EFFECT OF CLIMATE AND ELEVATION ON DISTRIBUTION AND ABUNDANCE IN THE MIDEASTERN UNITED STATES

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Abstract

The geographic association of good (i.e., warm) summer and good (i.e., cold) winter habitat is limiting for the Indiana bat (*Myotis sodalis*). During summer, the Indiana bat is most common in an area of the Midwest, comprised of southern Iowa, southern Michigan, the northern half of Missouri, most of Illinois, much of Indiana (excluding the two southern tiers of counties), and western Ohio. Detailed climatological maps indicate that this portion of the range is typically warmer in summer than parts of the bat’s range to the east and northeast. During summer, higher latitudes and elevations typically are cooler and wetter, and temperatures at higher elevations are more variable, adding significantly to the cost of reproduction. Cold winter hibernacula, in contrast, are essential for efficient hibernation. Hibernacula with large populations of Indiana bats are concentrated in Indiana, Kentucky, and southern Missouri, but generally, caves in the southern and mideastern United States are too warm for efficient hibernation. Implementing standardized management practices across the range of the species, based on ecological parameters appropriate for the Midwest, may provide little benefit to the species in outlying areas. More roost trees in areas not thermally suited to the species will not benefit the species, and searching for reproductive female Indiana bats in areas of high elevations and/or cool temperatures may not produce significant results. Regional customization of management plans and regulatory requirements to account for regional ecological constraints under which the species lives and reproduces seems reasonable.

Key words: climate, conservation, distribution, eastern United States, elevation, endangered species, Indiana bat, management, *Myotis sodalis*, range, temperature

Introduction

The Indiana bat (*Myotis sodalis*) is listed as endangered under the Endangered Species Act, and both the species and its habitat deserve protection. Managers of federal and state lands develop and implement plans that include the species, and private developers are required to survey for the species and address requirements of the Endangered Species Act, if the species is found. Surely, everyone who has dealt closely with this species has called it an enigma.

*Enigma 1*—The Indiana bat is considered a tree bat in summer, but it is most common in portions of its range where large, open, unforested lands are interspersed with wooded areas (Gardner and Cook 2002). It typically is not common in heavily forested regions. West Virginia, for example, has 5 million ha of wooded, potential habitat for these endangered bats but a wintering population of only 10,700 Indiana bats. Oak-hickory forest, which is commonly used by Indiana bats (e.g., Callahan et al. 1997), is the dominant forest type for 77% of that land. Virginia has 2.3 million ha of wooded habitat within the known range of the species but a very small population of Indiana bats—currently 833 bats, down from 2,500 bats in 1987. Pennsylvania has an enormous amount of woodland, 6.9 million ha, yet only 700–800 Indiana bats are known. In contrast, Indiana has only 1.7 million ha of forested lands but a population of 112,500 Indiana bats, which is more than any other state (Johnson et al. 2002).
Enigma 2—Although endangered, this bat is found in a variety of habitats, seemingly making it a generalist. It is not restricted to wilderness or pristine habitats. Maternity colonies of this species have been found roosting along the edge of woodlots and agricultural lands, in heavily logged woodlots, heavily grazed (savannah-like) woodlots and open pastures, and even pig lots (e.g., Gardner et al. 1991, Kurta et al. 1993, 1996).

Enigma 3—Indiana bats use a myriad of species of trees for roosts and are found in a variety of roost types and situations. Maternity colonies typically choose large trees, more than 38 cm in diameter at breast height, in Illinois (Gardner et al. 1991), Indiana (Whitaker and Brack 2002), Michigan (Kurta et al. 1996, 2002), and Missouri (Callahan et al. 1997). Individual bats, in contrast, occasionally use “trees” as small as 8.4 cm in diameter, and they often roost in areas of recent, restricted harvest (e.g., two-age shelterwood and highgrade cuts), especially during spring staging and autumn swarming (MacGregor et al. 1999). Indiana bats typically roost under exfoliating bark, but some individuals and even maternity colonies find shelter within tree crevices (Gardner et al. 1991, Kurta et al. 2002).

Enigma 4—In contrast to conventional wisdom for an endangered species, the range of the Indiana bat is very large, encompassing an enormous amount of geographic variability. Its range includes all or part of eight physiographic provinces and a dozen or more ecoregions, depending upon the classification used. The range of this bat includes most of the eastern United States (Gardner and Cook 2002), encompassing 11° of latitude and an estimated 1.56 million km².

An immense amount of money and time is spent meeting regulatory requirements for this endangered species. Land stewards, such as the U.S. Forest Service, develop management plans and implement them at significant cost to taxpayers, and private developers conduct summer netting surveys to ascertain whether projects may have an adverse effect on the Indiana bat or its summer habitat. Extensive netting surveys, collectively totaling ca. 3,000 net-nights since 1995, in West Virginia, Virginia (only within the species range), and Pennsylvania, have produced no reproductively active female Indiana bats, one male of unknown age, seven adult males, and one juvenile, or 0.003 Indiana bats/net-night. Cost, if this work were completed commercially, exceeds $210,000/bat. This is an underestimate, because all netting completed in Virginia and Pennsylvania could not be included due to missing data, although all known captures of Indiana bats were included in our calculation. The Indiana bat is not absent from these states during the summer reproductive season. Males, for example, can be caught at caves in West Virginia (Stihler in press), and reproductive females roost in an old church in Pennsylvania (Butchkoski and Hassinger 2002). Summer netting, however, is consistently unproductive. In comparison, five of our previous, unpublished studies in Indiana produced 0.025, 0.030, 0.148, 0.220, and 0.330 Indiana bats/net-night.

Across the range of the species and across elevational gradients, the Indiana bat is exposed to significant differences in climate that may affect its distribution and abundance. Clark et al. (1987), for example, indicate that climatic factors limit distribution of the Indiana bat in Iowa to areas south of 42° latitude. Cryan et al. (2000) state that abundance of reproductive female bats in the Badlands of South Dakota is inversely related to elevation, and Fenton et al. (1980) and Thomas (1988) report similar findings for bats in the Rocky and Cascade mountains, respectively. Areas of higher latitudes and elevations typically are cooler and wetter, and higher elevations experience greater seasonal variability, all of which can reduce the food supply, increase thermoregulatory demands, and reduce reproductive success of bats.

This study attempts to understand better why the Indiana bat, a bat that roosts in trees in summer, is uncommon in eastern states with extensive forests. To do this, we compare temperatures and other features of the core range of the species, where it is most common, to less populated portions of the range, and we look at elevation as a criterion to explain why seemingly suitable habitat is unoccupied. Finally, we examine management implications of these findings.

Methods

Ecoregional analysis—We examine climate, especially summer and winter temperatures, and other ecological differences across the range of the Indiana bat, using maps of Hargrove and Hoffman (1999). Using an iterative, multivariate, clustering technique, they divide the coterminous 48 states into “ecoregions” that have similar values of elevational, edaphic, and climatic variables. Resolution of the clustered maps is 1 km².
Each cell of the ecoregional map has contributions from nine variables, including elevation, soil nitrogen, organic matter of soil, water capacity of soil, depth to water table, mean precipitation, solar irradiance, degree-day heat sum, and degree-day cold sum. Each of these variables is mapped individually as well.

We relied most heavily upon maps of the degree-day heat sum, degree-day cold sum, and the ecoregional map of combined variables. The degree-day heat sum and degree-day cold sum are reflections of average temperatures in summer (summer warmth) and winter (winter cold), and for simplicity, we will refer to them as such. Importantly, the maps use a gradually changing spectrum of color to illustrate distribution of temperature and other variables across the continent; consequently, this part of our analysis is necessarily qualitative. These maps, however, are essential to our discussion, and although they cannot be reproduced here, the maps are available on the Internet at http://research.esd.ornl.gov/cgi-bin/pzs and at http://research.esd.ornl.gov/~hnw/esri98/. The former site allows one to manipulate the maps and focus on certain parts of the country, whereas the latter site provides a better description of the variables and how the maps were constructed. We encourage the reader to browse these sites before proceeding further.

**Effects of elevation**—We also examine the relationship between capture of Indiana bats and elevation for West Virginia, Virginia, and Pennsylvania. West Virginia has the highest average elevation of any state east of the Mississippi River; the lowest point is 75 m and the highest point is 1,482 m above sea level. Lowest points in Virginia and Pennsylvania are 0 m (sea level), whereas the highest points are 1,746 m in Virginia and 979 m in Pennsylvania.

We use surrogate species for the analyses because Indiana bats are so rarely captured within these states in summer. To explore the effect of elevation on presence of reproductive females, we use records of mistnetting captures obtained from state agencies. Such netting often is initiated to look for the Indiana bat, but netting sites typically are not located near sites known to be used by the species. We use topographic maps of the U.S.
Geological Survey to determine elevation of capture locations, and we pool captures by state because of differences in geography and elevation among states. Only netting between 15 May and 15 August is considered, and netting records with inaccuracies, inconsistencies, or missing values are excluded. Within each state, we subdivide each species into adult males, nonreproductive females, reproductive females (pregnant, lactating, and postlactating), and juveniles.

To begin the analysis, we determine the proportion of reproductive females among all adults captured in each 91.4-m (300-ft) interval of elevation. We use regression (Statistical Package for the Social Sciences, version 7.0) to examine the relationship between the log-transformed proportion of reproductive females and elevation, which is weighted by number of adults captured in each interval. Species with less than 10 captures of adult females are excluded.

Results

Range of the Indiana bat by ecoregion—During summer, maternity colonies of Indiana bats are most common in southern Iowa, southern Michigan, the northern two-thirds of Missouri and Indiana, Illinois, and the eastern edge of Ohio (Gardner and Cook 2002, U.S. Fish and Wildlife Service 1999). Summer and winter temperatures for this area are reasonably distinct from temperatures through most of the rest of the range of the species (http://research.esd.ornl.gov/~hnw/esri98/). Notably, summer temperatures in Pennsylvania, Virginia, and West Virginia are cooler than in the core range.

During winter, temperatures in Indiana, where large numbers of Indiana bats hibernate, are lower than temperatures in areas of Missouri and Kentucky containing major hibernacula. Indiana is also colder in winter than most of Virginia and West Virginia, and even portions of Pennsylvania. In addition, a mine in Preble County, Ohio, which has a recently discovered population of nearly 10,000 hibernating Indiana bats, and mines and caves used as hibernacula in New York are in areas that are colder than Missouri, Kentucky, Virginia, and much of West Virginia.

The combination of summer warmth and winter cold corresponds well with relative abundance of the species across its range (Fig. 1). The ecoregions of Hargrove and Hoffman (1999), formed from a combination of elevational, edaphic, and climatic factors, show strong associations with the range of the Indiana bat (compare maps on Internet with those in Gardner and Cook 2002).

Effect of elevation in the central Appalachians—We have suitable data from captures of 2,653 adult bats of 13 species (Table 1). Of these, 1,707 captures are from West Virginia, 476 from Virginia, and 470 from Pennsylvania. Reproductive females represent 31.1% of total adult captures.

Catches of evening (Nycticeius humeralis), hoary (Lasiurus cinereus), Indiana, Seminole (Lasiurus seminolus), silver-haired (Lasionycteris noctivagans), and Virginia big-eared (Corynorhinus townsendii) bats are too small for analysis in any state. Nonetheless, data are sufficient to perform regressions on six species in West Virginia and three species in Virginia and Pennsylvania, for a total of 12 analyses. Ten analyses indicate a significant effect of elevation—seven are negative and three are positive effects (Table 2).

The proportion of reproductive females among eastern pipistrelles (Pipistrellus subflavus) and red bats (Lasiurus borealis) is inversely related to elevation in West Virginia and among big brown bats (Eptesicus fuscus) in Pennsylvania. In addition, there was a decrease in proportion of reproductive female little brown bats (Myotis lucifugus) with increasing elevation in all three states (Table 2). Reproductive female little brown bats are 19.2% percent of the catch of adults of that species in Pennsylvania, 43.9% in Virginia, and 39.5% in West Virginia (Table 1). The predicted proportion of reproductive female little brown bats drops to ca. 10% of the adult population near 1,067 m (3,500 ft) in West Virginia and 244 m (800 ft) in Pennsylvania, but the predicted value is ca. 20% up to 1,067 m (3,500 ft) in Virginia. In contrast, the proportion of reproductive female northern bats (Myotis septentrionalis) in the catch is relatively constant across elevation in West Virginia but actually increases with elevation in Virginia and Pennsylvania, as does the proportion of reproductive small-footed bats (Myotis leibii) in West Virginia.

Discussion

Why is a tree bat less common where there are more trees?—There is no evidence that the Indiana bat was ever common in the eastern United States, despite vast forests that seemingly could be used by a tree-dwelling bat and caves that could be used for hibernation. Obviously, many other factors affect distribution,
Table 1.—Elevation (m) of sites where bats were captured, from 15 May through 15 August, by species, sex, and reproductive class.

<table>
<thead>
<tr>
<th>Species</th>
<th>Pennsylvania</th>
<th>Virginia</th>
<th>West Virginia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adult males</td>
<td>Nonreproductive females</td>
<td>Reproductive females</td>
</tr>
<tr>
<td></td>
<td>$\overline{X}$</td>
<td>$SD$</td>
<td>$n$</td>
</tr>
<tr>
<td>Big brown bat</td>
<td>429</td>
<td>120</td>
<td>64</td>
</tr>
<tr>
<td>Silver-haired bat</td>
<td>293</td>
<td>1</td>
<td>39</td>
</tr>
<tr>
<td>Red bat</td>
<td>374</td>
<td>101</td>
<td>32</td>
</tr>
<tr>
<td>Hoary bat</td>
<td>326</td>
<td>34</td>
<td>6</td>
</tr>
<tr>
<td>Small-footed bat</td>
<td>353</td>
<td>179</td>
<td>5</td>
</tr>
<tr>
<td>Little brown bat</td>
<td>320</td>
<td>94</td>
<td>35</td>
</tr>
<tr>
<td>Northern bat</td>
<td>354</td>
<td>105</td>
<td>27</td>
</tr>
<tr>
<td>Eastern pipistrelle</td>
<td>288</td>
<td>155</td>
<td>4</td>
</tr>
<tr>
<td>State total</td>
<td>229</td>
<td>93</td>
<td>91</td>
</tr>
<tr>
<td>Virginia big-eared bat</td>
<td>756</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Big brown bat</td>
<td>662</td>
<td>247</td>
<td>35</td>
</tr>
<tr>
<td>Silver-haired bat</td>
<td>440</td>
<td>33</td>
<td>3</td>
</tr>
<tr>
<td>Red bat</td>
<td>635</td>
<td>218</td>
<td>49</td>
</tr>
<tr>
<td>Hoary bat</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Gray bat</td>
<td>535</td>
<td>2</td>
<td>23</td>
</tr>
<tr>
<td>Small-footed bat</td>
<td>975</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Little brown bat</td>
<td>801</td>
<td>234</td>
<td>34</td>
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<tr>
<td>Northern bat</td>
<td>746</td>
<td>226</td>
<td>112</td>
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<tr>
<td>Indiana bat</td>
<td>436</td>
<td>57</td>
<td>5</td>
</tr>
<tr>
<td>Eastern pipistrelle</td>
<td>594</td>
<td>174</td>
<td>68</td>
</tr>
<tr>
<td>State total</td>
<td>331</td>
<td>54</td>
<td>91</td>
</tr>
</tbody>
</table>

Table 1.—Elevation (m) of sites where bats were captured, from 15 May through 15 August, by species, sex, and reproductive class.

abundance, and reproductive success of the species; climate, on a larger scale, and weather, on a more local scale, are notable examples. We believe that a unique association of summer and winter temperatures, a combination that is lacking over much of the range of the Indiana bat, accounts for substantial, geographic differences in abundance of this endangered species.

Detailed climatic maps indicate that summer temperatures are far from uniform across the range of the Indiana bat (Hargrove and Hoffman 1999). Summer temperatures in the eastern portion of the range and other outlying areas, are different from those in the core summer area where the species is most abundant. Portions of the bat’s range in West Virginia, Virginia, and Pennsylvania are slightly cooler in summer than are core areas, and there is a 6.4°C decrease in temperature...
The Indiana bat spends at least 5 months in hibernation. Caves are the natural winter habitat of the species, although some abandoned mines are used now. Caves must provide a cold, but not freezing, microclimate for hibernation. Although many factors affect the temperature of individual caves, cave temperatures in winter are a function of the surface temperature of that region. Detailed weather maps indicate that winter temperatures on the surface are not uniform throughout the range of the species. Major hibernacula of the Indiana bat are in areas of karst with cold winter temperatures. Much of Virginia and major portions of West Virginia, however, are warmer in winter than are areas where major hibernacula are located, and there is limited karst in these states. An exception is mideastern West Virginia, where there is an important hibernaculum for the Indiana bat (Hellhole Cave). The complex structure of this cave traps cold air and provides stable temperatures in winter. Other important eastern hibernacula for the species are in northern New York, where it is much cooler than in Virginia and West Virginia.

**Implications of elevation**—Northern latitudes and higher elevations, with shorter growing seasons and cooler weather, are a constraint for many species. Areas at higher elevation also suffer greater variations in temperature, both seasonally and daily. The Indiana bat, like most species of small bat in temperate areas, is capable of being a thermal conformist (Henshaw 1965). Although this allows the individual to withstand cold or wet spells when food is not available, such conditions, nevertheless, add to the cost of reproductive success. Indiana bats attempting to reproduce in mid- and northeastern states face the rigors of a cooler summer climate, which is intensified by elevation in many localities. The probability that the Indiana bat reproduces at higher elevations in these three eastern states is low. In Pennsylvania, the only known maternity colony of Indiana bats roosts in a building, which probably provides thermal benefits. Members of this colony roost and preferentially forage at lower elevations, and foraging seems concentrated in areas with a southerly aspect (Butchkoski and Hassinger 2002). In Virginia, all summer captures to date are male, and all, except one, are from the Appalachian Plateau (Hobson 1993) at a relatively low elevation (Table 1). One capture in Virginia is from the Ridge and Valley Province at an elevation of 750 m.

Within the three eastern states studied, reproductive females of several species of bat are proportionately less common at high elevations. One of these, the little brown bat, also is found at much higher latitudes than is the Indiana bat. The little brown bat often uses buildings that may provide a thermal advantage at higher elevations. Two additional species, the northern and small-footed bats, with ranges that go much farther north than that of the Indiana bat, have an increasing

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**Table 2.**—Regression analysis of the effect of elevation on reproductive activity for each species in each state for which more than 10 adult females were captured.

<table>
<thead>
<tr>
<th>Species</th>
<th>State</th>
<th>$r^2$</th>
<th>$F$</th>
<th>$P$</th>
<th>$b_0$</th>
<th>$b_1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big brown bat</td>
<td>West Virginia</td>
<td>0.02</td>
<td>3.53</td>
<td>0.06</td>
<td>-0.10</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Pennsylvania</td>
<td>0.55</td>
<td>674.78</td>
<td>&lt;0.0001</td>
<td>7.67</td>
<td>-1.02</td>
</tr>
<tr>
<td>Red bat</td>
<td>West Virginia</td>
<td>0.79</td>
<td>497.99</td>
<td>&lt;0.0001</td>
<td>1.78</td>
<td>-0.22</td>
</tr>
<tr>
<td></td>
<td>Virginia</td>
<td>0.01</td>
<td>0.74</td>
<td>0.39</td>
<td>-0.07</td>
<td>0.01</td>
</tr>
<tr>
<td>Small-footed bat</td>
<td>West Virginia</td>
<td>0.26</td>
<td>13.50</td>
<td>0.0007</td>
<td>-1.92</td>
<td>0.31</td>
</tr>
<tr>
<td>Little brown bat</td>
<td>West Virginia</td>
<td>0.89</td>
<td>3,963.82</td>
<td>&lt;0.0001</td>
<td>2.61</td>
<td>-0.30</td>
</tr>
<tr>
<td></td>
<td>Virginia</td>
<td>0.49</td>
<td>113.42</td>
<td>&lt;0.0001</td>
<td>4.28</td>
<td>-0.50</td>
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<td></td>
<td>Pennsylvania</td>
<td>0.93</td>
<td>2,250.30</td>
<td>&lt;0.0001</td>
<td>2.57</td>
<td>-0.36</td>
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<td>Northern bat</td>
<td>West Virginia</td>
<td>0.02</td>
<td>17.43</td>
<td>&lt;0.0001</td>
<td>0.68</td>
<td>-0.04</td>
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<td></td>
<td>Virginia</td>
<td>0.36</td>
<td>116.63</td>
<td>&lt;0.0001</td>
<td>-1.12</td>
<td>0.17</td>
</tr>
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<td></td>
<td>Pennsylvania</td>
<td>0.39</td>
<td>38.65</td>
<td>&lt;0.0001</td>
<td>-1.77</td>
<td>0.30</td>
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<tr>
<td>Eastern pipistrelle</td>
<td>West Virginia</td>
<td>0.75</td>
<td>332.88</td>
<td>&lt;0.0001</td>
<td>2.15</td>
<td>-0.27</td>
</tr>
</tbody>
</table>

* $^a$ Number of bats of each species caught in each state is provided in Table 1.
* $^b$ Formula for each regression line was: log$_{10}$ (proportion of reproductive females) = $b_0$ + ($b_1$ . . . elevation).
* $^c$ Although 12 adult females were caught, only one was reproductive.
proportion of reproductive females at higher elevations. Perhaps this helps reduce competition with both Indiana and little brown bats.

**Regulatory implications**—The Indiana bat is indeed very rare over most of its range, and areas of abundance are associated with a unique geographic association of summer and winter temperatures. Because optimal conditions are lacking over much of the range, it is unlikely that the species was or will be equally abundant in all parts of its range. It is probable that the species responds in varying degrees to the demands of a varying environment. Nevertheless, two conservation strategies for the species often are applied similarly across the range. First, management for summer habitat almost uniformly is designed with the primary goal of providing more trees, i.e., more summer nursery roosts, and second, regulatory agencies almost uniformly require determination of presence/absence of reproductive females by mistnetting in areas of potential impact.

The goal of managers and regulators alike is to maximize the good they do for the species with the time and money available. Many lands controlled by the U.S. Forest Service in the midwestern United States are in a region where both summer and winter temperatures are suboptimal for the Indiana bat. Implementing current standardized management practices in these areas, based on ecological parameters appropriate for the Midwest, may result in limited benefits to the Indiana bat (although other species may benefit). Providing more roost trees at higher elevations and on other cooler sites (e.g., north-facing slopes) is of questionable value to the Indiana bat, because more roosts trees in areas not thermally suited to the species simply will not result in more Indiana bats. Searching for reproductive female Indiana bats in summer in high and/or cool areas is unlikely to yield significant, positive results, and we believe that concentrating efforts in warmer habitats is justified. In short, regional customization of management strategies and regulatory requirements to match regional ecological constraints under which the species lives and reproduces is reasonable.

Like the mid- and northeastern United States, southern and southeastern portions of the range of the Indiana bat have more trees than the core summer area. The South and Southeast are as warm or warmer in summer than the core area, although this is not universally true. It seems implausible that managing for more trees (i.e., roosts) across the southern and southeastern United States will have a significant effect on recovery of the species. It is more likely that hibernacula with suitable (cool) temperatures are not readily available, especially given the species’ seeming reluctance to migrate long distances north and west to hibernate (Gardner and Cook 2002). More roost trees in southern forests will not produce more Indiana bats if appropriate hibernacula are lacking.

The goal of land managers and conservation biologists should be to minimize money, time, and effort spent managing areas that are unlikely to support the Indiana bat and to divert these resources to activities that more directly benefit the species. We believe our data can help reach that goal. As more information becomes available, our analyses should be refined and updated.

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