

Use of Species/Area Equations to Estimate Potential Species Richness of Bats on Inadequately Surveyed Mountain Islands

Ronnie Sidner and Russell Davis¹

Abstract.—Species richness of bats on selected mountains in southeastern Arizona was compared by regression to the area of montane habitat in each of these mountains. The resulting equation was then compared to similar equations generated from species-area curves that have been reported for birds in the Great Basin and small non-flying mammals in the Madrean Archipelago. Data from which these equations were calculated were then graphed and compared to the power model (log/log) regression curve. Outlier data points (apparently anomalous mountains), both above and below the regression line, were then examined. Inadequate sampling effort, size of forested area, and perhaps low habitat diversity are shown to be factors contributing to species richness on certain mountains that is lower than that which would be predicted from mountain (island) area alone. For bats, the contribution to species richness of sampling intensity may provide a caveat that could be important in certain management and conservation decisions: recorded species richness is not always the result of biological processes. This analysis also provides information that could prove useful in decisions regarding the most efficient use of funds for faunal surveys—it would allow these to be directed toward those mountains where recorded species richness is most likely to be increased.

INTRODUCTION

In general, the larger the region sampled, the higher the species richness. This positive correlation of the number of species in a region with the area of that region is one of the most ubiquitous and widely accepted ecological principles. The cause of this pattern, and the factors, other than area, that produce it, however, are topics of ongoing ecological debate. In the southwestern United States, patterns of species richness of both birds and mammals occurring on montane islands have received considerable attention (Brown 1978; Davis et al. 1988; Lomolino et al. 1989). In each case, as expected, when the number of species present on each mountain is plotted on the y-axis of a log-log graph, and the area of each mountain is plotted on the x-axis, the corresponding regres-

sion line (plotted from an equation determined by regression analysis) graphically displays a highly significant species/area relationship (see the "bird" and "mammal" curves in Figure 1).

Brown (1978) attempted to use the differences in the slopes of the species/area regression equations that were obtained for mammals and birds on mountain islands in the Great Basin to explain the differences in the patterns of species richness. The slope of the regression line for birds showed a flatter slope, he explained, because birds fly and the extent of isolation of the individual mountain ranges is thus inconsequential. The species/area relationship for birds on mountain islands in the Great Basin, therefore, is very much like that from data obtained from samples taken from a "mainland". On the other hand, Brown pointed out, the species/area regression line for small, non-flying mammals on these same mountain islands has a steeper slope—reflecting their lack of mobility and the extent of the relative isolation (to these

¹Department of Ecology and Evolutionary Biology, University of Arizona.

animals) of the various mountain ranges. A comparably steep slope was also obtained by Davis et al. (1988) for small, non-flying mammals on mountain islands in Arizona and New Mexico.

Bats have been omitted from the papers cited above and from most studies of species richness and area, because of the expectation of potential confusion that would result from bats behaving biogeographically much more like birds than other mammals, and because the distribution of bats generally was not well known (Brown 1978). Only recently have analyses of the influence of area on species richness of bats begun to emerge. Findley (1993) gives two examples of positive influence of area on species richness of bats, one from temperate zones and one from the tropics ($r^2=0.50$ and $P=0.0001$, and $r^2=0.17$ and $P=0.03$, respectively).

The present study is designed to determine first the pattern of species richness of bats on certain selected mountain islands of the Madrean Archipelago, and then to verify the expected role of area. The slope of the regression line obtained from the analysis necessary for that verification will be compared with regression lines reported for birds and small non-flying mammals. This comparison will provide a tentative test of the hypothesis that the slope of the species/area regression line for bats would be most similar to that of birds. An additional objective of this study, one of considerably more importance, is to determine mountain island characteristics, other than area, that influence the montane species richness of bats. Knowledge of such factors could play an

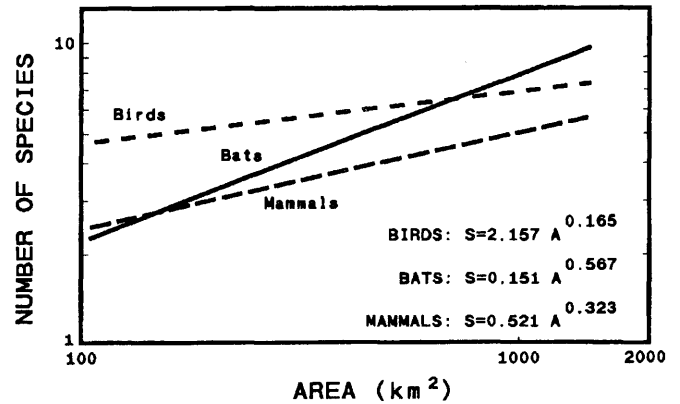


Figure 1.—Species-area curves. Both axes are logged. The equation for birds was derived from Brown's (1978) species-area curve for birds on mountain islands in the Great Basin; his data were first converted from area in mi^2 to km^2 . The equation for mammals is from Davis et al. (1988) for small, non-flying mammals (non-bats) on mountain islands in Arizona and New Mexico. The equation for bats is from data provided in this study.

important role in management and conservation decisions and thus have an important impact on the bat fauna of the Madrean Archipelago.

METHODS

We selected ten of the Madrean Islands for which there was either published information regarding bat distributions or for which we had gathered distribution data during recent field work (Table 1).

Table 1.—Characteristics of selected mountain ranges in the Madrean Archipelago. Total area is the area of montane habitat (oak woodland, chaparral, and forest) measured on the Brown and Lowe map (1980). Forest is the area only of forest habitats (pine and mixed conifer, and spruce-fir). Number of montane habitats (including woodland, chaparral, pine or mixed conifer, and spruce-fir forests) in each range are as mapped by Brown and Lowe (1980). Survey effort is a subjective ranking of surveying for bats by biologists. Species richness is the number of montane species of bats recorded from the range (see Table 3).

Mountain Range	Total Area (km^2) [Forest]	Number Montane Habitats	Highest Peak (m)	Survey Effort	Species Richness
Santa Catalina	549 [57]	3	2792	8	7
Rincon	338 [21]	3	2626	5	7
Santa Rita	410 [16]	2	2882	4	5
Whetstone	105 [0]	1	2343	1	2
Galiuro	668 [19]	3	2332	3	4
Pinaleno	537 [162]	3	3267	7	5
Chiricahua/Dos	1468 [122]	3	2986	10	8
Cabezas/Pedrogosa Complex					
Huachuca/	1056 [36]	2	2886	8	8
Patagonia Complex					
Animas	179 [27]	2	2601	6	6
Baboquivari	142 [0]	1	2357	1	1

Using the Brown and Lowe map (1980), we measured the basal area that corresponded to the total area of montane habitats (woodland, and chaparral and forest, if present) on each island and the area of forest habitat alone (excluding woodland and chaparral); see Table 1. The number of montane habitats on each island was counted by considering woodland and chaparral biotic communities each as distinct habitats, while subdividing forest into pine and mixed conifer forest or spruce-fir forest habitats. These habitat criteria resulted in a tally of one to three habitats for each island (Table 1); no montane island had four habitats—none had both chaparral and spruce-fir forest.

From various road and topographical maps we determined the elevation of the highest peak on each island (Table 1). In addition, we compiled, *a priori*, a subjective list of relative survey effort that had been devoted to, or had included, the bat fauna present on each of the mountain islands. The results of this subjective estimate were then ranked from 1 to 10 (Table 1). Criteria used in this estimate of survey effort included: published results of a survey of the mammals (and/or specifically of the bats) of a particular mountain range, accessibility by roads, number of sites known to be sampled, number of biologists known to have studied bats in that range, and the amount of our own field effort there (Appendix 1).

To determine species of Arizona bats that have montane affinity, we used Hoffmeister's table (Table 4.1 in Hoffmeister 1986) of the occurrence in Arizona of each species in each habitat as a percent of the total sites of collection of that species.

We chose those species of bats for which a total of 50% or more of their capture localities were in montane habitat: chaparral, oak woodland, and forest habitats (Table 2). Of the 11 species that qualified as "montane" bats, two were not used in our analysis. *Mormoops megalophylla* is known from only one locality in Arizona and was only observed during two nights in 1954. *Myotis evotis* is not known from any of our selected mountain islands nor from any locality in southern Arizona. Species names follow Jones et al. (1992) or Hoffmeister (1986).

We then compiled presence or absence data from the literature for the nine remaining species of bats (Table 3) on each of our selected mountains (Cockrum 1960, Findley et al. 1975, Cook 1986, Hoffmeister 1986, Sidner and Davis 1988, Davis and Sidner 1992, and Hoyt et al. 1994; and from our recent field surveys, Sidner and Davis, unpublished field notes).

Using regression analysis, we log-transformed both species richness of montane bats and total area in order to calculate a power model ($S = cA^z$), to allow us to conveniently compare the results of our study with results from Brown (1978) and Davis et al. (1988). Because we converted Brown's area data from mi^2 to km^2 to improve this comparison, the "intercept" portion of the equation for the Great Basin bird distribution data is different from that given in his paper (Brown 1978).

Of four characteristics of the mountain ranges that were tested (total area, forest area, elevation, and number of montane habitats), only forest area and elevation of highest peak were significantly correlated ($r=0.836$, $P=0.003$).

Table 2.—Species of Arizona bats for which $\geq 50\%$ of known localities (Hoffmeister 1986) occur in montane habitats: chaparral, woodlands (oak), and forests (pine, mixed, and spruce-fir). Two species indicated by * were not used in the analyses (see text).

Species	% Occurrence in Montane Habitat				No. Sites
	C	W	F	Total	
* <i>Mormoops megalophylla</i>	0	100	0	100	1
<i>Choeronycteris mexicana</i>	0	64	0	64	25
<i>Myotis occultus</i>	17	0	67	84	18
* <i>Myotis evotis</i>	7	0	73	80	15
<i>Myotis auriculus</i>	0	30	30	60	10
<i>Myotis thysanodes</i>	9	28	19	56	58
<i>Myotis volans</i>	9	26	31	66	35
<i>Myotis ciliolabrum</i>	9	25	25	59	32
<i>Lasionycteris noctivagans</i>	7	7	58	72	30
<i>Lasiurus cinereus</i>	10	10	32	52	31
<i>Idionycteris phyllotis</i>	6	6	38	50	16

Table 3.—Presence/absence records for montane species of Arizona bats used in this report. Presence is indicated by +, absence by —. Data are taken from Cockrum (1960), Findley et al. (1975), Cook (1986), Hoffmeister (1986), and Sidner and Davis (1988). An asterisk indicates new records of presence verified by unpublished data (Davis and Sidner 1992, and Sidner and Davis—field notes). A specimen of *M. occultus*, designated by ?, was collected by us 7 km south of the Catalina Mtn. and may occur there, but we have not counted it for species richness there. See Table 1 for full names of mountain ranges abbreviated here. See Table 2 for full names of species.

Species	Mountain Ranges										Total
	CA	RI	WH	SR	BA	HU	CH	GA	PI	AN	
<i>C. mexicana</i>	+	+	+	+	+	+	+	+	+	—	9
<i>M. occultus</i>	?	—	—	—	—	+	—	—	—	—	1
<i>M. auriculus</i>	+	+	—	+	—	+	+	—	+	+	7
<i>M. thysanodes</i>	+	+	+	+	—	+	+	+	+	+	9
<i>M. volans</i>	+	+	—	+	—	+	+	—	+	+	7
<i>M. ciliolabrum</i>	+	+	—	—	—	+	+	—	—	+	5
<i>L. noctivagans</i>	+	+	—	—	—	+	+	+	+	+	7
<i>L. cinereus</i>	+	+	—	+	—	+	+	—	—	+	6
<i>I. phyllotis</i>	—	—	—	—	—	—	+	+	—	—	2
Species	7	7	2	5	1	8	8	4	5	6	
Richness of Montane Bats											
Species	21	20	8	17	7	18	21	5	15	17	
Richness of all bats on Mtn											

Stepwise multiple regression was used to test for the influence of the following variables on species richness (untransformed data): total area, forest area, elevation of the highest peak, number of montane habitats, survey effort, and total species richness of bats on the mountain. Survey effort was also tested separately against species richness using simple linear regression.

RESULTS AND DISCUSSION

Species richness of bats for each island is given in Table 3. Values are provided for total species richness on the mountain (including non-montane habitats) and for those species of bats that are here characterized as montane species.

The equation resulting from the regression of species richness of bats and area of mountain islands is $S=0.151 A^{0.567}$ ($r^2=0.521$, $F=8.70$). However, the semi-log model provided a better fit of the species-area relationship than either the log-log or the unlogged models ($r^2=0.562$ v. 0.521 and 0.459, and $F=10.28$ v. 8.70 and 6.79, respectively).

As expected, our regression analysis shows a significant influence of area on species richness of bats ($P=0.018$) in the Madrean Archipelago, but the unexpectedly high z value is problematic.

The log-log model was used for comparison (fig. 1) with the power models obtained for birds, $S=2.157 A^{0.165}$ (modified from Brown 1978), and non-flying mammals, $S=0.521 A^{0.323}$ (Davis et al. 1988). Such comparisons may not be entirely appropriate, but they are at least interesting and they do suggest differences among taxa. We had predicted that the z value for bats on mountain islands in southeastern Arizona would be more similar to the z value that had been obtained elsewhere for birds than to that obtained for non-flying mammals. This prediction was based on the fact that bats have dispersal abilities more similar to those of birds, while small non-flying mammals have comparably poor dispersal ability. But not only is the z value for bats on montane islands not like that for birds, it is also considerably different (much higher) than that for non-flying mammals (fig. 1). The dispersal ability of bats must surely be more similar to that of birds. There must be other variables, in addition to area, that are influencing the species richness of montane bats in southeastern Arizona.

The result of a stepwise regression of six variables on species richness of bats is given in Table 4. We found a highly significant relationship between survey effort and species richness; 82% of the variation was explained by survey effort alone ($F=37.55$, $P=0.001$). The area of forest habitat entered second and significantly improved the r^2 value by 0.091 for a total model $r^2=0.915$. The vari-

able for number of montane habitats entered third but was not significant at the 0.05 level.

Our finding that mountain islands have not been sufficiently surveyed for bats is of no surprise. In fact, in the Great Basin work, Brown (1978) compiled species of mammals on mountain islands in addition to birds but he "ignored bats, because their distributions are incompletely documented."

We graphed the data (fig. 2) from which we calculated the species-area regression equation given above, and drew in the regression line. Each of the data points on the graph represents a mountain range, and each is labelled. Outlier data points (potentially anomalous mountains), both above and below the line, were then examined. Five mountains lie below the line; they have lower species richness than predicted by area. One of these, the Chiricahuas, appears to be spurious and will be discussed below. Of the remaining ones, three of the data points below the line are not surprising because they represent mountains (Whetstones, Baboquivaris, and Galiuros) where little survey effort has been accomplished (Table 1). The fifth point represents the Pinalenos, a range that ranked relatively high for survey effort, but which shows species richness lower than expected. This may also be an anomalous range in terms of distribution of bats. Or it may have been improperly ranked in survey effort; certainly it is surprising that the relatively common *Lasiurus cinereus* has not been recorded there, and this absence may indicate inadequate sampling.

As survey effort is increased, the slope of the species-area regression line will undoubtedly flat-

Table 4.—Results of regression analysis of variables that could influence species richness. Mountain characteristics (total montane area, forest area, elevation, and number of montane habitats) were tested for correlation; only forest area and highest elevation were significantly correlated ($r=0.836$, $P=0.003$). Stepwise multiple regression was used to test for the influence of the following variables on species richness (untransformed data): total area, forest area, elevation of highest peak, number of montane habitats, survey effort, and total species richness on the mountain. Survey effort entered first, followed by forest area, and number of habitats, but no other variables met the 0.15 significance level for entry into the model (SAS program).

Stepwise Multiple Regression

Variables	Contribution to r^2	F	P
Step			
1: Survey Effort	0.824	37.55	0.001
2: Forest Area	0.091	7.47	0.029
3: No. Habitats	0.033	3.75	0.101

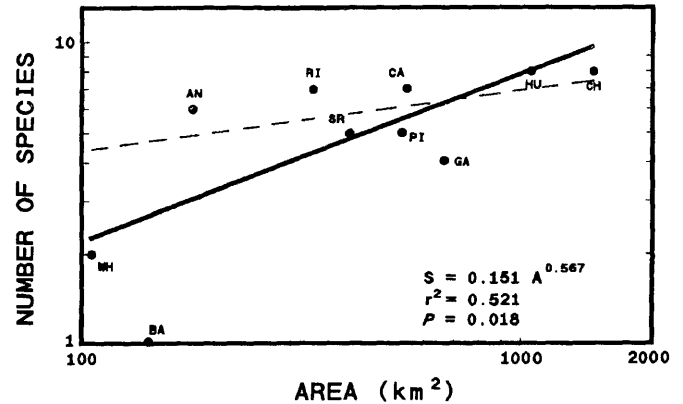


Figure 2.—Species-area curve for montane bats on selected mountains in the Madrean Archipelago. Both axes are logged. Solid curve is the regression line from current data. Dashed curve is a regression line from hypothetical future data with slight increases in the number of species recorded from two mountains ranges. See Table 1 for full names of mountain ranges abbreviated here.

ten out as more species are recorded from the least-studied mountains. To demonstrate this, we ran the species-area regression again after artificially increasing the species richness on the two least-studied mountains, the Whetstones and Baboquivaris, to that of the lowest diversity on the next least-studied mountain (i.e., four bat species). The resulting curve is shown as a dashed line in fig. 2. Using these artificial data points, the new power model is $S=1.606 A^{0.208}$. The z value (0.208) then is appropriately lower than that for non-flying mammals (Davis et al. 1988) and approaches that for birds (Brown 1978). Note also that the position of mountain data points below the line also changes. The Whetstones and Baboquivaris still have lower diversity values than expected, but they are much closer to the regression line than they were previously. The Galiuros have dropped to the lowest point below the line because they still have much area, but no more effort has been expended at finding new species. And the Chiricahuas, the spurious point mentioned earlier, has moved to where it belonged, above the line, since this range has the highest recorded diversity.

After adequate survey work has been completed so that all ranges have been equally well-studied relative to their size, we predict that all mountains will have nearly the same species richness regardless of island size. Variability in species richness will then be influenced more by other variables. If defined more precisely than we were able to do in our analysis, the number of habitats is then likely to be shown to be an influence of major importance (Rosenzweig 1992).

An examination of the data for non-flying mammals (Davis et al. 1988) shows two points where mammal diversity is zero, both islands that are $<100 \text{ km}^2$. There are no islands in the bird or bat analyses that are $<100 \text{ km}^2$ in size. It is interesting to speculate, however, whether there would be corresponding zero species richness. We would not predict zero richness for bats or birds.

CONCLUSIONS

For mountain islands in the Madrean Archipelago, inadequate sampling effort, area of forest habitat, (and perhaps low habitat diversity) have been shown to be factors contributing to species richness of bats that is lower on some mountain islands than that which would be predicted from area alone.

With bats, the contribution to species richness of sampling intensity provides a caveat that could be important in management and conservation decisions: the recorded patterns of species richness are not always the result of biological processes.

Distribution data obtained from survey effort may not be the most important information that can be provided by field biologists. Certainly information about roosts, fecundity and mortality data, or the factors affecting species diversity may be more interesting, but they are also more difficult to obtain. Simple faunal surveys, on the other hand, can be accomplished over relatively short periods of time for relatively small amounts of money. And for conservation purposes, as human use continues to affect environments, and where future comparisons will be made between what was and what is, it is critical to know what species exist on defined montane islands.

The analysis provided here provides useful information that could prove important in decisions regarding the most efficient use of funds for faunal surveys. Future effort should be directed toward those mountains where recorded species richness is most likely to be increased. There are some mountain islands in southeastern Arizona that have essentially been oversurveyed—where very little new information will be gained at very high time/effort cost, e.g., in the Chiricahua Mountains. On the other hand, there are other mountain islands where no or very little work has been done, and where even minimal effort will yield much new information about species richness, e.g., the Baboquivari Mountains.

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LITERATURE CITED

- Brown, D.E., and C.H. Lowe. 1980. Biotic communities of the Southwest. USDA Forest Service General Technical Report RM-78. 1 p. map. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Brown, J.H. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Naturalist Memoirs* 2:209-227.
- Cahalane, V.H. 1939. Mammals of the Chiricahua Mountains, Cochise County, Arizona. *Journal of Mammalogy* 20:418-440.
- Cockrum, E.L. 1960. The Recent mammals of Arizona. University of Arizona Press, Tucson, Arizona.
- Cockrum, E.L., and E. Ordway. 1959. Bats of the Chiricahua Mountains, Cochise County, Arizona. *American Museum Novitates* 1938:1-35.
- Cook, J.A. 1986. The mammals of the Animas Mountains and adjacent areas, Hidalgo County, New Mexico. Occasional Papers, Museum Southwestern Biology, University of New Mexico, 4:1-45.
- Davis, R., C. Dunford, and M.V. Lomolino. 1988. Montane mammals of the American Southwest: the possible influence of post-Pleistocene colonization. *Journal of Biogeography* 15:841-848.
- Davis, R., and R. Sidner. 1992. Mammals of woodland and forest habitats in the Rincon Mountains of Saguaro National Monument, Arizona. Technical Report NPS/WRUA/NRTR-92/06, CPSU/UANo. 47:1-62.
- Druecker, J.D. 1966. Distribution and ecology of the bats of southern Hidalgo county, New Mexico. University of New Mexico, Albuquerque, New Mexico, MS Thesis.
- Findley, J.S. 1993. Bats: a community perspective. Cambridge University Press, Cambridge, Great Britain.
- Findley, J.S., A.H. Harris, D.E. Wilson, and C. Jones. 1975. Mammals of New Mexico. University of New Mexico Press, Albuquerque, New Mexico.
- Hoffmeister, D.F. 1956. Mammals of the Graham (Pinaleno) Mountains, Arizona. *The American Midland Naturalist* 55:257-288.
- Hoffmeister, D.F. 1986. Mammals of Arizona. University of Arizona Press and Arizona Game and Fish Dept, Tucson, Arizona.
- Hoffmeister, D.F., and W.W. Goodpaster. 1954. The mammals of the Huachuca Mountains, southeastern Arizona. *Illinois Biological Monographs* 24:1-152.

- Hoyt, R.A., J.S. Altenbach, and D.J. Hafner. 1994. Observations on long-nosed bats (*Leptonycteris*) in New Mexico. *The Southwestern Naturalist* 39:175-179.
- Jones, J.K., Jr., R.S. Hoffmann, D.W. Rice, C. Jones, R.J. Baker, and M.D. Engstrom. 1992. Revised checklist of North American mammals north of Mexico, 1991. *Occasional Papers The Museum Texas Tech University* 146:1-23.
- Lange, K.I. 1960. Mammals of the Santa Catalina Mountains, Arizona. *The American Midland Naturalist* 64:436-458.
- Lomolino, M.V., J.H. Brown, and R. Davis. 1989. Island biogeography of montane forest mammals in the American Southwest. *Ecology* 70:180-194.
- Maza, B.G. 1965. The mammals of the Chiricahua Mountain region, Cochise County, Arizona. University of Arizona, Tucson, Arizona, MS Thesis.
- Rosenzweig, M.L. 1992. Species diversity gradients: we know more and less than we thought. *Journal of Mammalogy* 73:715-730.
- SAS Institute Inc. 1987. SAS/STAT guide for personal computers, version 6 edition. Cary, North Carolina: SAS Institute Inc.
- Sidner, R., and R. Davis. 1988. Records of nectar-feeding bats in Arizona. *The Southwestern Naturalist* 33:493-495.

APPENDIX

Appendix 1.—Survey effort by biologists in selected mountain ranges. A subjective number of points were designated for various criteria. Publications of mammal surveys, or specifically bat surveys, are as follows: Animas-Cook 1986, Druecker 1966; Catalinas-Lange 1960; Chiricahuas-Cahalane 1939, Cockrum & Ordway 1959, Maza 1965; Grahams-Hoffmeister 1956; and Huachucas-Hoffmeister & Goodpaster 1954. The presence of a main road and plentiful auxiliary roads were scored for road access. The presence of some or many known localities where bats were observed was noted for # localities. The number of known bat biologists that worked prominently on a mountain were recorded. The amount of surveying that we have accomplished in each range was added. The totals were then ranked and rank effort was used in regression analysis.

Criteria of Effort	Mountain Ranges		SR	WH	GA	PI	CH	HU	BA	AN
	CA	RI								
Publications	3					3	3+3	3		3+2
Road Access	2		1	1-	1-	2	2	2	1-	1
# Localities	2	1				1	2	2		
Known Bat Biologists	4	2	2		2	2	5	2	1	2
Our Work	1	5	1	1	1	1	1	3		
Totals	12	8	4	1+	3+	9	16	12	1+	8
Rank of Effort	8	5	4	1	3	7	10	8	1	6