbines prior to implementation of the treatment. However, we caution that data from our pre-treatment period in 2010 was collected prior to migration of migratory tree roosting species and the ratio of migrant to non-migrant species was different between these two periods in our study. Thus, different levels of fatality, different species composition, and possibly different behaviors of the bats during the two phases may have influenced our findings regarding inherent differences between control and Deterrent turbines. Future field tests of deterrent devices should better account for potential differences in fatalities among different species when determining inherent variation among sample turbines.

The effectiveness of ultrasonic deterrents as a means to prevent bat fatalities at wind turbines is limited by the distance and area that ultrasound can be broadcast. Unfortunately, the rapid attenuation of ultrasound, which is heavily influenced by humidity (see Appendix 1), in air limits the effective range that it can be broadcast. Nightly humidity in this region of Pennsylvania averaged 86.5% in August 2009, 84.8% in September 2009, 80% in August 2010, and 76.8% in September 2010 (source http://climate.met.psu.edu/www_prod/). Assuming a constant temperature of 20° C and air pressure of 101.325 kPa and 80% humidity, the theoretical distance to "jam" bats at the assumed 65 dB level only extends to 20 m for the 20-30 kHz range, and declines to only 5-10 m for the upper frequency ranges of broadcast (70-100 kHz; Appendix 1). Ultrasound emission in the perpendicular plane of the rotor-swept area may be adequate to affect approaching bats, particularly those species influenced at the lower frequencies. However, it is clear that effective emissions in the parallel plane of the rotor-swept area will be difficult if not impossible to achieve based on sound attenuation in humid environments. The effective airspace would be different and larger in more arid environments, however (Appendix 1). We also note that some devices were not operating all the time during our study, due to malfunctions. Although we were unable to account for this factor in our analysis, clearly the affected airspace was reduced when some devices were inactive, which further influenced our findings.

We assume that as bats encounter a gradient of increasingly strong emissions as they approach the deterrent device, they will respond by flying opposite to that gradient to escape the effect of the emissions. However, at present we know little about the general responses that various species have upon entering a large field of ultrasound emissions. It is therefore important to consider our assumptions when interpreting the results of this and our past studies of deterrents. Although our acoustic deterrent device could only generate a limited effective volume of uncomfortable airspace, bats could have detected the presence of such airspace from a

greater range, possibly beyond the rotor swept area. Bats previously experiencing the discomfort of ultrasound broadcast may avoid approaching other treated towers, which they could detect as treated from beyond the zone of discomfort. In this way, ultrasound broadcast may effectively serve as acoustic beacons to direct bats away from wind turbines. Over time, bats may learn to avoid all turbines from their experience with those equipped with deterrents. Conversely, bats may habituate to the presence of ultrasound emissions and acoustic deterrents may actually lose their effectiveness over time. However, Szewczak and Arnett (2007) reported that bats did not appear to habituate or accommodate to the presence of ultrasound emitted from a previous prototype deterrent. They found that over the five to seven days of monitored treatment, the number of bats entering the treated airspace declined to 4% of control levels, less than half of the first night of treatment. Just as bat capture success in mist nets declines on successive nights as bats apparently learn the presence of the nets and thereafter avoid them (Kunz et al 2009), Szewczak and Arnett (2007) speculated that after experiencing a disagreeable encounter with the ultrasound treated airspace bats may opt to subsequently avoid it. In practice, the actual decline of activity at any treated site will likely depend upon the immigration of naïve bats into the area. We did not monitor bat activity via night vision cameras (see Szewczak and Arnett 2006, 2007) or with thermal imaging cameras (Horn et al. 2007, 2008) and, thus, were unable to assess activity patterns of bats simultaneous with fatality searches. It is possible that insects preyed on by bats in this region were deterred from the turbines, which could represent the ultimate cause of avoiding treated turbines. Indeed, studies have demonstrated that ultrasound can repel insects (e.g., Belton and Kempster 1962) and influence their reproduction (Huang et al. 2011). However, we did not assess insect abundance and suggest future studies should attempt to address causal factors of avoidance including affect on insect prey.

The effectiveness of acoustic deterrents will likely vary among different species of bats. Hoary bats, for example, employ the lowest frequency range of the species we studied (~20–25 kHz) and may be affected more so than other species that use higher frequencies and perhaps fly at further distances from the device. Hoary bats had significantly fewer fatalities at turbines with deterrents relative to those without them in both years, and silver-haired bats also had fewer fatalities at turbines with deterrents in 2010. In 2010, however, we were able to compare the fatality rates during treatment with what was occurring at the same locations pre-treatment and after accounting for inherent differences between turbine sets prior to treatment, hoary and silver-haired bats killed per control turbine relative to Deterrent turbines during the treatment period represented about a 20% increase in fatality over the pre-treatment period. High variation among turbines, small numbers of carcasses found and frequent zero-counts of these and other species at each turbine prevented formal statistical tests of these ratios using the BACI design. Species-specific effectiveness warrants further investigation in a study with more power to detect differences among species. Such future studies hopefully will also elucidate whether deterrents can eventually serve as a mitigation tool for minimizing or eliminating take of threatened or endangered species such as the Indiana bat (*Myotis sodalis*). The limited range of ultrasound broadcast from a wind turbine tower or nacelle might have only a moderate contribution toward reducing impacts of bats randomly flying through the rotor-swept area. However, for bats that may be drawn to and approach turbine towers as potential roosts or gathering sites (Kunz et al. 2007, Cryan 2008), the combination of effective range and learned avoidance response to ultrasound broadcast may have longer term effects in reducing bat mortality at wind turbines.

This study, and previous experiments with earlier prototypes, revealed that broadband ultrasound broadcasts may affect bat behavior directly by discouraging them from approaching the sound source, or indirectly by reducing the time bats spend foraging near a turbine if insects are repelled by ultrasound (e.g., Belton and Kempster 1962, Huang et al. 2011; also recognizing not all insects have ears to detect ultrasound) and ultimately reduce bat fatalities at wind turbines. However, variation among turbines yielded inconclusive evidence of a strong effect of deterrents on bat fatality and while the approach may hold some promise, further refinement and investigation is needed. We did experience technical issues in both years of the study, including water leakage, that rendered some deterrents inoperable during portions of the study period which clearly influenced our findings. Thus, results from this study may reflect a more conservative estimate of potential fatality reduction achievable through application of the deterrent device we tested. Still, we caution that the response estimated in this study (~18–62%) falls generally within the range of variation for bat fatalities among turbines in this and other studies in the region (e.g., Arnett 2005, Arnett et al. 2009, 2010). Additionally, deterrents resulted in lower reductions in bat fatality relative to curtailing turbine operations by increasing cut-in speeds (44–93%; Arnett et al. 2011). We further caution that it would be premature and unwarranted to conclude or interpret from these initial results that this technology provides an operational deterrent device ready for broad-scale deployment at wind facilities. While we do not consider acoustic deterrents to be an acceptable mitigation strategy at this time, with further experimentation and modifications, this type of deterrent method may prove successful and broadly applicable for protecting bats from harmful encounters with wind turbine blades. Future research and development and field studies should attempt to improve the device and its weatherproofing and emission performance, and optimize the placement and number of devices on each turbine that would affect the greatest amount of airspace in the rotor-swept area to estimate potential maximum effectiveness of this tool to reduce bat fatalities. Future efforts also must evaluate the cost-effectiveness of deterrents in relation to different curtailment strategies to allow a cost-benefit analysis for mitigating bat fatalities.

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APPENDIX 1
(Select Specifications for Deterrent Device)

Appendix 1a. Calculated decibel level at different distances and frequencies at two different levels of relative humidity (10 and 40%) for acoustic deterrent devices used in this study. Calculations assume ambient temperature of 20° C and air pressure of 101.325 kPa (kilopascal).

Calculated Decibel Level at Distance and Frequency									
(Assumes 20° C at 10% relative humidity and pressure of 101.325 kPa)									
Distance (m)	Frequency (kHz)								
	20	30	40	50	60	70	80	90	100
1	102	107	112	122	122	117	114.5	114.5	117
5	87.0	91.6	96.2	105.6	104.7	99.1	95.7	94.5	95.8
10	79.7	83.9	87.9	96.6	94.4	88.1	83.7	81.0	80.8
15	74.8	78.7	82.0	90.1	86.7	79.7	74.2	70.0	68.3
20	71.0	74.5	77.2	84.6	80.0	72.3	65.7	60.0	56.8
25	67.8	70.8	73.0	79.6	73.9	65.4	57.7	50.6	45.8
30	64.9	67.5	69.1	75.0	68.1	58.9	50.2	41.6	35.3
35	62.3	64.5	65.5	70.7	62.6	52.6	42.8	32.7	24.9
40	59.8	61.6	62.0	66.5	57.2	46.5	35.7	24.1	14.8
45	57.5	58.8	58.7	62.5	52.0	40.6	28.6	15.6	4.7
50	55.3	56.2	55.5	58.6	46.9	34.8	21.7	7.2	-5.2
55	53.2	53.7	52.4	54.7	41.8	29.0	14.9	-1.1	-15.0
60	51.1	51.2	49.3	51.0	36.9	23.3	8.1	-9.4	-24.8

Calculated Decibel Level at Distance and Frequency									
(Assumes 20° C at 40% relative humidity and pressure of 101.325 kPa)									
Distance (m)	Frequency (kHz)								
	20	30	40	50	60	70	80	90	100
1	102	107	112	122	122	117	114.5	114.5	117
5	85.7	89.3	93.2	102.0	100.8	94.9	91.3	90.1	91.4
10	76.8	78.5	81.2	88.4	85.8	78.7	73.8	71.0	70.9
15	70.4	70.3	71.7	77.3	73.3	65.0	58.8	54.5	52.9
20	65.0	63.1	63.2	67.2	61.8	52.4	44.8	38.9	35.9
25	60.1	56.4	55.2	57.8	50.8	40.3	31.3	23.9	19.4
30	55.6	50.2	47.7	48.6	40.3	28.5	18.3	9.3	3.4
35	51.4	44.1	40.3	39.7	29.9	17.0	5.4	-5.1	-12.5
40	47.3	38.2	33.2	31.0	19.8	5.7	-7.2	-19.3	-28.1
45	43.4	32.5	26.1	22.4	9.7	-5.5	-19.8	-33.4	-43.7
50	39.6	26.9	19.2	13.9	-0.2	-16.5	-32.2	-47.3	-59.1
55	35.9	21.3	12.4	5.5	-10.0	-27.5	-44.5	-61.2	-74.4
60	32.2	15.9	5.6	-2.8	-19.8	-38.4	-56.8	-75.0	-89.7

Upper Target (dB) 65
 lower Target (dB) 35

Appendix 1a. - continued.

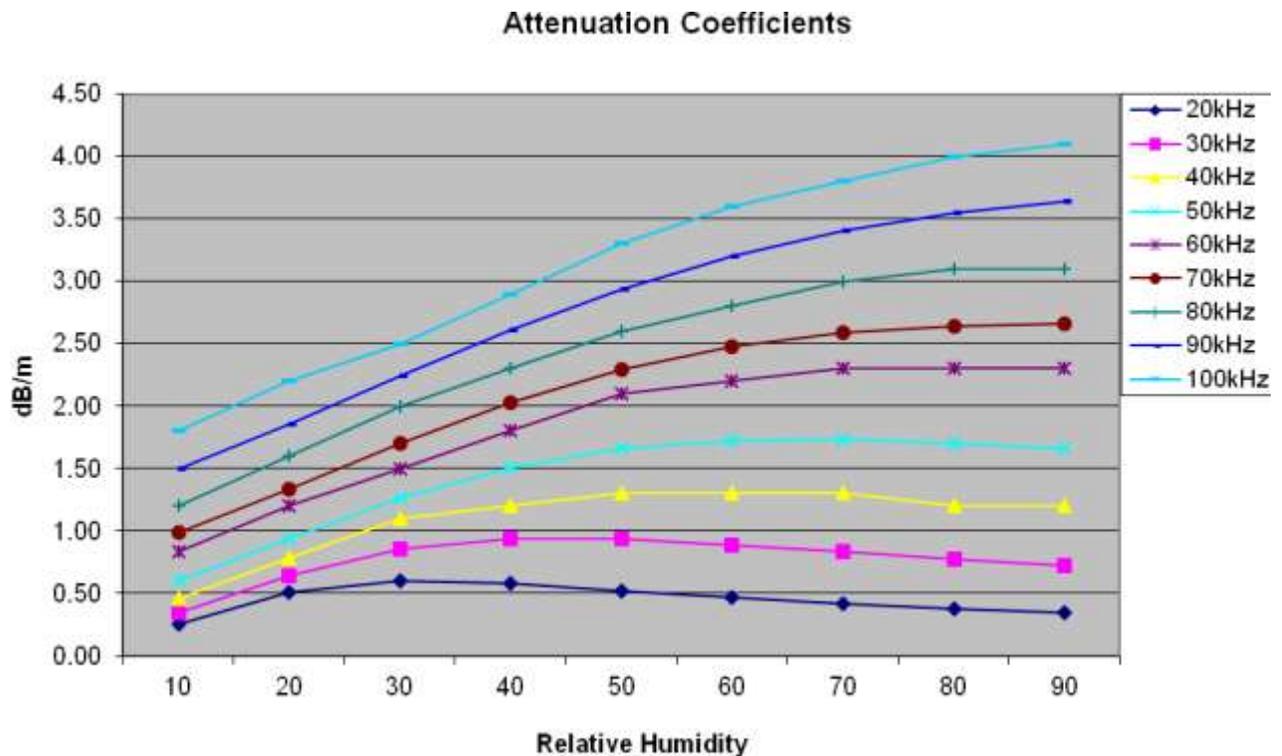
Calculated Decibel Level at Distance and Frequency									
(Assumes 20° C at 80% relative humidity and pressure of 101.325 kPa)									
Distance (m)	Frequency (kHz)								
	20	30	40	50	60	70	80	90	100
1	102	107	112	122	122	117	114.5	114.5	117
5	86.5	89.9	93.2	101.2	98.8	92.4	88.1	86.3	87.0
10	78.6	80.0	81.2	86.6	81.3	73.2	66.6	62.6	61.0
15	73.2	72.6	71.7	74.6	66.3	56.5	47.6	41.3	37.5
20	68.8	66.2	63.2	63.5	52.3	40.8	29.6	21.1	15.0
25	64.9	60.4	55.2	53.1	38.8	25.6	12.1	1.4	-7.0
30	61.4	55.0	47.7	42.9	25.8	10.8	-4.9	-17.9	-28.5
35	58.2	49.8	40.3	33.1	12.9	-3.7	-21.8	-36.9	-49.9
40	55.1	44.7	33.2	23.4	0.3	-18.1	-38.4	-55.8	-71.0
45	52.2	39.8	26.1	13.8	-12.3	-32.3	-55.0	-74.6	-92.1
50	49.4	35.0	19.2	4.4	-24.7	-46.5	-71.4	-93.2	-113.0
55	46.7	30.3	12.4	-5.0	-37.0	-60.5	-87.7	-111.8	-133.8
60	44.0	25.7	5.6	-14.3	-49.3	-74.5	104.0	-130.2	-154.6

Upper Target (dB) 65
 lower Target (dB) 35

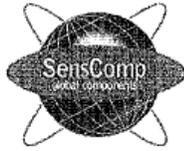
Appendix 1b. Attenuation of sound in air:

The attenuation of sound in air due to viscous, thermal and rotational loss mechanisms is simply proportional to f^2 . However, losses due to vibrational relaxation of oxygen molecules are generally much greater than those due to the classical processes, and the attenuation of sound varies significantly with temperature, water-vapor content and frequency. A method for calculating the absorption at a given temperature, humidity, and pressure can be found in ISO 9613-1 (1993). The table and figure below gives values of attenuation in dB m^{-1} for a temperature of 20°C and an air pressure of 101.325 kPa . The uncertainty is estimated to be $\pm 10\%$.

Absorption Coefficient (per ISO9613-1) at 20C and pressure of 101.325 kPa									
Frequency	Relative Humidity								
	10	20	30	40	50	60	70	80	90
20	0.26	0.51	0.60	0.58	0.52	0.47	0.42	0.38	0.35
30	0.34	0.65	0.86	0.94	0.94	0.89	0.83	0.78	0.72
40	0.46	0.78	1.10	1.20	1.30	1.30	1.30	1.20	1.20
50	0.60	0.94	1.27	1.51	1.66	1.73	1.74	1.71	1.66
60	0.84	1.20	1.50	1.80	2.10	2.20	2.30	2.30	2.30
70	0.98	1.33	1.70	2.03	2.29	2.47	2.59	2.64	2.66
80	1.20	1.60	2.00	2.30	2.60	2.80	3.00	3.10	3.10
90	1.50	1.85	2.24	2.61	2.93	3.20	3.40	3.55	3.64
100	1.80	2.20	2.50	2.90	3.30	3.60	3.80	4.00	4.10



Appendix 1c. Specifications for transducers (16 per device) used in acoustic deterrent devices used in this study.



SensComp, Inc.
 36704 Commerce Rd.
 Livonia, MI 48150
 Telephone: (734) 953-4783
 Fax: (734) 953-4518
 www.senscomp.com

600 Series Environmental Transducer

SensComp's Series 600 Environmental Grade electrostatic transducer is specifically intended for operation in air at ultrasonic frequencies. This transducer is identical to the 600 Series Instrument Grade Transducer except that the outer housing is made of 304 stainless steel for harsh environments.

Features

- 50 kHz Electrostatic Transducer
- Beam Angle of 15° at -6 dB
- Ranges from 6" to 35'
- Excellent Receive Sensitivity
- Better Suited for Harsh Environments
- Stainless Steel Housing, Perforated Protective Cover.
- Specifically Intended for Operation in Air at Ultrasonic Frequencies

Part No.

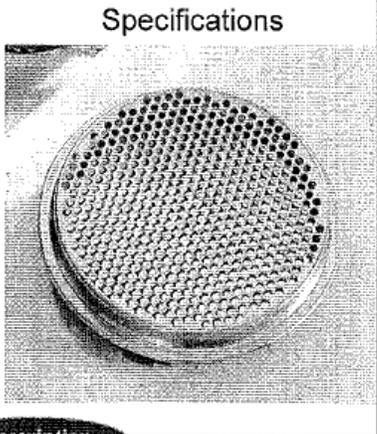
PID# 607281 – Series 600 Environmental Transducer

Benefits

- Able to Range from 6" to 35'
- Excellent Receive Sensitivity

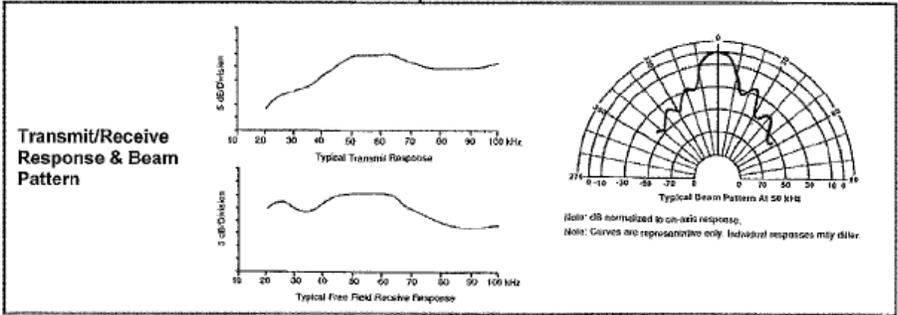
Applications

- Level Measurement, Proximity Detection, Presence Detection, Robotics, Educational Products
- Operation in Outdoor Environments



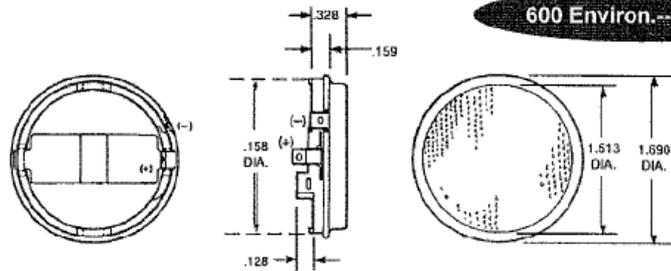
Description

The Series 600 ultra sensitive transducers feature ranging capability from 2.5 cm to 15.2 m when used with SensComp drive electronics. They are ideally suited for demanding applications where the most sensitivity possible is the highest priority. These ultrasonic transducers are among the best available when detecting soft targets. They have a broad band frequency response.



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Specifications

Usable Frequency Range		Suggested DC Bias Voltage	200V
Transmitting	See Graph	Suggested AC Driving Voltage	200V peak
Receiving	See Graph	Combined Voltage	400V max
Beam Pattern	See Graph	Capacitance at 1 kHz (typical)	400-500 pf
Typical: 15° at -6dB		(at 150 VDC bias)	
Transmitting Sensitivity	110 dB min	Operating Temperature	-30 to +70° C
at 50.0 kHz; 0dB re 20 µPa at 1 meter		(-20 to 160° F)	
(300 VAC _{pp} ; 150 VDC bias)		Storage Temperature	-40 to 120° C
Receiving Sensitivity	-42 dB min	(-40 to 250° F)	
at 50.0 kHz; 0dB = 1 volt/Pa		Relative Humidity (non condensing)	5% - 95%
(150 VDC bias)		Dimension	
Distance Range	0.15 to 10.7 M	Thickness	0.46 inch
(0.5 to 35 feet)		Diameter	1.69 inch
Resolution (± 1% over entire range)	± 3mm to 3m	Standard Finish	
(± 0.12 to 10 ft)		Foil	Gold
Weight	8.2 gm (0.29 oz)	Housing	304 Stainless Steel

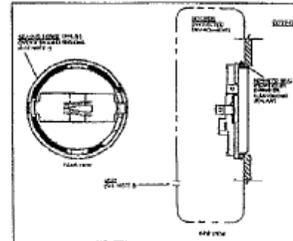
Specifications subject to change without notice

Environmental Characteristics & Exposures

Note: The following tests were performed in an environmentally controlled test facility with the transducer housed in a custom designed test enclosure. The test enclosure protects the transducer sides and back from exposure to any foreign matter. The rear of the transducer is vented to atmosphere pressure.

After each test, the transducers were cleaned and dried as necessary. Measurements were then taken at room temperature.

- Storage Temperature.....-40 TO 120° C (-40 to 250° F)
- Salt Spray Exposure (96 hours)....5% salt spray solution at 95°
- Shock and Vibration......50 G peak in each direction along 3 perpendicular axes, pulse duration: 6.5 ms; 6 G's RMS 20-2000 Hz for 6 minute.
- Water Immersion (24 hours).....(vent hole sealed)
- Freeze/Thaw Cycle (4 cycles)Spray with water, drain, expose to -20° F (-30° C) for 20 minutes, allow to warm to room temperature.
- Chemical Exposure.....Gasoline, acetone, sulphur dioxide. Samples sprayed with/ exposed to chemical, then placed in 120° F (49° C) / 90% relative humidity environment for 24 hours.



No claims are made for performance without an enclosure providing protection equal to or better than the test enclosure described above. Similarly, no claim is made for performance in any other environments or under any other condition than those controlled conditions described herein.

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APPENDIX 2
(Habitat Visibility Classes, Percent Area of Visibility Classes for Turbines)

Appendix 2a. Habitat visibility classes used during this study (following PGC 2007). Data for Classes 3 and 4 were combined during our final analyses.

% Vegetative Cover	Vegetation Height	Visibility Class
≥90% bare ground	≤15 cm tall	Class 1 (Easy)
≥25% bare ground	≤15 cm tall	Class 2 (Moderate)
≤25% bare ground	≤25% > 30 cm tall	Class 3 (Difficult)
Little or no bare ground	≥25% > 30 cm tall	Class 4 (Very Difficult)

Appendix 2b. Percentage of each habitat visibility class for the maximum plot area (120 x 126 m) for each turbine searched for the deterrent study at the Locust Ridge I and II facilities in 2009.

Deterrent:

Turbine	Easy	Moderate	Difficult	Very Difficult	Out
A2	13	10	0	3	74
B3	12	13	0	4	71
B6	13	15	2	2	69
B11	13	10	3	3	71
C1	10	13	0	9	69
C6	15	20	0	5	60
D21	12	20	6	1	61
T1	9	1	14	0	76
T5	17	2	5	10	66
T10	20	0	1	14	64

Control (PGC):

A1	11	8	1	2	78
A3	11	16	1	7	64
A5	10	8	2	4	76
B1	13	30	1	1	55
B4	12	12	0	5	71
B7	12	26	1	1	59
B9	16	18	10	3	53
B12	11	7	2	0	80
C3	11	3	8	1	77
C5	13	11	0	1	75
C7	12	10	1	3	73
C9	12	8	10	16	54
D4	11	9	3	6	71
D12	10	7	5	8	69
D25	15	6	4	0	76

Appendix 2c. Percentage of each habitat visibility class for the maximum plot area (120 x 126 m) for each turbine searched for the deterrent study at the Locust Ridge I and II facilities in 2010.

Deterrent:

Turbine	Easy	Moderate	Difficult	Very Difficult	Out
A2	13	10	0	3	74
B3	12	8	8	0	72
B6	13	15	4	0	69
B11	13	13	0	3	71
C1	10	13	0	6	72
C6	15	20	0	4	60
D21	12	21	3	1	63
T1	0	10	14	0	76
T5	20	0	5	11	64
T10	17	2	9	6	66

Control (PGC):

A1	11	8	1	2	78
A3	11	16	1	7	64
A5	10	8	2	4	76
B1	13	30	1	1	55
B4	12	12	0	5	71
B7	12	26	1	1	59
B9	16	18	10	3	53
B12	11	7	2	0	80
C3	11	3	8	1	77
C5	13	11	0	1	75
C7	12	10	1	3	73
C9	12	8	10	16	54
D4	11	9	3	6	71
D12	10	7	5	8	69
D25	15	6	4	0	76

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Issue: *The Year in Ecology and Conservation Biology***Ecosystem services provided by bats**Thomas H. Kunz,¹ Elizabeth Braun de Torrez,¹ Dana Bauer,² Tatyana Lobova,³ and Theodore H. Fleming⁴¹Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, Massachusetts.²Department of Geography, Boston University, Boston, Massachusetts. ³Department of Biology, Old Dominion University, Norfolk, Virginia. ⁴Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona

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Ecosystem services are the benefits obtained from the environment that increase human well-being. Economic valuation is conducted by measuring the human welfare gains or losses that result from changes in the provision of ecosystem services. Bats have long been postulated to play important roles in arthropod suppression, seed dispersal, and pollination; however, only recently have these ecosystem services begun to be thoroughly evaluated. Here, we review the available literature on the ecological and economic impact of ecosystem services provided by bats. We describe dietary preferences, foraging behaviors, adaptations, and phylogenetic histories of insectivorous, frugivorous, and nectarivorous bats worldwide in the context of their respective ecosystem services. For each trophic ensemble, we discuss the consequences of these ecological interactions on both natural and agricultural systems. Throughout this review, we highlight the research needed to fully determine the ecosystem services in question. Finally, we provide a comprehensive overview of economic valuation of ecosystem services. Unfortunately, few studies estimating the economic value of ecosystem services provided by bats have been conducted to date; however, we outline a framework that could be used in future studies to more fully address this question. Consumptive goods provided by bats, such as food and guano, are often exchanged in markets where the market price indicates an economic value. Nonmarket valuation methods can be used to estimate the economic value of nonconsumptive services, including inputs to agricultural production and recreational activities. Information on the ecological and economic value of ecosystem services provided by bats can be used to inform decisions regarding where and when to protect or restore bat populations and associated habitats, as well as to improve public perception of bats.

Keywords: arthropod suppression; biological pest control; ecosystem valuation; insectivory; pesticide reduction; pollination; seed dispersal; sustainable agriculture

Introduction

Ecosystems consist of living organisms and their interactions with the abiotic environment (both physical and chemical). Terrestrial ecosystems include forests, grasslands, deserts, wetlands, and caves. Aquatic ecosystems include rivers, streams, lakes, ponds, estuaries, and oceans. For thousands of years, both terrestrial and aquatic ecosystems have been subject to human alterations, including conversion of natural ecosystems to agricultural ecosystems that were needed to sustain increasing human population growth. Natural ecosystems throughout

the world have become increasingly threatened by human-generated or anthropogenic factors such as urbanization, mining, deforestation, chemical and light pollution, and invasive species. Healthy ecosystems are especially important in providing various regulatory processes (e.g., insect suppression, pollination, seed dispersal, purification of water and air, stabilization of soils, decomposition of wastes, binding of toxic substances, mitigation of diseases, mitigation of floods, and regulation of climate, etc.); products or provisions (e.g., food, fuel, fiber, and medicines); supporting processes (e.g., nutrient cycling, soil formation, and primary production); and

cultural benefits (e.g., aesthetic, spiritual, educational, and recreational) that improve human well-being.¹ These processes and products are commonly referred to as *ecosystem services*^{2,3} and have been duly recognized by the United Nations Millennium Ecosystem Assessment.^{4,5} Ecosystem services vary depending on the ecosystems and the organisms that they constitute. In this paper, we consider the role of bats in providing ecosystem services, focusing primarily on those that both regulate and provide services needed to sustain humankind, with brief references to supporting and cultural services. One of the grand challenges that society faces is how best to identify, protect, and conserve services that are critical for human and ecosystem health.^{1,6}

In their present form, bats have been on Earth for over 52 million years⁷ and during this period have diversified into at least 1,232 extant species.^{8,9} Bats have evolved an incredibly rich diversity of behavioral, roosting, and feeding habits.^{10,11} By day, many species occupy caves and cave-like structures, such as tombs and mines;¹² others roost in tree cavities and foliage,¹³ sometimes modifying foliage into unique tent-like structures.^{14–16} By night, bats fill the skies to forage on a diversity of food items ranging from insects, nectar, and fruit, to seeds, frogs, fish, small mammals, and even blood.

Unfortunately, many threats face bats today. Bats in western cultures have long been subjects of disdain and persecution and have often been depicted in the popular media as rampant vectors of disease, blood-sucking demons, ingredients of witches brew, and, at times, associated with the dark side of some religious practices.¹⁷ Common myths include that bats are attracted to and become caught in women's hair, are associated with the devil, and that extracts from the skin of bats can cure baldness.^{18,19} As with many myths and folklore, there may be some elements of truth, yet the vast majority of real or imagined images of bats often portrayed in art, poetry, books, movies, television, and the press convey them as having little redeeming value except to frighten for the sake of corporate or personal profit. By contrast, in many eastern cultures, especially those that prevailed during the middle and late Qing Dynasty (1644–1911) in China, bats were considered to be symbols of good fortune, such as long life, health, wealth, virtue, and serenity of mind.^{18,19} Today, these cultural symbols persist, but appear to be less important to modern Chinese society.²⁰

Since their evolutionary origin, some species of bats have become locally extirpated or regionally extinct, mostly for unknown reasons.²¹ In recent years, increased evidence of anthropogenic activities such as depletion or destruction of forests and other terrestrial ecosystems, disturbances to caves, depletion of food resources, overhunting for bush meat,²² increased use of pesticides,^{11,23} and the proliferation and operation of utility-scale wind energy facilities^{20,24–26} have contributed to unintended and, in some cases, unprecedented mortality of bats. Bats that roost in caves, for example, are often disturbed by unsuspecting visitors either during maternity periods or hibernation, which can lead to death or abandonment. Bats known to roost in buildings are sometimes excluded or even exterminated for perceived or real threats to human health, and sometimes simply from unfounded fear stirred by the media.

Increased human populations and associated habitat degradation have been linked to the decline of many fruit-eating and nectar-feeding species, especially of endemic taxa and certain tropical species that evolved on remote islands.²⁷ Increased human pressures by indigenous cultures in Asia, Africa, and the Pacific Islands for bush meat have also led to the local or regional extirpation of some species. The recent decline of the little brown myotis, *Myotis lucifugus*, one of the most common and widespread species in North America, has been attributed to white-nose syndrome,²⁸ an emerging disease associated with the putative fungal pathogen, *Geomyces destructans*,^{29,30} which may have been introduced from Europe.^{31,32}

Bat biologists are often asked, “Why should we care about bats?” The simple answer is that scientists care about the fate of animals and as a consequence have invested their careers in studying and, perhaps more importantly, protecting these marvelous flying mammals. Benefits that humans inadvertently and unsuspectingly derive from bats will be forever lost or severely diminished, causing both known and unknown consequences to the ecosystems in which they have evolved.

The rich diversity of dietary habits of bats, ranging from species that feed on insects and other arthropods to those that feed on fruit, nectar, and flowers,^{10,11} provide valuable ecosystem services and, thus, are the subjects of this paper, although other species that feed on seeds, frogs, fish, small

mammals, and even blood also assume important roles in ecosystems as predators or prey in sustainable ecosystems. Bats provide value to ecosystems as primary, secondary, and tertiary consumers that support and sustain both natural and human dominated ecosystems ranging from the simple to the complex. In this review, we describe the ecosystem services provided by bats that feed on insects and other arthropods, on nectar and pollen, and on fruit. Insectivorous species, largely feeding on airborne insects and other arthropods, suppress both naturally occurring and anthropogenically-generated insect populations (such as agricultural pest species and insects that annoy or transmit specific pathogens to humans and other mammals) and contribute to the maintenance of ecosystem stability. Frugivorous bats help maintain the diversity of forests by dispersing seeds across different ecosystems, often introducing novel plant species into previously disturbed landscapes³³ and to oceanic islands.³⁴ Similarly, nectarivorous bats that visit flowers provide valued ecosystem services by pollinating plants, dispersing pollen, and, thus, helping to maintain genetic diversity of flowering plants. In addition to suppressing insect populations, pollinating flowers, and dispersing seeds, insectivorous, nectarivorous, and frugivorous species may redistribute nutrients and energy through their guano to sustain terrestrial, aquatic, and cave ecosystems. Lastly, where data are available, we consider the economic value of bats to terrestrial ecosystems. While data on the economic value of bats to ecosystems are limited, we present a framework that is needed to make such assessments and to examine why the diverse forms of this group of mammals deserve respect, protection, and conservation.

The role of bats in arthropod suppression

Among the estimated 1,232 extant bat species,⁸ over two thirds are either obligate or facultative insectivores (Table 1). They include species that glean insects from vegetation and water in cluttered forests to those that feed in open space above forests, grasslands, and agricultural landscapes (Fig. 1). Although popular literature commonly recognizes bats for their voracious appetites for nocturnal and crepuscular insects,³⁵ the degree to which they play a role in herbivorous arthropod suppression is not well documented. In this section, we review the available literature on the predator–prey interactions between



Figure 1. Brazilian free-tailed bat (*Tadarida brasiliensis*) flying with a moth in its mouth (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org).

bats and arthropod pests—including the magnitude of arthropod consumption by bats, the responses of prey to threats of predation, and the quantitative impacts of bats on arthropod populations—and discuss the various methods used to obtain these data. This type of information could ultimately be used to estimate the ecological and economic value of bats in both natural and agricultural systems, a topic that we discuss in detail in the section on economic valuation of ecosystem services.

Dietary considerations: what's on the menu?

Foraging modes. Insectivorous bats use various methods for capturing and consuming insect prey (Table 1). Aerial hawking bats hunt prey on the fly, often scooping insects from the air with their wing or tail membrane and transferring them to their mouths.^{36–38} Gleaning bats, those that take prey from surfaces, generally forage in cluttered environments (e.g., dense foliage) where background echoes can mask echoes from insects.^{38,39} Some gleaners are able to finely discriminate targets using low-intensity, broadband echolocation calls,^{40,41} whereas others passively listen for prey-generated sounds or use vision and/or olfaction.³⁸ Trawling bats glean insects off the surface of water using their long feet and/or tail membrane. Fly-catching and perch-hunting bats hang from perches and wait for aerial and ground-dwelling prey, respectively. These foraging modes, however, are not mutually exclusive, and it is often difficult to categorize a given species.

General insect consumption. Studies of dietary habits of insectivorous bats date back many

Table 1. An ecological classification of bats, Order Chiroptera. Taxonomy follows Wilson and Reeder.²⁴¹

Family (common name)	Number of genera, species	Distribution	Diet and foraging modes
Pteropodidae (Old World fruit bats)	42, 186	Old World tropics and subtropics	Plant visitors that feed nearly exclusively on nectar and fruit; most species feed in forest canopies, but a few feed in forest understories
Rhinolophidae (horseshoe bats)	1, 77	Old World tropics and subtropics	Insectivorous: use aerial hawking, gleaning, fly catching, perch hunting; many forage very close to the ground, hover in place, and pluck prey from spider webs
Hipposideridae (Old World leaf-nosed bats)	9, 81	Old World tropics and subtropics	Insectivorous: use aerial hawking, gleaning, fly catching, perch hunting; fly close to the ground
Megadermatidae (false vampire and yellow-winged bats)	4, 5	Old World tropics	Both insectivorous and carnivorous: primarily use perch hunting; consume arthropods and small vertebrates (e.g., fish, frogs, lizards, birds, mice, or other bats)
Rhinopomatidae (mouse-tailed or long-tailed bats)	1, 4	Old World tropics	Insectivorous: little information on foraging behavior; fly at least 6–9 m above ground; slit-like nostrils that can exclude sand and dust
Craseonycteridae (Kitti's hog-nosed bat)	1, 1	Thailand	Insectivorous: use aerial hawking, gleaning; glean insects and spiders from tree-top foliage and can hover
Emballonuridae (sac-winged, sheath-tailed, and ghost bats)	13, 51	Pantropical	Insectivorous: use primarily aerial hawking; have long narrow wings for swift flight; occasionally eat fruit
Nycteridae (slit-faced or hollow-faced bats)	1, 16	Old World tropics	Primarily insectivorous: consume insects, spiders, small scorpions; one species specializes on vertebrates (e.g., frogs, small birds); forage close to surfaces
Myzopodidae (Old World sucker-footed bat)	1, 1	Madagascar	Insectivorous: little is known about its foraging behavior
Mystacinidae (New Zealand short-tailed bats)	1, 2	New Zealand	Primarily insectivorous: use aerial hawking but well adapted to hunting arthropods on the ground; also pollinate certain terrestrial flowers and eat fruit

Continued

Table 1. Continued

Family (common name)	Number of genera, species	Distribution	Diet and foraging modes
Phyllostomidae (New World leaf-nosed bats)	55, 160	Neotropics	Diverse foraging and feeding habits, including gleaning and aerial insectivores, carnivores, blood-feeders, nectar-feeders, and fruit-eaters. Plant-visiting species forage in forest understory and canopy
Mormoopidae (ghost-faced bats, moustached bats, and naked-backed bats)	2, 10	Neotropics	Insectivorous: primarily feed on insects close to or on surfaces of water
Noctilionidae (bull dog bats)	1, 2	Neotropics	Both species capture insects in or from the surface of water; <i>Noctilio leporinus</i> eats fish, frogs, and crustaceans by trawling its long feet and claws through the water
Furipteridae (smoky bats and thumbless bats)	2, 2	Neotropics	Insectivorous: may specialize on moths and butterflies
Thyropteridae (disc-winged bats)	1, 3	Neotropics	Insectivorous: characterized by fluttery, moth-like flight; consume small insects
Natalidae (funnel-eared bats)	3, 8	Neotropics	Insectivorous: characterized by fluttery, moth-like flight; consume small insects
Molossidae (free-tailed bats)	16, 100	Cosmopolitan in tropics and subtropics	Insectivores: use aerial hawking; most species forage in open areas and are swift, straight fliers
Vespertilionidae (evening and vesper bats)	48, 407	Cosmopolitan	Primarily insectivorous: diverse foraging modes including aerial hawking (often using their tail membrane as a scoop), gleaning, trawling; a few species eat scorpions, fish, and small birds

years,^{42–49} but few have assessed the potential impacts of prey consumption on human health or natural and agricultural systems. Although it is beyond the scope of this review, there has been considerable debate as to the degree of prey selection by bats.^{38,50} While some studies have shown individuals to actively select among available prey,^{51–54} others have concluded that insectivorous bats are generalist predators, feeding on a wide diversity of taxonomic groups and opportunistically consuming appropriately sized prey according to its avail-

ability within a preferred habitat.^{48,50,55} Insectivorous bat activity and diversity are strongly correlated with arthropod abundance,^{56–58} suggesting that bats seek out areas of concentrated prey sources. Although there is considerable variation in the relative proportions consumed by different species, most insectivorous bats eat large quantities of lepidopterans (moths), coleopterans (beetles), dipterans (flies), homopterans (cicadas, leaf hoppers), and hemipterans (true bugs).^{44,47,59–63} Some species also eat unusual prey items such as scorpions and

spiders.⁶⁴ Prey size can vary from as small as 1 mm (midges and mosquitoes) to as large as 50 mm long (beetles and large moths), depending on the species of bat.^{52,59,60,65–68} Bats often forage throughout the night, returning to their roosts to nurse young and to rest during periods of low insect activity.^{59,69,70}

The magnitude of arthropod consumption by a bat varies considerably by species, season, and reproductive cycle. On average, insectivorous bats maintained in captivity have been estimated to consume up to 25% of their body mass in insects each night (*Myotis lucifugus* and *Eptesicus fuscus*,⁴⁶ *M. lucifugus* and *M. thysanodes*,⁷¹ *Lasiurus cinereus*,⁷² *Lasiorycteris noctivagans*⁷³). Under natural conditions, these estimates increase, most likely due to higher energy demands. Using field metabolic rates based on turnover of doubly labeled water, Kurta *et al.*⁷⁴ estimated that at the peak night of lactation, a 7.9 g little brown bat (*M. lucifugus*) needs to consume 9.9 g of insects (over 100% of its body mass) to account for the marked increase in energy expenditures due to this costly stage of the reproductive cycle.⁷⁵ At peak lactation, a female Brazilian free-tailed bat (*Tadarida brasiliensis*) can consume up to 70% of her body mass in insects each night; furthermore, she frequently culls her prey, consuming only the nutrient-rich abdomen of moths while discarding the wings, head, and appendages, which greatly increases feeding efficiency and hence the quantity of insects consumed.⁶¹ To put this in perspective, an average maternity colony of one million Brazilian free-tailed bats weighing 12 g each could consume up to 8.4 metric tons of insects in a single night. These studies hint at the immense capability of nightly insect consumption and at the potential role of bats in top-down suppression of arthropod populations.

Agricultural pests and pesticide use. Herbivorous arthropods destroy approximately 25–50% of crops worldwide.^{76,77} The response to these threats by modern agriculture has been predominantly through the application of synthetic pesticides, a practice that has led to many unintended consequences including human health risks, degradation of ecosystem function, evolved toxicity resistance by pests, and severe alterations of the dynamics of agribusiness.^{76,78–80} The World Resources Institute estimates that over 400 pest species have evolved resistance to one or more pesticides,

and that despite an increase in pesticide use, the proportion of crops destroyed by insect pests in the United States has doubled (to 13%) since the 1940s.⁸¹ By eliminating beneficial invertebrate and vertebrate predators through indiscriminate use of broad-spectrum insecticides, insect species that are not normally considered pests are often elevated to pest status.^{80,82} Efforts to curb the widespread and indiscriminate use of chemical pesticides include the promotion of biological controls.⁸³ An estimated 99% of potential crop pests are limited by natural ecosystems,^{80,84} of which some fraction can be attributed to predation by bats. Naylor and Ehrlich⁸⁰ estimated that the value of the global pest control ecosystem service ranges between \$54 billion and \$1 trillion, an estimate that includes reductions in both crop losses due to pests and direct/indirect costs of pesticide use. Pimentel *et al.*⁷⁷ concluded that a 50% reduction in pesticide use could be achieved with only a 0.6% increase in the cost of purchased food, provided that biological, cultural, and environmental pest control technologies are used.

Consumption of specific agricultural pests by bats. Various species of prominent agricultural insect pests have been found in the diets of bats based on identification of insect fragments in fecal samples and stomach contents. These insects include, but are not limited to, June beetles (Scarabidae), click beetles (Elateridae), leafhoppers (Cicadellidae), planthoppers (Delphacidae), the spotted cucumber beetle, (*Diabrotica undecimpunctata*, Chrysomelidae), the Asiatic oak weevil (*Cyrtopistomus castaneus*, Curculionidae), and the green stinkbug (*Acrosternum hilare*, Pentatomidae) (Table 2 and Appendix A).

Based on the dietary composition, minimum number of total insects per guano pellet, number of specific agricultural pest species in each pellet, and the number of active foraging days per year, Whitaker⁸⁵ calculated that a colony of 150 big brown bats (*Eptesicus fuscus*) in the midwestern United States annually consumes approximately 600,000 cucumber beetles, 194,000 June beetles, 158,000 leafhoppers, and 335,000 stinkbugs. Subsequently, assuming that each female cucumber beetle lays 110 eggs,⁸⁶ this average-sized bat colony could prevent the production of 33,000,000 cucumber beetle larvae (corn rootworms), which are severe crop pests (Appendix A). While these calculations include a

large number of assumptions and ignore various sources of natural variation, this study took the extra step of translating ecological data into a form more readily appreciated by the public. With the addition of data on corn rootworm damage to crops in the study area, an economic value for this colony could be estimated.

A common challenge in these investigations is the overwhelming lack of basic ecological information regarding foraging behavior and diet for many species of bats. For example, traditional dietary analyses through fecal or stomach contents have historically only identified arthropod fragments to the ordinal or familial level, rather than to species,^{46,60,69,87} and in cases where species identification is possible, it has typically been restricted to hard-bodied insects, such as beetles, that remain partially undigested. Recently, novel molecular techniques have allowed detection and species identification of both hard- and soft-bodied insects, such as lepidopterans, within guano collected from bats.^{88–93} Whitaker *et al.*⁹⁰ described the development of quantitative polymerase chain reaction (qPCR), coupled with controlled feedings of known insects to captive bats, as an approach to estimate the number or percent volume of specific insects consumed by wild bats. qPCR has been used to document consumption of the corn earworm moth (*Helicoverpa zea*) and the beet armyworm (*Spodoptera exigua*), both major pests of corn, cotton, and other crops throughout the United States, by Brazilian free-tailed bats, *Tadarida brasiliensis*, in south-central Texas.^{88,90,92} Brown⁹¹ used qPCR to identify the pecan nut casebearer moth (*Acrobasis nuxvorella*), the hickory shuckworm moth (*Cydia caryana*), and *H. zea* moths in the diet of Brazilian free-tailed bats from guano collected beneath bat houses located in organic pecan orchards. This author also identified the southern green stink bug (*Nezara viridula*) by sequencing insect fragments found in the guano (see Appendix A).

To date, Clare *et al.*⁸⁹ conducted the most comprehensive dietary analysis of an insectivorous bat. These authors extracted DNA from insect fragments found in fecal samples and used a polymerase chain reaction (PCR) coupled with a sequence-based technique to assess the diet of the eastern red bat, *Lasiurus borealis*, in Canada. Through comparison of fecal DNA sequences to a reference database, they were able to identify 127 prey species (5 orders, 16 families

of lepidopterans), some of which were notable agricultural, forest, and orchard/garden pests including gypsy moths (*Lymantria dispar*), tent caterpillars (*Malacosoma sp.*), coneworms (*Dioryctria sp.*), cutworms (*Noctua pronuba*), snout moths (*Acrobasis sp.*), and tortrix moths (*Cydia sp.*) (see Table 2 and Appendix A). All bats were captured in a provincial park that was adjacent to agricultural land. Although this study provides unprecedented detail regarding the diversity of insects consumed by the eastern red bat, the techniques used did not allow for quantification of pest consumption, and the authors did not have sufficient data to estimate the ecological or economic value of these bats to any particular ecosystem.

Direct and indirect impacts of insectivorous bats

Understanding complexities of predator–prey interactions. The studies reviewed in the previous sections document the consumption of herbivorous arthropods by bats; however, few studies have measured their actual impacts on natural or agroecosystems. Top- and midlevel predators can have direct effects on herbivore communities and indirect effects on plant communities through both density-mediated (consumption) and trait-mediated (behavioral) interactions.⁹⁴ The following sections address the research that has begun to document these interactions between insectivorous bats and their prey.

A pioneering study by Buckner dating back to the 1960s, which examined the role of vertebrate predators in the biological control of forest insects,⁹⁵ illustrates the complexities involved with assigning a value to natural predators and may serve as a template for the assessment of the ecosystem services provided by bats. Buckner asserted that three basic measurements must be made to understand a predator–prey system: density of the prey, density of the predators, and the extent of destruction of prey by the predators. Few studies have thoroughly evaluated these seemingly simple questions. Equally fundamental, but perhaps more ecologically complex, is the evaluation of an individual predator species in relation to its local ecological community. What is the predator's capacity for consumption of the prey? What are the effects of the density of prey or the presence of alternative prey on the predator's density and/or rate of consumption? What defense

Table 2. Examples of studies found in the literature documenting the consumption of agricultural insect pests by different species of bats, analytical methods used for dietary analysis, and estimated quantity of consumption^a

Pest species	Species of bat predator	Analysis	Estimate of consumption (%)
Coleoptera			
June beetles (Scarabidae)	Cave myotis, <i>Myotis velifer</i> ⁵⁹	Stomach content	15.9 of Coleoptera
	Brazilian free-tailed bat, <i>Tadarida brasiliensis</i> ⁶⁶	Fecal dissection	19.7 of Coleoptera
	Eastern red bat, <i>Lasiurus borealis</i> ²⁴²	Fecal dissection	11.2
	Northern long-eared myotis, <i>M. septentrionalis</i> ²⁴²	Fecal dissection	5.5
	Big brown bat, <i>Eptesicus fuscus</i> ^{45, 85, 242*243}	Fecal dissection	29.6
Click beetles or wire worm (Elateridae)	Big brown bat, <i>E. fuscus</i> ²⁴³	Fecal dissection	31.2
Spotted cucumber beetle, <i>Diabrotica undecimpunctata</i> (Chrysomelidae)	Big brown bat, <i>E. fuscus</i> ^{45, 85*242}	Fecal dissection	28.2
	Brazilian free-tailed bat, <i>T. brasiliensis</i> ⁶⁶	Fecal dissection	Unreported
	Evening bat, <i>Nycticeius humeralis</i> ²⁴⁴	Fecal dissection	23.5
	Indiana myotis, <i>Myotis sodalis</i> ²⁴⁵	Fecal dissection	1.1 (3.9 by frequency)
Asiatic oak weevil, <i>Cyrtopistomus castaneus</i> , (Curculionidae)	Little brown myotis, <i>Myotis lucifugus</i> ²⁴²	Fecal dissection	5.3
	Indiana myotis, <i>Myotis sodalis</i> ^{245*242}	Fecal dissection	7.7 (23.2 by frequency)
	Eastern red bat, <i>Lasiurus borealis</i> ²⁴²	Fecal dissection	29
	Big brown bat, <i>Eptesicus fuscus</i> ²⁴²	Fecal dissection	13.9
Homoptera			
Leaf hoppers (Homoptera: Cicadellidae)	Cave myotis, <i>M. velifer</i> ⁵⁹	Stomach content	17.4 of Homoptera
	Big brown bat, <i>E. fuscus</i> ^{45, 85}	Fecal dissection	8.2
	Brazilian free-tailed bat, <i>T. brasiliensis</i> ⁶⁶	Fecal dissection	37.3 of Homoptera
	Big free-tailed bat, <i>Nyctinomops macrotis</i> ²⁴⁶	Fecal dissection	26.7 (58.9 by frequency)
	Eastern pipistrelle, <i>Perimyotis subflavus</i> ²⁴²	Fecal dissection	14.5
White-backed planthopper, <i>Sogatella sp.</i> (Delphacidae)	Indiana myotis, <i>M. sodalis</i> ²⁴²	Fecal dissection	1.8 (17.9 by frequency)
	Wrinkled-lipped bats, <i>Tadarida plicata</i> ⁶³	Fecal dissection	25.3 by frequency**

Continued

Table 2. Continued

Pest species	Species of bat predator	Analysis	Estimate of consumption (%)
Hemiptera			
Stink bugs (Pentatomidae)	Brazilian free-tailed bat, <i>T. brasiliensis</i> ⁶⁶	Fecal dissection	26.8
Green stink bug, <i>Acrosternum hilare</i>	Indiana myotis, <i>Myotis sodalis</i> ²⁴⁵	Fecal dissection	0.1 (1.4 by frequency)
	Hoary bat, <i>Lasiurus cinereus</i> ²⁴²	Fecal dissection	43.8
	Eastern red bat, <i>Lasiurus borealis</i> ²⁴²	Fecal dissection	2.1
	Big brown bat, <i>E. fuscus</i> ^{45,85,242,243*}	Fecal dissection	18.3
Brown stink bug, <i>Euschistus servus</i>	Big brown bat, <i>E. fuscus</i> ²⁴²	Fecal dissection	2.5
	Northern long eared myotis, <i>M. septentrionalis</i> ²⁴²	Fecal dissection	1.0
Lepidoptera			
Corn earworm moth, <i>Helicoverpa zea</i> (Noctuidae)	Brazilian free-tailed bat, <i>T. brasiliensis</i> ^{88,92}	Molecular: qPCR	N/A
Gypsy moths, <i>Lymantria dispar</i> (Lymantriidae)	Eastern red bat, <i>Lasiurus borealis</i> ⁸⁹	Molecular: sequence based	N/A
Cutworms, <i>Noctua pronuba</i> (Noctuidae)			
Coneworms, <i>Dioryctria spp.</i> (Pyralidae)			
Tent caterpillars, <i>Malacosoma spp.</i> (Lasiocampidae)			
Tortrix moths, <i>Cydia sp.</i> (Tortricidae)			
Diptera			
Mosquitos (Culicidae)	Indiana myotis, <i>M. sodalis</i> ²⁴⁵	Fecal dissection	1.0 (4.3 by frequency)
Hessian fly, <i>Mayetoila destructor</i>	Indiana myotis, <i>M. sodalis</i> ²⁴⁵	Fecal dissection	<0.1 (0.4 by frequency)

^aEstimates of consumption are in percent volume of the total diet unless otherwise specified. See Appendix A for descriptions of pest species.

*The study from which estimates of consumption are taken if more than one.

**Estimate refers to Homoptera: “most” were *Sogatella sp.*

mechanism does the prey have and use against the predator? Buckner argued that until these aspects are studied thoroughly, the understanding of predation as a biological control factor will be incomplete. Researchers investigating invertebrate and aquatic systems have begun to do this (reviewed in Refs. 96 and 97), but few if any studies of vertebrate predators have fully addressed these important questions.

Ecosystem services of the Brazilian free-tailed bat: a case study. Of the approximately 900 insectivorous bat species, the Brazilian free-tailed bat, *Tadarida brasiliensis*, provides one of the most impressive examples of continental-scale natural pest suppression in the world.⁹⁸ Several studies have attempted to document the nightly foraging behavior and prey consumption patterns in this species



Figure 2. Brazilian free-tailed bats (*Tadarida brasiliensis*) dispersing over agricultural landscapes from a maternity roost in south-central Texas (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org).

to better understand its ecosystem service.^{62,66,99,100} Millions of Brazilian free-tailed bats migrate northward each year in the spring from Mexico to form enormous maternity colonies in limestone caves and bridges throughout the southwestern United States.^{43,101} Each evening, large numbers of bats emerge from these roosts (Fig. 2) and disperse across natural and agricultural landscapes in high enough densities to be detected by NEXRAD WSR-88D Doppler weather radars.⁹⁹ As recently as the 1950s and early 1960s, midsummer colonies of Brazilian free-tailed bats in 17 caves in the southwestern United States were estimated to total about 150 million individuals.¹⁰² However, recent estimates, based on improved census methods using thermal infrared imaging and computer detection and tracking algorithms, conclude that these same caves now house closer to nine million bats, indicating either a marked population decline or an overestimation in past observations.¹⁰³ The likelihood of historic overestimates is supported by further quantitative assessments of colony dynamics and emergence behavior of Brazilian free-tailed bats that roost in Carlsbad Caverns, New Mexico.¹⁰⁴

Although Brazilian free-tails are known to consume a wide variety of prey items (12 orders, 35 families), numerous studies indicate that moths (Lepidoptera) are their primary food source,^{61,62,66,105} including devastating agricultural pests such as the corn earworm or cotton bollworm moth (*Helicoverpa zea*) and the tobacco budworm moth (*Heliothis virescens*).^{88,98} Studies have found that the proportion of moths consumed by Brazilian free-tailed bats increases markedly during their early morning for-

aging bouts in comparison to evening foraging bouts from May to the end of June,^{66,105} a time period that coincides with the immigration of swarms of corn earworm moths and fall armyworms, *Spodoptera exigua*, into Texas from northern Mexico on prevailing winds.^{106,107} In a study on the foraging activity of these bats at high altitudes, McCracken *et al.*¹⁰⁰ documented that echolocation search calls and feeding buzzes were most abundant at ground level and at 400–500 m above ground level, the latter of which corresponds with the low-elevation southerly wind jet, a major aeroecological corridor for the nocturnal dispersal of corn earworm moths, fall armyworms, and other insects. Des Marais *et al.*¹⁰⁸ used stable isotope ratios of carbon from bat guano to estimate that more than one-half of all insects eaten by Brazilian free-tailed bats that roost in Carlsbad Caverns fed on crops, based on landscape data showing that 90% of the crops surrounding the cave were C3 plants while the majority of the native plants were C4. Similarly, Mizutani *et al.*¹⁰⁹ estimated that two-thirds of the guano sampled from a cave housing several million Brazilian free-tailed bats in Arizona included insects or other arthropods that fed on C3 crops (cotton and alfalfa) in an area dominated by native C4 vegetation.

These studies strongly suggest that Brazilian free-tailed bats opportunistically forage over agricultural fields that both produce and attract large insect populations. Research suggests that after initial arrival into Texas from northern Mexico, corn earworm and tobacco budworm moths and their progeny undergo an annual migration northward through the southern and central croplands of the United States.^{106,107} Thus, the benefits conferred to agriculture by consumption of these moths by bats may not be limited to their local foraging areas (e.g., in Texas and New Mexico) but may extend to agricultural landscapes hundreds of kilometers away. Several recent studies have estimated the economic value of the pest suppression service provided by Brazilian free-tailed bats^{98,103,110,111} and are further discussed in the section on valuation of ecosystem services.

Density-mediated direct and indirect effects: consumption. Research evaluating ecosystem services of other insectivorous bat species fall far behind that of the Brazilian free-tailed bat; however, several recent studies have provided compelling evidence that

bats can limit insect populations in both agricultural and natural systems.

For example, Williams-Guillén *et al.*¹¹² and Kalka *et al.*¹¹³ separated the effects of insectivorous birds and bats on pest suppression by conducting predator enclosure experiments in a coffee plantation in Mexico and a lowland tropical forest in Panama, respectively. Both studies placed agricultural netting around individual plants to exclude bats at night and birds during the day. Previous studies using predator enclosures attributed any results of arthropod suppression to bird predation,^{114,115} ignoring bats as potential contributors. Williams-Guillén *et al.*¹¹² found that, by excluding bats, total arthropod densities increased by 84% per coffee plant in the wet season but were not affected in the dry season. They attributed the seasonal difference to the increased abundance, reproductive activity, and hence energy demands of bats during the wet season. In both seasons, bats and birds together had the highest impact on arthropod densities, suggesting an additive effect. Although there was a clear direct effect of bats and birds on herbivorous arthropods, the authors did not find a significant indirect effect on leaf damage for any of the treatments. By contrast, Kalka *et al.*¹¹³ demonstrated that the exclusion of bats from five common tropical understory plants significantly increased both arthropod densities (by 65%) and leaf damage (by 68%) relative to control treatments. They also found that bats consistently had a higher impact on insect populations than birds. These authors emphasize that their estimates of direct and indirect impacts of both groups are likely conservative due to predation by aerial insectivores outside of the enclosures, the exclusion of large arthropods along with bats and birds, the presence of predatory arthropods in the enclosures, and their focus on understory plants rather than the more-productive forest canopy. For both of these studies, a list of insect orders that were suppressed is available in their supporting online material; however, neither study identified pests to the species level, nor did they attempt to estimate the economic value of bats in these systems.

Reiskind and Wund⁶⁷ provided compelling evidence that northern long-eared bats (*Myotis septentrionalis*) suppress mosquito (*Culex spp.*) populations through direct predation. Although bats are commonly credited for their role in mosquito control, this is the first study documenting a quanti-

tative impact on mosquito populations. Predator enclosures were erected in the field that contained artificial oviposition sites and allowed passage of naturally occurring mosquitoes. These researchers released wild-captured northern long-eared bats into the enclosures to forage for a total of nine nights. They found that nightly oviposition by mosquitoes was reduced by 32% in enclosures that contained bats when compared to control enclosures with no bats. Based on their finding of no difference between control enclosures and unenclosed artificial oviposition sites adjacent to bat enclosures, they concluded that these effects were due to predation rather than the alteration of mosquito behavior.

Enclosure and enclosure studies, such as those described above, have the potential to provide valuable information on the direct and indirect effects of bats as arthropod predators; however, results should be interpreted with caution. Enclosures effectively exclude bats that glean insects directly from vegetation but most likely have a limited effect on aerial insectivores that capture insects on the fly often far from the plant of interest. Enclosures, on the other hand, may inflate estimates of prey suppression due to unnatural conditions such as an elevated density of bats or limited availability of other suitable prey items within the enclosures.

Trait-mediated indirect interactions: ecology of fear. Predator–prey interactions are central features in all ecological communities, yet traditional models of predator–prey dynamics treat individuals as unresponsive units and do not consider the prey’s physical or behavioral response to the presence of a predator.¹¹⁶ In a fear-driven system, prey enact an inducible defense in response to the presence or threat of a predator in order to reduce the risk of consumption by altering such behaviors as predator vigilance, foraging decisions, and mate attraction.^{97,116} This behavioral plasticity may have significant impacts on species interactions, community structure, and ecosystem function.^{97,117}

The threat of predation by bats has led to the evolution of both physical and behavioral defense mechanisms in many species of moths, including aposematic signaling,^{118,119} the production of ultrasonic jamming clicks,¹²⁰ and evasive flight maneuvers¹²¹ to avoid consumption. In an agricultural setting, the presence of bats may alter the behavior

and/or population dynamics of moth pests within that system. Belton and Kempster¹²² found that the infestation rate of sweet corn (maize) by the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Pyralidae), was reduced by over 50% in test plots that were exposed to ultrasound broadcast at frequencies, amplitudes, and pulse rates characteristic of bat calls. This result provides an excellent example of the ecology of fear; however, the sample size of the study was very small (only two replicates over one season), the broadcasts may not have represented natural levels of bat activity, and possible changes in predation due to bat responses to the broadcast were not accounted for. In a laboratory study, the true armyworm, *Pseudaletia umpuncta* (Lepidoptera: Noctuidae), and the European corn borer, altered their mating behavior in response to high levels of simulated predation risk (ultrasonic bat calls) by reducing their mate-seeking behavior, pheromone production, and mating calls.¹²³ Huang *et al.*^{124,125} documented that when exposed to ultrasound in the laboratory, female Indian meal moths, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) received fewer spermatophores from males, produced fewer and smaller larvae, reduced mate calling, and reduced the length of mating time when compared to female moths not exposed to ultrasound. These studies suggest that the mere presence of bats, whether foraging due to high prey availability or being attracted to roosting opportunities, may aid in reducing damaging activities or disrupting population dynamics of insect pests in a given agricultural landscape.

Conclusions, future directions, and management of arthropod suppression services

The studies reviewed in this section hint at the immense potential for bats to provide pest suppression services in both natural and agroecosystems; however, more research is needed to adequately document the extent to which bats interact with and limit insect pest populations across the geographical landscape and over time. Some of the authors have attempted to address one or all of the three basic measurements outlined in Buckner:⁹⁵ density of predator, density of prey, and capacity of destruction of prey; however, uncertainties lie in each of these parameters. Determining the degree of spatial and temporal overlap between predator and prey, how

the densities of the predator and prey are affected by third party effects, such as alternative prey sources or competition, and how crop production affects these relationships are all examples of sources of variation and uncertainty. This information is essential in models predicting the ecological and economic value of a predator.

Unfortunately, small-scale temporal and spatial variation in the diet is often difficult to detect through traditional methods and requires extensive fieldwork. The findings by Whitaker *et al.*¹⁰⁵ and Lee and McCracken,⁶⁶ that dietary composition is markedly different between the evening and morning foraging bouts of female Brazilian free-tailed bats living in caves near major agricultural regions, illustrate the importance of taking into consideration temporal variation when characterizing the diet of a species as well as assessing any potential ecosystem service. Other studies have shown temporal variation in the diet of bats by season,^{126,127} year,^{60,128} and age class.^{129,130} Dietary variation also exists between co-occurring species and geographically within a given species.^{48,60,131–133} Additionally, many frugivorous and nectarivorous bat species (e.g., *Glossophaga soricina*;^{134,135} *Phyllostomus discolor* and *Phylloderma stenops*¹³⁶) include insects in their diets as a supplement to their dominant food sources. For example, among the 39 species of bats captured in an agricultural mosaic in Mexico, 22 were classified as omnivorous (i.e., consuming insects in addition to fruit, nectar, or meat).¹³⁷ These species are not typically considered when evaluating potential pest suppression yet undoubtedly contribute to the overall service. Findings from these studies highlight the importance of encouraging high bat diversity (not only species richness, but also reproductive class and functional diversity) in a given area to maintain ecosystem function.

A detailed resolution of dietary composition across bat species, in which identification of prey items is to species rather than only to the familial or ordinal level, is needed to track patterns of consumption of agricultural pests spatially, seasonally, and relative to other benign insects. Molecular techniques used by McCracken *et al.*^{88,92} and Clare *et al.*⁸⁹ have the potential to yield this scale of resolution and offer exciting new avenues for research in mapping food webs and trophic cascades; however, studies on quantifiable effects of bats on crop yields and damage should be coupled with

these dietary analyses to avoid making assumptions of impact based purely on evidence of consumption. Similarly, studies investigating the biology of bat populations within specific agroecosystems—roosting dynamics, habitat selection, and estimates of density—are critical for a complete evaluation of the role of bats in pest suppression, leading ultimately to an estimate of the economic value of this service.

Beyond the studies reviewed here, there have been many other studies investigating habitat use by insectivorous bats in agricultural systems that have not specifically addressed the effects of bats on pest suppression (e.g., organic farms in the United Kingdom,^{56,57} shade cacao plantations in Brazil,¹³⁸ olive orchards in Greece,¹³⁹ Midwestern agricultural land,¹⁴⁰ cereal crops in England,¹⁴¹ arboreal crops in Mexico,¹³⁷ and agricultural riparian areas¹⁴²). These, and other agroecosystems where high bat activity has been documented, are ideal candidates for further research investigating the potential ecosystem service provided by insectivorous bats.

Incorporating the results of ecosystem service studies into integrated pest management (IPM) programs designed to restore the natural predator–pest balance⁸³ has the potential to lead to beneficial results for both farmers and bats. Natural predators may not control 100% of forest and agricultural pests, but a combination of factors can keep populations, and therefore crop losses, in check. With white-nose syndrome causing massive declines of up to 90% and expected regional extinctions of insectivorous bat populations in the eastern and midwestern United States,²⁸ the loss of this important regulating service may severely impact agricultural production in affected areas.¹⁴³ Identification and measurement of the magnitude and value of this natural pest control service can be an effective tool in influencing public support, policy, and private land management toward conservation of natural ecosystems; however, due to the complexities and large scale at which natural pest control acts, cross-disciplinary approaches, collaboration, and creativity are essential.

Pollination and seed dispersal

In addition to insect suppression through predation, some bat species also play important roles as pollinators and seed dispersers in tropical and subtropical habitats throughout the world. These ecosystem ser-

vices are provided primarily by bats in two families, Pteropodidae in the Old World and Phyllostomidae in the New World (Table 1). These two families are distantly related and differ in evolutionary age. Current information suggests that Pteropodidae evolved in Asia about 56 mya (million years ago), whereas Phyllostomidae evolved in the northern Neotropics about 35 mya.¹⁴⁴ Because feeding on nectar and pollen requires relatively specialized morphology (e.g., elongated snouts and tongues), relatively few members of these families are obligate (or nearly so) pollinators. Only 15 species in six genera are morphologically specialized nectar-feeders in the Pteropodidae; other members of this family are primarily fruit-eaters, although species in genera such as *Cynopterus*, *Epomophorus*, and *Pteropus* also visit flowers opportunistically (Fig. 3). The Phyllostomidae contains a diverse array of feeding adaptations (Table 1), but over one half of its species are plant-visitors. About 38 species in 16 genera are specialized nectar-feeders; 90 species in 22 genera are primarily frugivorous, although a number of these in genera such as *Artibeus*, *Carollia*, and *Phyllostomus* also visit flowers (Fig. 4).

Unlike predation, which is an antagonistic population interaction, pollination and seed dispersal are mutualistic population interactions in which plants provide a nutritional reward (nectar, pollen, and fruit pulp) for a beneficial service: pollen and seed dispersal. Bats, along with many other flower-visiting and fruit-eating animals, provide important mobility for plant gametes and propagules. As a result, there has been extensive coevolution between plants and their pollinators and seed dispersers.



Figure 3. Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) approaching a baobab flower of which it pollinates (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org).

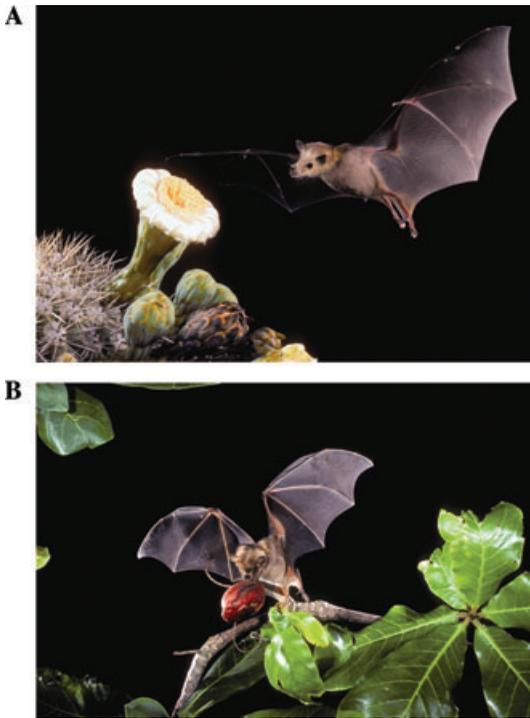


Figure 4. (A) Lesser long-nosed bat (*Leptonycteris curasoae*) approaching a Saguaro cactus flower of which it pollinates (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org). (B) Jamaican fruit bat (*Artibeus jamaicensis*) removing a ripe tropical almond fruit (*Terminalia catappa*) before taking off in flight (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org).

Bat pollination occurs in about 528 species in 67 families and 28 orders of angiosperms worldwide (Fig. 4). Pteropodid bats are known to pollinate flowers of about 168 species in 100 genera and 41 families; phyllostomid bats pollinate flowers of about 360 species in 159 genera and 44 families.¹⁴⁵ Most of the plants pollinated by pteropodid

bats, which are substantially larger than phyllostomids, are canopy trees or shrubs, whereas those pollinated by the smaller phyllostomids are epiphytes and lianas as well as trees and shrubs.¹⁴⁶ The fruit diets of phyllostomids are much better known than those of pteropodids. A total of at least 549 species in 191 genera and 62 families are dispersed by bats in the Neotropics.¹⁴⁷ Pteropodid bats are known to eat fruit from at least 139 genera in 58 families.¹⁴⁸ As in the case of flowers, most fruits eaten by pteropodid bats are produced by trees or shrubs, whereas those eaten by phyllostomids include fruits produced by epiphytes and vines as well as trees and shrubs.

Major plant families (in terms of number of genera) containing species either pollinated or dispersed by the two families of bats are listed in Table 3. Reflecting the independent evolution of bat–plant interactions in Old and New World plant lineages, only a few families are common in the diets of both bat families. For flowers, these include Fabaceae, Malvaceae (especially subfamily Bombacoideae, formerly known as Bombacaceae), and Bignoniaceae (in which bat flowers occur in different clades in the Old and New Worlds). For fruits, these include Araceae (palms) and Sapotaceae. Although only represented by a few genera in the diets of bats, a few additional families are notable for containing many species of bat-pollinated flowers or bat-dispersed fruit. In the New World, these include flowers (Campanulaceae and Marcgraviaceae) and fruit (Araceae, Cecropiaceae, Clusiaceae, Piperaceae, and Solanaceae). In the Old World, these include fruit (Moraceae). Figs (Moraceae) are very important in the diets of both pteropodid and phyllostomid bats worldwide (Fig. 5).

The evolution and ecology of bat–plant interactions are discussed in detail in Fleming,¹⁴⁹ Fleming

Table 3. Examples of the most important angiosperm families (in terms of number of plant genera, in parentheses) whose flowers are pollinated and/or seeds dispersed by pteropodid and phyllostomid bats^a

Bat family	Pollination	Seed dispersal
Pteropodidae	Bignoniaceae (10), Fabaceae (11), Malvaceae (7), Myrtaceae (8), Sapotaceae (7)	Anacardiaceae (8), Araceae (7), Meliaceae (8), Rubiaceae (7), Sapotaceae (10)
Phyllostomidae	Cactaceae (26), Fabaceae (23), Malvaceae (18), Solanaceae (7), Bignoniaceae, Bromeliaceae, Gesneriaceae (6)	Araceae (15), Cactaceae (11), Moraceae (10), Myrtaceae (10), Sapotaceae (6)

^aSources of data: work by Fleming *et al.*;¹⁴⁵ Lobova *et al.*;¹⁴⁷ and Mickleburgh *et al.*¹⁴⁸



Figure 5. Gambian epauletted fruit bat (*Epomophorus gambianus*) taking flight after plucking a fig infructescence (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org).

and Kress,¹⁵⁰ Fleming and Muchhala,¹⁴⁶ Fleming *et al.*,¹⁴⁵ Lobova *et al.*,¹⁴⁷ and Muscarella and Fleming.¹⁵¹ Here, we discuss these interactions in terms of the ecosystem services that provide direct and indirect benefits to humans.

Services providing direct benefits to humans

Although bat pollination is relatively uncommon compared with bird or insect pollination in angiosperms, it involves an impressive number of economically and/or ecologically important plants (Table 4). In arid habitats in the New World, two families, Agavaceae and Cactaceae, have enormous economic and ecological value. Many species of paniculate *Agave* rely heavily on phyllostomid bats for pollination, and many of these same bats are also major pollinators and seed dispersers of columnar cacti.¹⁵² Three species of *Leptonycteris* bats are especially important in this regard in the southwestern United States, Mexico, and northern South America (Fig. 4). The bat-pollinated *A. tequilana* is the source of commercial tequila, a multimillion dollar industry in Mexico; other species of *Agave* are used locally to produce similar alcoholic beverages such as pulque, mescal, and bacanora. Agaves are also important sources of sisal fiber in many tropical localities. Although bats are not the exclusive pollinators of most species of *Agave*, they are critically important pollinators in tropical latitudes in the New World.¹⁵³ This is also true of bats pollinating columnar cacti. For example, bats are minor pollinators of the two northernmost columnar cacti, *Carnegiea gigantea* and *Stenocereus thurbei*, in the Sonoran Desert, but they are the nearly exclu-

sive pollinators of columnar cacti in south-central Mexico and northern Venezuela.¹⁵²

Large-scale cash crops produced by plants either (originally) pollinated or dispersed by bats include nonnative bananas and mangos in the New World and native bananas, breadfruits, durians, mangos, and petai (*Parkia speciosa*) in the Old World (Table 4). Of these, only durians and petai currently rely on bats (among other animals) for pollination. The same is true for trees such as *Ceiba pentandra*, the kapok tree, and *Ochroma lagopus*, the balsa tree. Other bat-fruits that are harvested and sold locally include sapodilla and organ pipe cactus (*Stenocereus*) in the New World and the shea butter tree (*Vitellaria (Butyrospermum) parkii*) in Africa.^{154–156} Many other species are listed in Table 4. Placing a dollar value on the economic services of plant-visiting bats is important but is beyond the scope of this paper for at least two reasons: lack of readily accessible information about the economic value of many crops, especially ones that are sold locally, and, more importantly, lack of detailed knowledge about the actual contribution of bats to the pollination and/or seed dispersal of many of these plants. In the case of cultivated plants, bats are no longer needed to pollinate their flowers or disperse their seeds. But the ecological services these bats provide for their wild relatives are important for preserving genetic diversity in these plants.

In India, the Mahwa tree (*Madhuca indica*), also called the honey tree, sugar tree, or Indian butter tree, is pollinated by *Pteropus giganteus*, *Rousettus leschenaulti*, and *Cynopterus sphinx*.¹⁵⁷ These pollination services highlight one of the highly valued ecosystem services provided by plant-visiting bats both culturally and economically. The timber of this tree is used for making wagon wheels in India. The flowers, also called honey flowers, are used as food and for preparing a distilled spirit (matkom duhli). Sun-dried fruits are directly consumed by humans, and the oil extracted from flowers and seeds, known locally as *mahwa*, *mowrah butter*, or *yallah*, is incorporated into soaps, candles, cosmetics (e.g., lipstick, lotions), and lubricants, and used medicinally as an emetic, an antirheumatic, and in the treatment of leprosy. Extracts from the fruits are also thought to prevent wrinkles and restore skin flexibility.^{158,159} Seedcakes made from *M. indica* are used as food for cattle and goats^{160–163} and are known to increase their milk production.¹⁶⁴

Table 4. Examples of economically and ecologically important plants that are either pollinated (P) or dispersed (D) by bats^a

Plant family and subfamily	Taxon	Service	Comments
Economically important plants			
Anacardiaceae	<i>Anacardium occidentale</i>	D	Cashew, yields three major global and local economic products: cashew (seed), cashew apple (hypocarp), and cashew nutshell liquid (mesocarp resin) ^{262,263}
	<i>Mangifera indica</i>	D	Mango, commercial crop globally and locally ¹⁴⁷
	<i>Spondias</i>	D	<i>S. cytherea</i> , <i>S. mombin</i> , and <i>S. purpurea</i> fruits are important locally in tropical America and consumed fresh or preserved ¹⁴⁷
Annonaceae	<i>Annona</i>	D	<i>A. muricata</i> (soursop), <i>A. reticulata</i> (custard apple), <i>A. squamosa</i> (sweetsop) with edible syncarps are locally important in tropical America ¹⁴⁷
Araceae	<i>Anthurium</i> , <i>Philodendron</i>	D	Commonly cultivated as ornamental plants ¹⁴⁷
Araliaceae	<i>Dendropanax arboreus</i>	D	Cultivated ornamental and timber plant in tropical America ^{135,264,265}
Arecaceae	<i>Acrocomia</i> , <i>Astrocaryum</i> , <i>Bactris</i> , <i>Euterpe</i> , <i>Prestoea</i> , <i>Roystonea</i> , <i>Sabal</i> , <i>Socratea</i>	D	Used as source of “palm-hearts,” especially <i>Euterpe edulis</i> and <i>E. oleraceae</i> ¹⁴⁷
	<i>Euterpe edulis</i>	D	Source of popular açai fruits ²⁶⁶
	<i>Phoenix dactylifera</i>	D	Date palm, commercial crop and staple food for Arabia and North Africa; leaves for matting and thatch ^{135,267,268}
	<i>Roystonea regia</i>	D	Royal palm, commonly cultivated ^{267,269}
	<i>Sabal palmetto</i>	D	Leaves are commercially important source of fibers and thatch; stems used for furniture and wharf-piles ²⁶⁷
Agavaceae	<i>Socratea exorrhiza</i>	D	Wood used for construction ^{135,147,262,270–272}
	<i>Agave</i> , subgenus <i>Agave</i>	P	Paniculate agaves such as <i>A. tequilana</i> are used to make tequila, mescal, bacanora, etc., with high economic value; leaf fiber is used as sisal ^{153,273}
Boraginaceae	<i>Cordia dodecandra</i>	D	Cultivated for edible fruits and fine timber in tropical America ¹³⁵
Cactaceae	Many genera in tribe Pachycereae, subfamily Cactoideae	P, D	Native populations in the southwestern U.S. and Latin America harvest fruits of bat-pollinated cactus species in genera such as <i>Carnegiea</i> , <i>Pachycereus</i> , and <i>Stenocereus</i> . Some species of <i>Stenocereus</i> are grown commercially for their fruits ^{152,156}

Continued

Table 4. Continued

Plant family and subfamily	Taxon	Service	Comments
Caricaceae	<i>Carica papaya</i>	D	Papaya, widely cultivated in tropics for fruits and as a source of papain used in culinary and medical products ¹⁴⁷
Caryocaraceae	<i>Caryocar</i>	P, D	Many species have seeds that are oil source in tropical America; <i>C. glabrum</i> (soapwood) inner bark used for washing ^{135,274,275}
Cecropiaceae	<i>Cecropia peltata</i>	D	Wood used for pulp, also cultivated as ornamental in tropical America ¹⁴⁷
Chrysobalanaceae	<i>Chrysobalanus icaco</i>	D	Grown for edible fruits; seed oil used for candles in West Africa ¹⁴⁷
Clusiaceae	<i>Clusia, Symphonia, Vismia</i>	D	Resins are locally medicinal in South America ¹⁴⁷
Combretaceae	<i>Terminalia catappa</i>	D	Tropical almond, source of valuable timber, edible seeds, tannins for dye, bark extract for medicine in Indomalaya ¹⁴⁷
Cyclanthaceae	<i>Carludovica palmata</i>	D	Panama hat palm, grown for hat manufacture, important export plant for Ecuador, also used for mats and baskets in tropical America ^{135,136,149,276}
Ebenaceae	<i>Diospyros digyna, D. kaki</i>	D	Grown for edible fruits (black sapote, Japanese persimmon) in Central America and Asia ¹⁴⁷
Fabaceae	<i>Dipteryx odorata</i>	D	Fragrant seeds used for scenting tobacco and snuff ¹⁴⁷
Faboideae	<i>Andira inermis</i>	D	Valuable timber, bark used for medicine, planted for shelter belts in West Indies (cabbage-tree) ¹⁴⁷
Fabaceae, Mimosoideae	<i>Inga vera</i>	D	Guaba, widely grown in South America for edible fruit pulp, timber, shade, medicine, and alcoholic beverage cachiri ^{277,278}
	<i>Parkia speciosa</i>	P	Commercially important fruit species in Southeast Asia ¹⁵⁴
Lecythidaceae	<i>Lecythis pisonis</i>	D	Paradise nuts, cultivated in South America for edible seeds ^{147,279}
Malpighiaceae	<i>Malpighia glabra</i>	D	Barbados cherry, edible fruits high in vitamin C, also ornamental in tropical America ^{135,262,280}
Malvaceae, Bombacoideae	<i>Ceiba</i>	P	Fibers from fruits of <i>C. pentandra</i> and other species of <i>Ceiba</i> are used to make kapok ¹⁵⁴
Malvaceae	<i>Ochroma</i>	P	Balsa, world's lightest commercial timber ¹³⁵

Continued

Table 4. Continued

Plant family and subfamily	Taxon	Service	Comments
Malvaceae, Helicteroideae	<i>Durio</i>	P	<i>D. zibethinus</i> (durian) and several other species of <i>Durio</i> are cultivated widely for edible fruits and seeds in Southeast Asia and elsewhere in the tropics ^{135,154}
Moraceae	<i>Artocarpus</i>	D	<i>A. altilis</i> (breadfruit) and other species are cultivated and sold commercially throughout tropical Asia and Australasia as a source of starch-rich infructescences ¹⁴⁷
	<i>Brosimum alicastrum</i>	D	Breadnut, seeds are edible and valuable source of fiber, vitamins, and microelements; leaves used for fodder; latex and wood are also utilized ¹⁴⁷
	<i>Ficus</i>	D	Numerous species of fig used for rubber, fibers, paper, timber, medicine, and as ornamentals throughout the world tropics ¹⁴⁷
Muntingiaceae	<i>Muntingia calabura</i>	D	Firewood crop in tropical America ¹⁴⁷
Musaceae	<i>Musa</i>	P, D	Bananas, pteropodid bats both pollinate flowers and disperse seeds of wild bananas. Cultivated bananas have very high economic value ¹⁴⁷
Myrtaceae	<i>Anamomis umbellulifera</i>	D	Edible fruits in West Indies ^{135,262,280}
	<i>Psidium guajava</i>	D	Guava, cultivated for edible fruits, commercial crop in tropical America ¹⁴⁷
	<i>Syzygium cumini</i> , <i>S. jambos</i> , <i>S. malaccensis</i>	D	Rose apple, cultivated for edible fruits in Old World tropics ¹⁴⁷
Passifloraceae	<i>Passiflora</i>	D	Passionfruit, important edible tropical fruits ¹⁴⁷
Piperaceae	<i>Piper aduncum</i>	D	Fruits edible in Puerto Rico ¹⁴⁷
Polygonaceae	<i>Coccoloba uvifera</i>	D	Seaside grape, cultivated for edible fruits in tropical America ¹⁴⁷
Rhamnaceae	<i>Hovenia dulcis</i>	D	Japanese raisin tree, swollen, fleshy pedicels are sweet and edible; also used in medicine and for timber in Asia ²⁸¹
Rosaceae	<i>Eriobotrya japonica</i>	D	Loquat, native to Asia but widely cultivated throughout world tropics for edible fruits ¹⁴⁷
Rubiaceae	<i>Coffea arabica</i>	D	Coffee, native to Old World but cultivated for seeds as source of coffee throughout the world ²⁶⁷
Rutaceae	<i>Casimiroa edulis</i>	D	White sapote, cultivated for edible fruits in Central America ¹³⁵
Salicaceae	<i>Flacourtia indica</i>	D	Fruits edible and medicinal in Old World tropics ^{135,262,280}
Sapindaceae	<i>Melicoccus bijugatus</i>	D	Mamoncillo, edible fruits in tropical America ¹⁴⁷

Continued

Table 4. Continued

Plant family and subfamily	Taxon	Service	Comments
	<i>Sapindus saponaria</i>	D	Soapberry, fruits used as soap substitutes in tropical America ^{135,149,280}
Sapotaceae	<i>Chrysophyllum cainito</i>	D	Star-apple, cultivated for edible fruits in tropical America ¹⁴⁷
	<i>Manilkara</i>	D	Species of <i>Manilkara</i> , including <i>M. zapota</i> (sapodilla), produce commercially valuable fruits ¹⁴⁷
	<i>Mimusops elengi</i>	D	Cultivated for fragrant flowers throughout tropics ^{135,262,280}
	<i>Pouteria</i>	D	<i>P. sapota</i> (sapote) is important Caribbean fruit; <i>P. campechiana</i> is also a source of edible fruits in Central America ¹⁴⁷
Sterculiaceae	<i>Guazuma ulmifolia</i>	D	Light timber for boats, barrels, and fuelwood in tropical America ^{263,267}
Ulmaceae	<i>Trema micrantha</i>	D	Used for pre-Hispanic barkcloth in tropical America; soft timber for matches and chests; also used in shade coffee plantations ^{265,282,283}
Vitaceae	<i>Vitis vinifera</i>	D	Grape vine, source of edible fruits and alcoholic beverages, native probably to Asia, broadly cultivated throughout the world ^{135,280,284}
Ecologically important plants			
Agavaceae	<i>Agave</i>	P	Many species of paniculate agaves are conspicuous members of arid upland habitats in the Neotropics ^{153,273}
Arecaceae	Many New and Old World genera	D	Palms are common elements of many tropical forests, especially in the Neotropics ^{147,148}
Cactaceae, Cactoideae	Many columnar cacti in several tribes of this subfamily	P, D	Columnar cacti are keystone species in many arid Neotropical habitats ^{152,156}
Cecropiaceae	<i>Cecropia</i>	D	Species of <i>Cecropia</i> are important pioneer trees throughout the Neotropics ^{151,285}
Clusiaceae	<i>Vismia</i>	D	<i>Vismia</i> shrubs are important pioneer species in the Neotropics ¹⁵¹
Malvaceae, Bombacoideae	<i>Adansonia</i> , <i>Bombax</i> , <i>Ceiba</i> , <i>Pachira</i> , <i>Pseudobombax</i> , etc.	P	Trees of this subfamily are often dominant (in terms of basal area) members of tropical forests worldwide ^{135,286,287}
Moraceae	<i>Ficus</i>	D	Fig trees are often keystone members of tropical forests worldwide ¹⁶⁹
Piperaceae	<i>Piper</i>	D	<i>Piper</i> shrubs are pioneer plants and common members of Neotropical forest understories ²⁸⁸

Continued

Table 4. Continued

Plant family and subfamily	Taxon	Service	Comments
Solanaceae	<i>Solanum</i>	D	<i>Solanum</i> shrubs are pioneer plants and common members of Neotropical forest understories, particularly at mid-elevations ²⁸⁹
Ulmaceae	<i>Trema micrantha</i>	D	Fast-growing pioneer tree ^{265,282,283}

^aSource of commercial uses of these plants comes from work by Mabberley,¹⁵⁵ unless noted. In cases when there are more than three references of a particular bat–plant interaction, a reference to the appendices of the review, by Lobova *et al.*,¹⁴⁷ is given. Please note that for most of these plants, the precise quantitative role that bats play as pollinators and dispersers is unknown.

Throughout much of India, there appears to be a social taboo against cutting *M. indica*, probably due to its recognized value in tribal regions. However, in the North Karanpura Valley, this is one of the most threatened species, where it is being destroyed by the thousands in coal mining regions.¹⁶⁵ The economic importance of pollination by fruit bats and the products derived from species such as the Mahwa tree extend well beyond the borders of India. Increased efforts are needed to educate government agencies, industries, international corporations, and the general public about the ecological and economic value of plant-visiting bats to this species and other native flowering and fruit-bearing trees.¹⁶⁶

The tropical almond tree, *Terminalia catappa* (Combretaceae) of Indomalaya, is an example of a bat-dispersed tree with many human uses. This tree is dispersed by *Cynopterus* bats throughout Asia. In India, it is important in coastal communities where it provides shade, fuel-wood, and edible nuts.¹⁶⁴ The timber derived from almond trees makes a decorative general-purpose hardwood and is well suited for making furniture and for interior building timbers. Tannin is extracted from the bark, leaves, roots, and the fruit shell. The large leaves are also used as wrapping material and have many medicinal uses, including diaphoretic, antiindigestion, and antidysentery. Young leaves are used to cure headaches and colic. A black dye is obtained from the bark, fruit, and foliage. Its leaves and bark have a wide range of other medicinal uses. Children sometimes consume the outer flesh of agreeable fruit types. In the Philippines, a wine is made by fermentation of mature fruits. The nuts may be consumed fresh after ex-

tracted from the shell or preserved by drying or smoking and consumed up to a year later. Sun-dried kernels yield 38–54% of bland, yellow oil that is edible. The bark is used as an astringent for dysentery and thrush.^{167,168}

Services providing indirect benefits to humans

Over and above the economic value of their pollination and seed dispersal services, plant-visiting bats provide important ecological services by facilitating the reproductive success of their food plants, including seed set and the recruitment of new seedlings and saplings. Many of these plants are among the most important species in terms of biomass in their habitats (Table 4). In the New World, bat-pollinated columnar cacti and agaves are dominant vegetation elements in arid and semiarid habitats as are various species of Bombacoideae in dry and wet tropical forests throughout the world. Bat-dispersed palms and figs are also common in many tropical forests worldwide. Because they are also eaten by many birds and mammals, figs often act as keystone species (i.e., species whose ecological impact often exceeds their biomass) in tropical forests.¹⁶⁹ Figs are important bat-fruits throughout the tropics. Bat-dispersed, soft-fruited species of *Cecropia*, *Piper*, *Solanum*, and *Vismia* are critically important early pioneer species that are among the most abundant plants during early primary and secondary succession in the Neotropics.¹⁵¹ Fruit-eating phyllostomid bats thus play an extremely important role in forest regeneration in the New World. This is not necessarily true in the Paleotropics, where most early successional plants are bird dispersed. Pteropodid

bats play a more important role in the dispersal of later successional trees than in the dispersal of pioneer species.¹⁵¹ Some of these plants, such as species of *Pouteria* and *Plaquium* (both Sapotaceae) in Asia and *Milicia* (*Chlorophora*) *excelsa* and *Antiaris africana* (both Moraceae) in Africa, are important timber trees.¹⁷⁰ An exception to this is the dispersal of seeds of pioneer species of *Ficus* in the Old World. During the recolonization of Krakatau, for example, bird- and bat-dispersed figs were early colonists and attracted frugivores that brought in seeds of other plant taxa.¹⁷¹ Thus, bat-dispersed figs likely “jump-started” forest regeneration on these islands.

One of the most important ecological services that bats provide for their food plants is long-distance dispersal of pollen and seeds. This is especially true in arid New World habitats where *Lep- tonycteris* species visiting the flowers of columnar cacti have a large foraging area.¹⁷² Flower-visiting phyllostomid and pteropodid bats forage in both continuous forest and forest fragments and, thus, help to maintain genetic connections among fragmented plant populations. For example, phyllostomid bats pollinating *Hymenaea courbaril* trees in tropical dry forest fragments in Puerto Rico often move pollen 600–800 m between individuals.²²⁶ In Brazil, *Phyllostomus* species are known to move the pollen of *Hymenaea courbaril* trees 18 km between individuals in riverine forest.¹⁷³ Glossophagine bats regularly move pollen between individuals of the canopy tree *Ceiba pentandra* within continuous forest and between forest trees and isolated pasture trees in western Mexico.¹⁷⁴ The Australian pteropodid *Syconycteris australis* usually moves pollen < 200 m between *Syzygium cormiflorum* trees but also moves pollen up to about six km between individuals in different habitat patches.¹⁷⁵

Most seed dispersal systems, including those involving vertebrates, produce leptokurtic dispersal distributions. That is, most seeds are dispersed close to parent plants with only a few being dispersed 100s to 1,000s of meters away. Seeds dispersed by frugivorous bats undoubtedly conform to this pattern, but bats can also provide relatively long seed-dispersal distances for their food plants. For example, in central Panama the Jamaican fruit bat *Artibeus jamaicensis* carries single fig fruits 100–250 m away from fruiting plants before beginning to feed in a night roost; it often feeds at several

trees located a kilometer or more apart in a single night.¹⁷⁶ Similarly, *Cynopterus sphinx*, the Asian pteropodid ecological analogue of the Neotropical *A. jamaicensis*, is known to forage on more than one island in the Krakatau group in a single night.¹⁷¹ Although it is generally a short-distance seed disperser, the phyllostomid *Carollia perspicillata* is known to move 1–2 km between foraging areas and frequently moves seeds between habitats.^{149,177} In contrast to forest-dwelling frugivorous birds, phyllostomid and pteropodid bats readily fly over open areas and defecate seeds in flight. As a result, phyllostomid bats eating the small seeds of pioneer plant species provide substantial mobility for their seeds and help them to quickly colonize forest treefall gaps and disturbed areas such as abandoned pastures and logged forests.¹⁵¹

We close this section with a brief discussion of an important conservation concern associated with plant-visiting bats. Many species of nectar- or fruit-eating bats annually migrate between a series of landscapes, and these movements are driven by seasonal fluctuations in the availability of flower or fruit resources. In western Mexico, for example, many individuals of the lesser long-nosed bat, *L. yerbabuena*, spend the fall and winter in tropical dry forest where they mate. Here, they feed on the flowers and fruit of dry tropical forest trees and shrubs. In the spring, many females migrate up to 1,000 km north to form maternity colonies in the Sonoran Desert where they feed on flowers and fruit of columnar cacti. In late summer and early fall, females and their offspring move into upland areas of southern Arizona and Sonora, Mexico, where they feed at flowers of paniculate agaves before migrating south again.¹⁷⁸ Seasonal movements among landscapes by flower-visiting bats are also known to occur in northeastern Costa Rica, lowland Malaysia, and in the eucalypt forests of eastern and northern Australia.^{179–181} Similarly, some frugivorous phyllostomid and pteropodid bats undergo altitudinal or latitudinal movements.^{182,183} For example, populations of the African pteropodid *Eidolon helvum* migrate over 1,000 km annually from the Democratic Republic of Congo to central Zambia.¹⁸⁴ Most of the foraging areas along the migration route are not protected by conservation legislation.

Because they often move across international borders, as well as among habitats that often do not have state or federal protection, migratory species

are of special conservation concern.¹⁸³ This is especially true of vertebrate pollinators and seed dispersers whose movements and survivorship are of critical importance for the reproductive success of their food plants. Protection of migratory pathways and critical feeding areas of migrants must be major conservation goals worldwide.

Finally, some of the greatest conservation concerns in bats involve island-dwelling species, including nectar- and fruit-eaters.^{185,186} Because of their remoteness, oceanic islands usually have reduced biodiversity and disharmonic (unbalanced) faunas in which bats play an especially important role in the pollination and dispersal biology of trees, vines, and shrubs.¹⁸⁷ As a result of overhunting, persecution, and habitat destruction, many island bats are critically endangered, and their conservation is of substantial concern to bat biologists and ecologists.^{183,188,189}

Provisioning and cultural services

Bats provide additional provisioning and cultural ecosystem services beyond the regulatory services (i.e., arthropod suppression, pollination, and seed dispersal) that we have emphasized throughout this paper. In this section, we briefly discuss these underappreciated benefits to humans provided by bats and then revisit them in the section on valuation of ecosystem services.

Redistribution of nutrients from guano

Guano from bats has long been mined from caves for use as fertilizer on agricultural crops due to the high concentrations of nitrogen and phosphorous, the primary limiting nutrients of most plant life.^{190,191} Although the benefits of nitrogen to plants are well known, most of the evidence supporting bat guano as fertilizer is anecdotal, and few studies have explicitly measured its effects on plant growth parameters.¹⁹² Because bats regularly or occasionally roost in caves, they are thought to provide the primary organic input to cave ecosystems, which are inherently devoid of primary productivity.^{193–196} Cave-dwelling salamander and fish populations and invertebrate communities, for example, are highly dependent upon the nutrients from bat guano.^{197,198}

Several researchers have begun to investigate the potential ecological role of guano in nutrient redistribution over the landscape via the “pepper-shaker effect.”^{191,192,199,200} Because insectivorous bats con-

sume energy rich prey, experience rapid digestion during flight, and forage significant distances over heterogeneous habitat types, it is expected that guano is sprinkled over the landscape throughout the night.²⁰¹ Thus, bats contribute to nutrient redistribution from nutrient-rich sources (e.g., lakes and rivers) to nutrient-poor regions (e.g., arid or upland landscapes). However, to date, no studies have explicitly tested this prediction. Reichard¹⁹² estimated that a colony of one million Brazilian free-tailed bats, *Tadarida brasiliensis*, in Texas could contribute 3,600,000 kJ/day of energy and 22,000 g of nitrogen in the form of guano. He also demonstrated that moderate applications of guano in a controlled greenhouse experiment promoted growth in a grass species native to Texas (Indian grass, *Sorghastrum nutans*), but reduced root/stem ratio and had a neutral effect on two other native species: little bluestem, *Schizachyrium scoparium*, and prairie coneflowers, *Ratibida columnifera*, respectively. He further speculated that guano deposition may have species-specific effects on plant communities and thus emphasize the need for more in-depth experimental and field studies. Other trophic ensembles (e.g., nectarivorous, frugivorous, carnivorous bats) may similarly contribute to nutrient cycling through guano redistribution; however, we were not able to find any studies investigating this potential service.

Bats in medicine and culture

As described in the introduction, bats have long been feared in a diversity of human cultures. Although it is beyond the scope of this paper to provide a full treatment of this topic, it is important to also note the value of bats to ancient and contemporary religions and cultures worldwide. Bat symbols appear in priceless artifacts, such as wall paintings in Egyptian tombs from 2000 B.C., Chinese bowls carved of white jade, Japanese prints, and ancient temple paintings of the Mayan bat god.¹⁸ In fact, the Mayan “Zotzil,” the bat people, continue to live in southern Mexico and Guatemala in cities with the same name: “Tzinacantan,” or the Bat City. These and other cultural heirlooms are not only symbolically cherished for their historical significance but also generate direct revenue for the countries and museums that display them to curious tourists.

Bats have also long been used for food and medicine.^{18,22} Witches and sorcerers used bats in ancient magic to induce desire and drive away sleep.

Shamans and physicians used bats to treat ailments of patients ranging from baldness to paralysis.^{18,202} Some of these traditions continue today, though bats are now consumed primarily as meat.²² One exception is the anticoagulant compound that is found in the saliva of the common vampire bat, *Desmodus rotundus*. This compound, *Desmodus rotundus* salivary plasminogen activator (DSPA), has drawn considerable attention from the medical community as a potential treatment for strokes because, unlike the alternatives, it can be administered much later after a stroke has occurred and still be effective.²⁰³

Today, bats provide aesthetic value through cave visits, nocturnal tours in national parks, and educational nature programs. These activities provide adventure and life memories for the public and revenue for the communities and companies involved.²⁰⁴ Bats also commonly appear as symbols or logos in popular movies (e.g., *Batman*), products (e.g., Bacardi rum), and holidays (e.g., Halloween), all major revenue-generating endeavors.²⁰⁵ Finally, the study of bat echolocation and locomotion has provided inspiration for novel technological advances in such fields as sonar systems, biomedical ultrasound, sensors for autonomous systems, wireless communication, and BATMAVs (bat-like motorized aerial vehicles).^{206,207} Although extremely difficult to quantify, it is important to recognize the extraordinary value of bats to ancient and contemporary traditions and science.

Valuation of ecosystem services provided by bats

As described in the preceding sections, bats provide a variety of ecosystem services that improve human well-being. To date, few studies have attempted to place an economic value on these ecosystem services. This section describes various methods that could be used to value ecosystem services provided by bats and then reviews the available studies that have attempted to do so. Although some of these services provide direct benefits to humans (e.g., food, fuel, fiber, and fertilizer), most ecosystem services offer indirect benefits (e.g., pest suppression, seed dispersal, and pollination). Often times, little attention is paid to the “free” (i.e., nonmarketed) services provided by ecosystems either because the benefits of the services are not fully understood by decision

makers or because the benefits accrue to nonowners of the ecosystem providing the service. Moreover, little consideration has been given to the role of bats in supporting entire cave ecosystems by providing essential organic input that supports assemblages of endemic cave flora and fauna. Information on non-market values of ecosystem services can be used to inform decisions regarding whether to protect existing ecosystem services, improve the current provision of ecosystem services, or restore previously lost ecosystem services.^{4,208}

The economic approach to valuation

Traditionally, economic valuation is the process of measuring the human welfare gains or losses that result from changes in the provision of ecosystem services. The purpose of economic valuation is to provide a common metric with which to compare the impacts of alternative management or policy decisions among ecosystem services and other market-based goods and services.⁴ Consumer surplus and producer surplus are the welfare measures commonly used in economic valuation.^{208,209} Consumer surplus is the amount that consumers would be willing to pay for a good or service above the amount that they actually pay, while producer surplus is the amount that producers receive for a good or service less what it costs them to produce it. Consumer and producer surplus can be measured for market-based goods (e.g., food) by direct estimation of demand and supply functions. For nonmarketed goods and services, including most ecosystem services, alternative valuation methods have been developed.^{208,209} These methods fall into two broad categories. Revealed preference approaches value of ecosystem services through observing consumer or producer behavior for related goods and services.²¹⁰ For example, crop production often uses a variety of ecosystem services as inputs.²¹¹ However, it is not always possible to directly observe consumption or production of ecosystem services. In addition, some ecosystem services have nonuse or existence values. In these cases, stated preference methods of valuation, whereby individuals state their individual willingness to pay for ecosystem services, can be used.²¹² While a complete assessment of valuation methods is beyond the scope of this paper, Appendix B provides brief descriptions for the various methods that could be used to value the ecosystem services provided by bats.

Applying economic valuation to ecosystem services provided by bats

Few studies have attempted to value the ecosystem services provided by bats. In this section, we highlight those that have been published. We also discuss a small number of nonbat studies that describe an interesting approach or present results that might be similar to those used to value bats.

Regulating services. As described earlier, bats provide a number of regulating services including pest suppression, seed dispersal, and pollination within both agricultural and natural ecosystems. Determining the economic value of regulating services provided by bats to natural ecosystems is extremely challenging and no studies were found. Thus, we focus here on studies where the ecosystem service is provided directly to the production of goods and services consumed by humans.

One early study describing the economic importance of bats is that of Fujita and Tuttle,¹⁵⁴ in which the authors identify 289 Old World tropical plant species that rely on the pollination and seed dispersal services of bats for their propagation (see also Table 4). These plants, in turn, contribute to the production of 448 bat-dependent products in a variety of categories, including timber and other wood products (23%); food, drinks, and fresh fruit (19%); medicines (15%); dyes, fiber, animal fodder, fuel wood, ornamental plants, and others. Fujita and Tuttle¹⁵⁴ describe the economic value of some of these products; for example, fiber produced from kapok trees is reported to be worth \$4.5 million. However, because bat-provided services represent one input within a multi-input production process, only a portion of the total value of the end product can be attributed to bats. The primary contribution of this study is in highlighting the expansive role that bats play in the production of goods that contribute to human well-being.

More recently, three studies assess the economic importance of pollination services provided to world agriculture.^{213–215} In each study, the contribution of animal pollinators, including bats, to global primary crop production is assessed. In an extensive literature review, Klein *et al.*²¹³ evaluate the dependence on animal pollinators of primary agricultural crops. Dependence categories are based on the percentage of crop production that would be lost without animal-mediated pollination, a damage

function type of analysis but without an economic component. Their results show that while 87 primary crop species depend to some degree on animal pollination, these crops account for only 35% of global production. Of the crops directly consumed by humans, pollinators were found to be essential for 13, highly dependent for 30, moderately dependent for 27, slightly dependent for 21, unimportant for 7, and of unknown significance for 9. The majority of these crops are pollinated by bees; however, birds, bats, and other insects also contribute to the pollination of the world's leading crops.²¹⁶ In particular, bats are important pollinators of durian (*Durio zibethinus*), star apple (*Chrysophyllum cainito*), and velvet bean (*Mucuna pruriens*). Production data for these bat-dependent crops are not reported separately but rather appear in aggregated crop groupings, so there is no way to extract the specific value of bat pollination services from this study or other studies that use Klein *et al.*'s dependence values.

Gallai *et al.*²¹⁴ combine pollination dependence ratios with regional measures of crop production and prices in an economic valuation of the pollination services provided to 100 world food crops. Of these, 46 crops depend to some degree on animal pollinators (6 essentially dependent, 13 highly dependent, 13 moderately dependent, and 14 slightly dependent), accounting for 39% of world production value. The economic value of the portion of crop production due to animal-dependent pollination is calculated by multiplying the total production value of each crop by its pollinator dependence ratio, a damage function approach to valuation. Summing over all crops, the total economic value of global pollination services is estimated to be €153 billion (~\$200 billion), representing 9.5% of the value of world food crop production in 2005. A small portion of this total is due to bat pollination services. Using rough approximations for demand functions, Gallai *et al.* also estimate consumer surplus values for pollination services to be between €191 and €310 billion (\$250 and \$405 billion), indicating that the damage function approach may underestimate the true economic value for pollination services.

Bauer and Sue Wing²¹⁵ develop a multiregion, multisector model of global agricultural production and trade that incorporates Klein *et al.*'s²¹³ pollinator dependence ratios as exogenous neutral shocks

to four broad crop sectors. Pollinator loss scenarios are implemented as catastrophic shocks to each regional economy, with the services of animal pollinators being completely lost and the productivity of pollinator-dependent crops declining by the corresponding dependence ratio. This general equilibrium analysis estimates the crop sector losses to be \$10.5 billion globally, but total economy-wide losses that account for price effects on downstream sectors (e.g., processed foods) and households to be \$334.1 billion, an order of magnitude greater. Once again, a small portion of this amount is due to bat pollination services.

We found no studies that estimated the economic value of seed dispersal services provided by bats. However, multiple studies describe the ecological relationship between bat-mediated seed dispersal and timber volume for economically important tree species.^{151,217} To estimate the economic value of the seed dispersal service due to bats, the quantitative relationship between the seed dispersal contribution of bats and the volume of marketable timber by species, similar to Klein *et al.*'s²¹³ pollinator dependence ratio, would first need to be established. This information could then be fed into economic analyses similar to those described earlier for pollination services.

One study estimating the economic value of seed dispersal services provided by the Eurasian jay to regeneration of giant oak in a Stockholm National Urban Park in Sweden²¹⁸ mentions that bats do reside in the park, but it is unlikely that insectivorous bats (the only bat feeding ensemble present in Sweden) would contribute to seed dispersal. Notwithstanding, the study uses a replacement cost approach that could be used to estimate the economic value of seed dispersing bats. By first quantifying the number of oaks that are due to jays, the authors then estimate the costs associated with two different types of manual replacement, seeding acorns, or planting saplings. The value of seed dispersal services per pair of jays was estimated at SEK 35,000 (\$4,935) for seeding acorns and SEK 160,000 (\$22,560) for planting saplings, which aggregates up to between SEK 1.5 million and SEK 6.7 million (\$212,000 and \$945,000). The authors acknowledge Shabman and Batie's²¹⁹ three conditions for use of the replacement cost approach and argue that the first two conditions are met by their study but concede uncertainty whether the third condition is met, although

they contend that public support for preservation of giant oak is great.

Three related studies approximate the economic value of pest suppression services provided by Brazilian free-tailed bats to the production of cotton in Texas.^{98,103,110} In the first study, Cleveland *et al.*⁹⁸ employed both damage function and replacement cost approaches in approximating the economic value of bats' pest control service across a 4,000 Ha region. The damage function approach required a detailed assessment of the ecological relationships between Brazilian free-tailed bats, cotton bollworm adults, cotton bollworm larvae, and cotton crops detailing how these relationships vary over the course of the growing season. The value of the avoided damage to cotton is approximately \$0.02 per bat per night in mid-June (dropping to zero by August) for a total annual value of \$638,000. The replacement cost approach was based on an estimated reduction of at least one pesticide application early in the growing season due to high bat predation rates keeping the number of cotton bollworm larvae below the economic threshold for pesticide use. The value of pesticides not used (i.e., replaced by the bat service) is approximately \$100,000 per year across the region. Betke *et al.*¹⁰³ used data collected with thermal imaging technology to update the estimate of bat population across this same cotton-producing region. Feeding this information into the pesticide allocation model used by Cleveland *et al.*,⁹⁸ Betke *et al.* present an updated measure for the pesticide replacement cost of \$500,000 annually.

The Cleveland *et al.*⁹⁸ study, using values from Pimentel *et al.*,⁷⁷ also estimates the reduction in external environmental costs resulting from lower pesticide use at \$3,000 per year. These external costs are those nonprivate costs incurred by society including loss of natural enemies, loss of wild pollinators, groundwater and stream contamination, and the impact on local bird and fish populations.

Federico *et al.*¹¹⁰ develop a more detailed dynamic model of the bat–bollworm–cotton agroecosystem, which includes multiple life stages for both bats and bollworm and compares conventional and transgenic cotton crops. Once again, the pest control services provided by bats are approximated through estimates of crop damage avoided and number of pesticide applications reduced. Four different crop–pesticide scenarios were assessed,

resulting in a range of per-hectare values for bat pest suppression services: (i) \$86 for conventional-spray, (ii) \$757 for conventional-no spray, (iii) \$46 for transgenic-spray, and (iv) \$214 for transgenic-no spray. By combining two valuation methods, both Cleveland *et al.*⁹⁸ and Federico *et al.*¹¹⁰ go beyond the basic damage function approach by allowing producers to vary a second production input (pesticide applications) in their simulations. This use of the replacement cost method seems appropriate as it is based on the economic pest threshold concept that cotton producers use in their decision-making process for pesticide applications.

In an unrelated study, Gándara Fierro *et al.*¹¹¹ estimate the economic value of a population of Brazilian free-tailed bats in Nuevo León, Mexico to range from 6.5 to 16.5 million Mexican pesos (\$479,000–1.2 million) with an average value of 260 pesos (\$19) per hectare. The authors use a simple replacement cost method, basing their estimate on the identification of potential insect pests in the guano of a large colony of bats, surveys of 101 local farmers attesting to the cost and use of pesticides and the presence or absence of bats in different crops, and estimates by Federico *et al.*^{220,221} that bats reduce crop damage by 25–50%.

Rather than valuing the direct contribution of regulating services to agricultural production, some studies value the indirect contribution that natural landscapes make by providing forage and nesting habitat for pollinators, seed dispersers, and natural enemies.^{222,223} In this case, crop production is a function of the quantity of nearby natural habitat. While these studies have predominantly focused on coffee production, which is bee-pollinated, the same methods could be applied to bat-serviced crops resulting in values for conservation of natural habitat used by bats.

Provisioning services. Bats provide a direct source of food in many countries.²² Although no studies were found estimating market demand or supply of bat bushmeat, several studies reported anecdotal pricing information for local consumption of bats (\$2.50–3.50 per bat in Malaysia and \$10 per bat in Jakarta for *Pteropus vampyrus* and *P. hypomelanus*);¹⁵⁴ (65 Naira [\$0.43] per kg for *Eidolon helvum*);²²⁴ (\$0.50–1.25 for *P. vampyrus natunae*;²²⁵ [\$0.50–1.50 for *P. rufus*]²²⁶). In an analysis of several types of bushmeat for vitamin and mineral

composition, bats were found to have the highest value (i.e., lowest cost per kilogram) of protein.²²⁴

Several studies have reported on the overhunting of bat bushmeat, indicating a need for further conservation efforts including recommendations for the establishment of protected areas.^{186,225,227,228} However, a note of caution may be in order, as Fa *et al.*²²⁹ reported a negative relationship between the quantity of bushmeat harvested and the distance between settlements and national parks for many species, although bats were a very small percentage of the total bushmeat harvested in their study area.

Bats also provide another marketable product, bat guano, which is used as a natural fertilizer. Once again, we were not able to find any formal studies estimating market demand and supply of guano. However, an Internet search (keywords: *bat guano price*) conducted in September of 2010 revealed more than 950 bat guano products, clearly indicating a market for the product. Prices for bat guano organic fertilizer varied between \$1.25 and \$12.00 per pound, depending on the size of the package (larger packages have lower per-unit prices) and the mix of ingredients.

Cultural services. Although perhaps not as widely practiced as bird watching or whale watching, bat watching is a growing recreational activity. The majority of bat viewing takes place at cave entrances where nightly emergences can be viewed. Many sites charge small fees ranging from \$5 to \$12 per visitor, which can be interpreted as an individual's minimum willingness to pay to view bats.²³⁰ The 5th Annual Austin Bat Fest reportedly drew over 40,000 participants to the area surrounding the Congress Avenue Bridge, a roosting site for an estimated 1.5 million Brazilian free-tailed bats.²³¹ Tickets to the day-long event cost \$7.00 and included a number of band performances, crafts exhibits, and educational displays. The bridge is home to one of the largest urban bat colonies in the United States, and bat viewing at the bridge is typically free. A fiscal impact study of bat-watching visitors estimated tourist bat-related expenditures of \$3 million per year, with one third of the visitors coming from outside of Texas.²³² Ecotourism clearly is one way to support bat conservation.²³³

In terms of general conservation or existence values for bats, one recent contingent valuation study included one species of bat (*Myotis emarginata*) in

its assessment of willingness to pay for biodiversity conservation in a national park in Spain.²³⁴ Through a photo questionnaire, bats (along with snakes and spiders) were valued five times less than other species (lynx and eagle) due in part to a lack of understanding regarding their ecological role as well as a potential aversion factor. This study highlights the need for further public education on the ecosystem services provided by bats.

Challenges associated with valuation of ecosystem services

It is not possible within this paper to fully describe the process involved in economic valuation of ecosystem services. The National Research Council (NRC)²⁰⁸ provides a book-length treatment of the subject, and Appendix C offers a five-step summary of guidelines. Here, we describe the major challenges one might encounter when conducting a valuation study.

The fundamental challenge of valuing ecosystem services lies in providing an explicit description and adequate assessment of the links between the structures and functions of natural systems, the benefits (i.e., goods and services) derived by humanity, and their subsequent values. (NRC 2005, p. 2)²⁰⁸

As can be seen in the studies by Klein *et al.*,²¹³ Cleveland *et al.*,⁹⁸ and others, development of detailed descriptions of ecological production functions that quantitatively articulate relationships between bats and the marketed output requires much effort at great cost. But these details are necessary in order to estimate the economic value of the pollination, seed dispersal, and pest suppression services provided by bats to agricultural and natural systems. It is tempting to try to use values from previous studies in new applications, a practice known as benefits transfer. However, great care should be taken when applying benefits transfer or when conducting original studies that might be used in later studies.^{235,236} Similar care should be taken when scaling up results from field- or farm-level analyses to regional or global analyses, as it is possible that stakeholder values will vary at different spatial scales.²³⁷ It is also important to clearly define the change (increase or decrease) in the ecosystem service that is being valued.²³⁸

As noted above, direct estimation of supply or cost functions is difficult due to lack of data that in-

cludes measurements of the ecological entities (e.g., bats and bollworms). Efforts should be made to collect these types of data, at least for important crop systems. This includes getting information on other inputs into the production process and assessing producer decision making when various inputs change. It is likely that many agricultural producers are unaware of the services that bats provide because much of this activity occurs at night. Producer surveys could be used to provide education as well as elicit information on producer decision making.

The majority of valuation studies of ecosystem services focus on a single service. Additional challenges exist when attempting to measure values for multiple ecosystem services because double-counting of services is possible and tradeoffs between services may exist.^{238–240}

Summary and conservation considerations

Ecosystem services are the benefits that humans obtain from ecosystems that enhance their well-being. As reviewed here, bats provide many ecosystem services. Humans derive direct benefits from bats as food, guano for fertilizer, and through contributions to medicine and culture. Perhaps more significantly, yet much more difficult to quantify, humans derive indirect benefits from bats through arthropod suppression, forest regeneration, and maintenance via seed dispersal and pollination of a wide variety of ecologically and economically important plants. In turn, the contribution of these services by bats to healthy, functioning ecosystems provides additional benefits to humans by supporting vital regulatory processes such as climate regulation, nutrient cycling, water filtration, and erosion control. Unfortunately, many misconceptions about bats persist, especially in the neotropics, where humans regularly have negative interactions with vampire bats;²⁰⁵ thus, conservation efforts often fall short. Assigning values to the different ecosystem services provided by bats is one way of positively influencing the public's perception of these beneficial mammals; however, economic valuation of these services remains in its nascency. Here, we have reviewed most of the existing literature on the three primary ecosystem services provided by bats and highlighted areas of research that deserve further attention. We have also outlined both market and nonmarket valuation methods that either have been or could be used to estimate the economic value of these ecosystem

services. As was noted by the few published studies, these values can be quite substantial. However, a distinct challenge exists in that most of these efforts require detailed descriptions of ecological production functions (e.g., Klein *et al.*'s²¹³ pollinator dependence ratios) or consumer surveys of households in developing countries that require substantial time and monetary investments. Nevertheless, at a time when critical threats face bat populations (e.g., white-nose syndrome) and biodiversity as a whole is rapidly declining worldwide, the development of alternative conservation strategies—such as the valuation of ecosystem services—should become a priority.

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Appendix A:

Examples of economic and ecological damage caused by insect pests consumed by bats

June beetles. Adults are herbivorous and have the potential to defoliate trees in large numbers; their larvae, white grubworms, attack the roots of grasses and various crops such as corn, wheat, oats, barley, sugarbeets, soybeans, and potatoes.^{247,248}

Wireworms/Click beetles. Wireworms, click beetle larvae, cause several million dollars worth of damage annually, and no crop is known to be entirely immune.²⁴⁹

Leafhoppers and planthoppers. These true bugs are vectors of plant pathogens such as the rice dwarf and the maize mosaic viruses, as well as phytoplasmas and bacteria.²⁵⁰ The brown planthopper has resulted in cumulative losses of rice estimated in the hundreds of millions of dollars, and other species act as serious agricultural pests to potatoes, grapes, almonds, citrus, and row crops.²⁵¹

Spotted cucumber beetles (*Diabrotica undecimpunctata*). Serious pests of corn, spinach, and various cucurbit vines.⁸⁶ In their larval stages, *Diabrotica spp.* (referred to as corn rootworms) decimate corn crops, costing farmers in the United States an estimated \$1 billion annually in crop yields and costs of pesticide applications. The United States Department of Agriculture (www.usda.gov) reports that more hectares of cropland are treated with insecticide to control corn rootworm than any other pest in the United States.

Stinkbugs. Serious pests of various crops including apples, pecans, soybeans, cotton, field corn, grain sorghum, peaches, and vegetables.²⁵² Stinkbugs pierce plant tissues with their mandibular and maxillary stylets to extract plant fluids, which results in staining of the seed, deformation and abortion of the seed and fruiting structures, delayed plant maturation, and the predisposition to colonization by pathogenic organisms.

Gypsy moths. Serious pests of several hundred species of trees, bushes, and shrubs, both hardwood and conifer, and can lead to the complete defoliation when in high enough densities.²⁵³ Introduced into North America in the late 1800s, their range has continually expanded westward and now threatens temperate forested ecosystems throughout the northeast.²⁵⁴

Tent caterpillars. Have irruptive population dynamics, generally advancing to pest status every year in some regions of the United States and causing considerable defoliation of trees over extensive areas.²⁵⁵

Coneworms. Larvae feed within cones on cone scales and seeds of various species of firs and western pines,²⁵⁶ and can cause significant damage to fertilized conifer plantations and loblolly pine seed orchards.^{257,258}

Cutworms. Destructive garden pests, causing fatal damage to nearly any type of vegetable, fruit, or flower.²⁵⁹

Tortrix moths. Many moths of the genus *Cydia* are economically important due to the damage they inflict on fruit and nut crops, and include notable pests such as the codling moth, pear moth, alfalfa moth, and hickory shuckworm moth.

Snout moths. Members of the genus *Acrobasis* feed on a wide variety of shoots, nuts, and fruits

including alders, birches, hickories, pecans, and cranberries.

Corn earworm and tobacco budworm moths. Rank among the top pests in the United States in damage caused to crops and number of insecticides applied to crops to control them.²⁶⁰ In Texas, corn earworms are present in an estimated 98% of cornfields. Each female corn earworm moth potentially lays over 1,000 eggs in her lifetime,²⁶¹ which then develop into larvae that infest corn, cotton, or other crops.

Appendix B:

Methods for the valuation of ecosystem services

Revealed preference methods of valuation

Ecosystem services such as pest suppression, seed dispersal, and pollination are often inputs into the production of agricultural crops.²¹¹ A *production function* approach to valuation can be used to compare the levels of agricultural production with and without the ecosystem service or with a reduction in the service.²⁹⁰ In these situations, the ecosystem service input appears as an argument in the supply or cost function along with other inputs to production such as labor, capital, and materials (e.g., fertilizers). Estimation of consumer and producer surplus welfare measures using a production function approach often requires substantial time-series or cross-sectional panel data that include, among other things, measurements of the ecosystem service input (e.g., the number of bats feeding in each farm across several farms across multiple growing seasons). Because there is often a lack of sufficient data, a *damage function* approach to valuation is sometimes used.²⁹⁰ This approximation is based on the idea that arthropod predators, seed dispersers, and pollinators reduce the loss of agricultural crops that would otherwise result without the associated ecosystem service. It is an approximation rather than a true estimate, because it assumes that use of all other inputs to the production process remain constant, and that the price of the agricultural output does not change. Although fewer data are required with the damage function approach, challenges with establishing clear ecological relationships between the ecosystem service and agricultural output remain.

A related valuation method is the *replacement cost* method in which the value of the ecosystem service

is estimated by what it would cost to replace the service using an alternative approach. For example, pest suppression services may be estimated by the cost of the chemical pesticides that would be required to provide the same level of production output. However, caution must be exercised when using replacement costs as they do not reflect actual consumer or producer behavior and, thus, are not true welfare measures.²⁰⁸ For example, farmers might not be willing to pay the full amount for equivalent pest control. Shabman and Batie²¹⁹ describe three conditions that should be met when using replacement costs in valuations of ecosystem services: the alternative must provide the same level of service, the alternative must be the least-cost alternative, and there should be substantial evidence that individuals would be willing to pay for the alternative if the ecosystem service were eliminated. It is this last criterion that is typically difficult to ascertain.

Another revealed preference method for valuation of ecosystem services is the *hedonic pricing* method in which property values reflect a number of characteristics of a parcel of land including any ecosystem services provided from within the parcel itself or from neighboring parcels. The price of a parcel can be broken down into a set of implicit prices for each of the characteristics. This method is commonly used for valuing air and water quality or open space amenities, but could potentially be used to value ecosystem services provided by bats.

A fifth revealed preference valuation technique is the *travel cost* method, which estimates the recreation values associated with ecosystem services. Using the opportunity cost of time and actual costs incurred with traveling to a particular recreation site, the demand for recreation can be estimated. Expanding the analysis to multiple sites with varying levels of ecosystems services can elicit values for particular services. Travel cost studies are often used to assess ecotourism or sport hunting values.²¹⁰

Food, fuel, and other goods are often harvested directly from the ecosystem rather than being purchased through markets. For example, bats are hunted for local consumption in many developing countries.²² In these situations, *time allocation* models can be used to estimate the time invested in hunting and gathering versus other household activities. These studies are typically conducted through household surveys although a researcher may directly observe the behavior.

Stated preference methods of valuation

Stated preference methods of valuation such as *contingent valuation* and *conjoint analysis* involve surveys that contain hypothetical scenarios of ecosystem services and elicit individual willingness to pay for well-defined changes to one or more ecosystem service.²¹² Despite some early concern over the use of stated preference surveys, the techniques have improved considerably over the past two decades and are commonly accepted methods for eliciting non-market values.^{4,208} Stated preference surveys are the only economic valuation method available for assessing existence values.

Appendix C:

Steps used in the valuation of ecosystem services

There is no one-size-fits-all process for valuing ecosystem services. Each valuation study has its own policy context, within which is an associated set of ecosystem services. The following five steps, adapted from work by Hein *et al.*,²³⁷ NRC,²⁰⁸ and MEA,⁴ are offered as valuation guidelines. For each step, a set of qualifying questions is provided.

Step 1. Identify the policy or decision context for the valuation exercise:

- What is the purpose and how will the results be used?
- Which ecosystem services will be included?
- What is the appropriate geographic scale?
- How is the valuation question framed?

Step 2. Assess the underlying ecology (structure, functions, processes):

- How well understood is the ecosystem of interest?
- Are important dynamics understood?
- Are important nonlinearities and thresholds understood?
- Are the complexities of the system understood?
- Are the linkages between policy alternatives and ecological responses understood?

Step 3. Translate ecological functions to ecosystem services:

- Can the outputs from the ecological models be used as inputs to the economic models?

- Are all direct and indirect linkages between ecological functions and ecosystem services understood?

Step 4. Translate ecosystem services to values:

- What valuation methods are appropriate?
- What data are available?
- How will aggregation of values across individuals, services, and time be handled?
- How will double-counting be avoided?

Step 5. Assess the level of uncertainty:

- What are the primary sources of uncertainty?
- What methods will be used to address uncertainty?
- Are there important gaps in our knowledge?
- Are there important potential irreversibilities?

Conflicts of interest

The authors declare no conflicts of interest.

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