AN ABSTRACT OF THE THESIS OF

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Title: Human influence on mammalian biodiversity of public lands in the United States

Abstract Approved: Elmer J Finck

Many factors affect biodiversity and species richness such as size of reserve, habitat diversity, land use outside the reserve, latitude, precipitation, degree of isolation, distance to species "source", and rate of disturbance. I determined the effects of reserve size, habitat diversity, and land use outside the reserve on mammalian species richness and assemblage, number of disturbed site species and undisturbed site species on reserves in the conterminous United States. In January of 1995, 429 letters were sent to the offices of national parks, national wildlife refuges, and national forests requesting information on mammals found within the reserves. Managers from 308 reserves replied. Questionnaires requesting additional information on acreage of the reserve, habitat types, surrounding land use, and confidence that the mammal list accurately represented the mammalian assemblage found on the reserve were sent back to the 308 reserve managers. After receiving the confidence rating for each reserve, 175 were found to be insufficient to use in my study. The remaining 133 produced useable data. To investigate the relationship between the size of an area and species richness, curvilinear regression and species-area curve equations were used. These data fit the species-area curve ($R^2=0.45$, $z = 0.12$), therefore, the rest of the analyses was conducted with confidence these data accurately represented a true relationship between size of reserve and species richness. Size of the reserve had more of an influence on undisturbed species richness ($R^2=0.63$)

than on disturbed species richness (R^2=0.20). When using simple linear regression to determine the relationship between habitat diversity and species richness, only a slight trend was noted ($P = 0.02$; $r^2 = 0.04$). Since the number of habitats are discrete groups, an analysis of covariance was used to determine the differences in species richness among number of habitats. In reserves with 7 to 9 habitat types, the overall species richness and undisturbed species richness was significantly higher. The number of habitat types within a reserve did not have a significant effect on disturbed species richness due to the habitat requirements of disturbed species. Within each habitat type group, undisturbed species richness was significantly less than disturbed species richness. Land use outside the reserve did not have a significant effect on overall, disturbed, and undisturbed species richness. Within each land use group, undisturbed species richness was significantly less than disturbed species richness.

Species area curve equations can explain conditions of the habitat for particular species being tested. The *z* value for undisturbed species richness was 0.26, which is consistent with true, oceanic islands showing the strong isolating effect of disturbance outside the reserve on the species inside the reserve. The *c* value for undisturbed species was very low, which means the environmental conditions for these types of species is poor.

Human influence on mammalian biodiversity of public lands in the United States

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Preface

My thesis follows the style of Conservation Biology.

Running heading: Human influence on biodiversity in US.

Key words: biodiversity, island biogeography, habitat fragmentation, species-area curve, habitat diversity.

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North America was once teeming with plants and animals. Today, in many urban and agricultural areas, only species with the most general habitat requirements remain. An important topic for many biologists and a concern of people all over the world is the status of the earth's biodiversity. Biologists spanning all aspects of science, from conservation biology and geology to physiology are concerned about the health of the earth's ecosystems and the rapid decrease in biodiversity. Wilson (1992) predicted that there are 10 to 100 million species on the planet today. Currently, there are approximately 1.8 million known organisms. As reported by Wilson (1992), the rate of extinction was 400 times that of extinction rates recorded through recent geological time, and increasing rapidly. Therefore, many species are being lost to extinction without ever being discovered, named, or identified, let alone studied.

Extinction is a natural process and necessary step in natural selection and evolution. In natural extinction, a species that is unable to adapt to a slowly changing environment will go extinct. However, the increased rate of extinction caused by the exponential increase in human population has caused change at a rate too rapid for many species to adapt. The current rate of decline of biodiversity exceeds that of any natural mass extinction in the past 65 million years (Wilson 1988). There are many causes of extinction including the inability to adapt to changing environments and direct exploitation and extirpation of a species by humans. However, the main cause for the decrease in biodiversity is the increase in human population and, thus, an increase in the rate of destruction and fragmentation of a species' habitat. Natural habitats are replaced by houses, agriculture, condominiums, hotels, malls, streets, parking lots, and highways.

With human development come other problems, such as logging, invasion by exotic species, acid rain, and water and air pollution. Species are not only impacted by the direct destruction of their habitat by these factors, but also by the fragmentation of their habitat.

Many governments have set aside parcels of land as reserves to protect natural resources because habitat is now the limiting resource for many species. In some areas, strides have been and are being taken to accomplish the habitat enhancement goal. However, only about 2.8% (about 4.25 million km^2) of the world's land surface is protected in reserves (Western 1989). Many of these reserves initially functioned as recreation areas or geographical attractions rather than protection for natural resources or specific species. In addition, these areas do not represent all of the types of biomes on the planet, therefore, many habitat types are not being protected. Since many types of habitats are so scarce, design and size of a reserve are important. Reserve managers must ask several important questions before deciding their management goals when acquiring new land or designing a wildlife reserve. How does the size of an area affect the species assemblage found in that area? Is species richness a function of the size of an area, numbers of habitat types, or both? How does the land use around the reserve affect the species inside the reserve? The answers to these questions depend on the goal of reserve managers, policy makers, and the public. The decision makers need to cooperate with one another and make their decisions regionally. The first decision to be made is whether the area should be managed for high species richness or managed for a particular species, perhaps an indicator species, game species, endangered species, threatened species, or keystone species. Another decision to be made is whether or not to break the reserve into many different habitat types to attract a diversity of species, thus increasing species richness, or to manage the reserve as a homogeneous area. Before making any of these decisions, managers must know how the land use outside their reserve, for example, urban or agricultural use, will affect the species richness and assemblage within their reserve.

Theories on how habitat fragmentation affects species richness were first derived from the concepts and mathematical models of island biogeography as proposed by MacArthur and Wilson (1967). One model, the species area curve, can be used to predict species richness in a particular sized area and has also been used to predict the number of species lost by habitat destruction and fragmentation (Myers 1988). The model shows that as area increases so does species richness. The formula for this relationship is

$$S = cA^{z} \qquad (1)$$

where S = species richness, A = area, c = constant dependent on habitat condition and population density, and z = phylogenetic constraints of the organism. The Arrhenius equation

$$\log S = z \log A + \log c \qquad (2)$$

(Preston 1962) is used to calculate the c and z values. To determine these values, the log of species richness is plotted against the log of reserve size where the slope of the line is z and the y-intercept is c. A tenfold increase in area results in doubling the species richness (MacArthur & Wilson 1967). Since the relationship between species richness and reserve size is curved and not linear, the transformation of Equation 2

$$\mathrm{EXP}(\log S) = \mathrm{EXP}(z \log A + \log c) \qquad (3)$$

will give the species-area curve equation (Equation 1).

Both theoretical and empirical data demonstrate that the size of an area has a direct effect on the number of species found in that area (Diamond 1975; Humphreys & Kitchner 1982; Glenn 1990; Soule et al. 1992; Enoksson et al. 1995). Species richness will change as a function of the equilibrium of colonization and extinction rates of an area (Forman & Godron 1986). On a small isolated island, there is more competition, lower colonization, and higher extinction, resulting in fewer species. On larger and less isolated islands, the extinction rate and competition are both lower, resulting in a greater number of species (Simberloff & Wilson 1969; Diamond 1974; Soule et al. 1992). Island biogeography theory states that species richness is a function of an island's area, isolation, and age. However, when applying these concepts to terrestrial "islands", which are equated to fragmented habitats, the rules are somewhat changed. As the contrast between preserved habitat types and the surrounding matrix decreases, the original theories of island biogeography become less applicable to the terrestrial "islands" (Diamond 1975). In these terrestrial situations, the following components must be taken into consideration when predicting species richness:

> S = f(+ habitat diversity, -(+) disturbance, + area, + age, + matrix heterogeneity, - isolation, - boundary discreetness)

(Forman & Godron 1986). The different components of the function (f) of species richness (S) are listed in presumed order of importance. The + indicates the component is positively correlated with species diversity and - signifies the component is negatively correlated with species diversity (Forman & Godron 1986). Obviously, there are many factors affecting species richness, however, the two components of this equation my thesis will concentrate on are the habitat diversity component, the most important component according to the above equation, and the area component. In addition to the components proposed by Forman and Godron (1986), I tested land use outside the reserve and its effect on mammalian species richness.

Much empirical data support the theory that the larger the reserve, the more species are present (Preston 1962; Connor & McCoy 1979; Humphreys & Kitchner 1982; Glenn 1990; Enoksson et al. 1995) because the large preserves have lower extinction rates and can hold more species at equilibrium (MacArthur & Wilson 1967; Diamond 1975). However, the equilibrium theory is not without criticism. Margules et al. (1982) have several criticisms of the assumptions of the equilibrium theory. First, the species-area relationships and equilibrium theory are only concerned with maximizing species richness. If every reserve manager's goal was to conserve the most species rich sites, many species might be neglected and eventually lost. Forgetting the differences between true islands and terrestrial “islands”, researchers apply island biogeography theory to terrestrial islands and they tend to make blanket statements that are not necessarily correct. Second, Margules et al. (1982) criticized the equilibrium theory because previous supporters of the theory never defined when a habitat becomes heterogeneous or homogeneous. However, MacArthur and Wilson (1967) acknowledged habitat heterogeneity and other factors, not size alone, will have a great effect on species richness. Margules et al. (1982) stated that researchers need to define heterogeneity as a heterogeneous habitat profoundly affecting species richness in an area. One could argue that a positive relationship between species richness and reserve size could be a function of, or have a strong effect on, the number of different habitat types found in a larger reserve (Forman & Godron 1986). In a large reserve, more habitat types will be included within its boundaries and more species would be present. MacArthur (1958) was the first to test the habitat heterogeneity theory empirically by dividing habitats of birds into groups based on the height of certain vegetation and measuring avian richness and habitat density in each group. Bird species diversity increased with the increasing number of habitats. The habitat diversity theory had been shown to work for soil mites (Anderson 1978), mammals in the wheatbelt of Australia (Humphreys & Kitchener 1982), lizards (Pianka 1967; Recher 1969), and other bird species (Rosenzweig & Winakur 1969).

Habitat fragmentation and land use outside a reserve can affect the assemblage of species that are in an area, as well. An operational definition for species assemblage is the types of species found in a reserve based on their habitat requirements (see Fauth et al. 1996). Humphreys and Kitchener (1982) divided species from three taxa (mammals, passerine birds, and lizards) into two groups depending on their habitat requirements. The first group was undisturbed site species (*u* species), which were species that require habitats undisturbed by humans, e.g., continuous habitats, old growth forest, and interior habitats. The second group was disturbed site species (*d* species), which included species that can tolerate habitats disturbed by humans, e.g. agriculture, buildings, and lawns. Humphreys and Kitchener (1982) then tested the effect of size of a reserve on these two types of species. They found the proportion of *u* species decreased as the size of the reserve drops below approximately 600 ha. The authors also concluded the smaller reserves contained relatively more *d* species.

The effect of reserve size on species assemblage has also been studied for mammalian species in Canada by Glenn (1990). She collected species lists from 28 parks of different sizes across Canada, divided the species into appropriate *d* and *u* species groups depending on the species' tolerance of disturbed habitat, and clustered mammals into "mammal providences" based on their coincident distributions as listed by Hagmeir (1966). She found a single large park in Canada will support equal or fewer mammalian species than several small parks with the same area. She also found that in highly populated regions of Canada, where many parks were isolated by cities and agriculture, the species assemblage had more *d* species than *u* species.

Many think of habitat fragmentation affecting only vertebrates because that is where much of the attention and research is directed. However, one must keep in mind that habitat fragmentation alters plant communities, that in turn affect vertebrate communities. Rudis (1995) studied how surrounding land uses and anthropogenic influences affect the types of bottomland plant communities in the southeastern United States. Rudis (1995) concluded the community types that historically occurred in areas unsuitable for agriculture, road construction, or non-agricultural human disturbance, or timber production were represented in the largest fragments studied. Larger fragments had older, wetland plant community types, whereas the smaller fragments had younger and drier plant community types. Rudis (1995) suggested fragmentation affects the assemblage of different types of bottomland plant communities.

Within the conterminous United States, I investigated the effects of reserve size, habitat diversity, and land use outside reserves on species richness for mammal species representatives of the families Didelphidae, Dasypodidae, Canidae, Felidae, Mustelidae, Procyonidae, Ursidae, Suidae, Tayassuidae, Cervidae, Bovidae, Antilocapridae, Aplodontidae, Sciuridae, Castoridae, Erethiziontidae, Myocastoridae, Ochotonidae, and Leporidae. I examined the relationship between size of the reserve and species richness and assemblage on these data collected from public lands across the United States. I tested the role of number of habitat types in determining species richness and assemblage. To determine how habitat diversity and reserve size affects the mammalian species assemblage in reserves, I compared the frequency of *u* species to *d* species in reserves surrounded by human disturbance. I determined whether small reserves surrounded by cities or agriculture (fragments) have the same proportion of *d* species and *u* species as those reserves homogeneous with the surrounding areas.

I used species lists from national parks, national forests, and national wildlife refuges to study the above objectives. I made the following assumptions before analyzing data. First, I assumed the data are reliable and accurate. The screening process for the data (described below), and the high visibility and profile of taxa selected for the study gave me confidence that the data I used were reasonably accurate. The second assumption concerns the variance of these data. There are many factors influencing species richness such as distance to another reserve, distance to a species "source", habitat diversity, and land use outside a reserve (MacArthur & Wilson 1967). Rosenzweig (1995) discuses other factors such as latitude, precipitation and evapotranspiration, rate of disturbance, and productivity that can influence species richness. I chose to test size of a reserve, habitat diversity within the reserve, and land use outside of the reserve as three influences on species richness and assemblage. Therefore, since the other factors do affect species richness and assemblage the variance is large. The large sample size used in my analysis should decrease the variance.

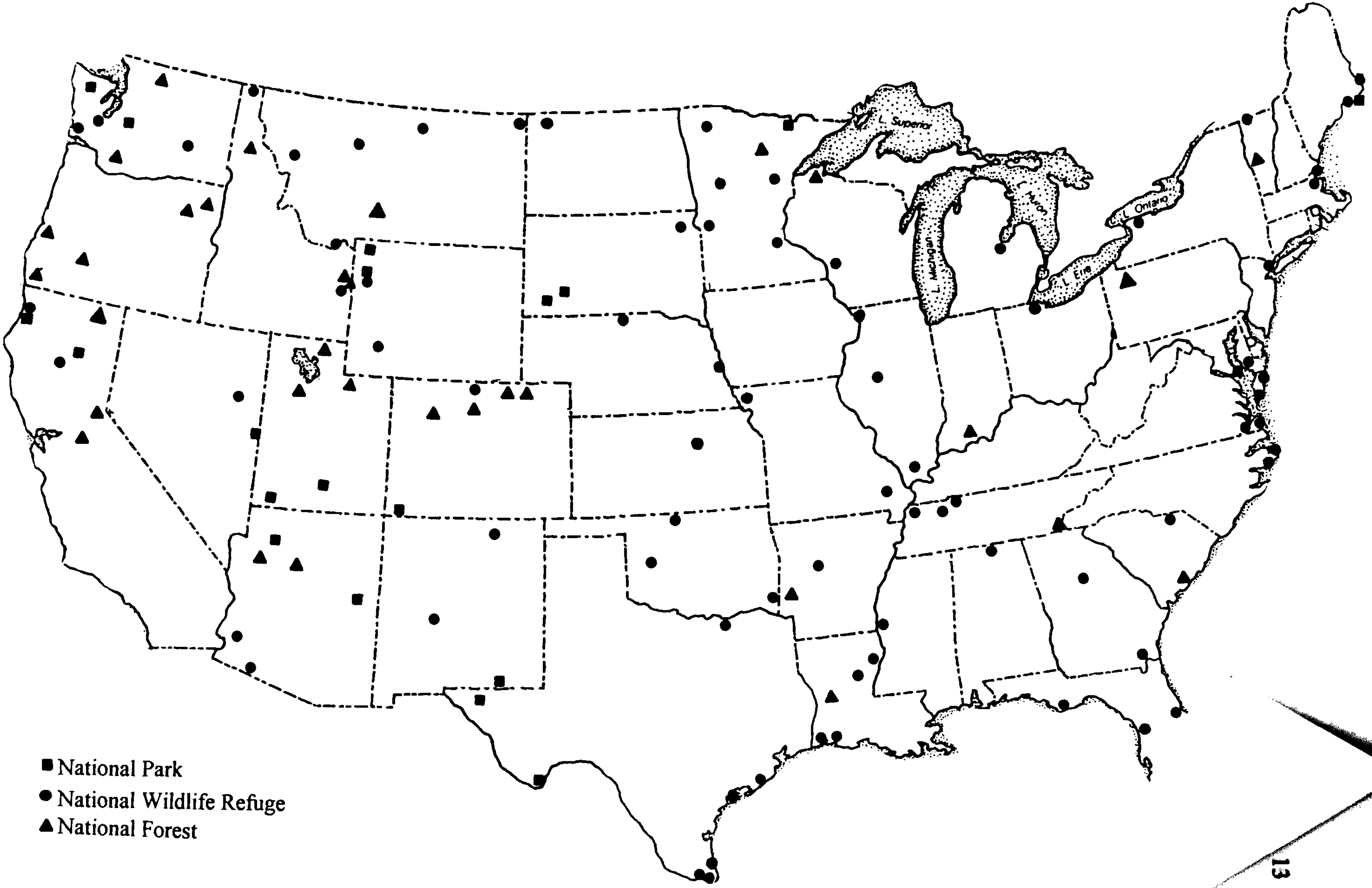
Materials and Methods

Collection and Organization of Data

I sent 429 letters requesting mammalian species lists from national wildlife refuges, national parks, national forests, and state parks in January of 1995 (Figure 1). To confidently say the lists of mammals represented the mammalian species on the refuge, I sent a questionnaire (Appendix A) to the reserve managers. In the questionnaire, the managers were asked their confidence (scale 1-5) that the lists of mammals accurately represented the mammalian species present on the reserve. If the confidence rating was a four or five and the list had been updated in the last 20 years, I considered the list valid. Through this screening process, the data used in my project were reasonably accurate and representative of the mammalian species on the reserves. To increase confidence in the data, I used groups of highly visible mammals. The groups I used were the conterminous United States mammalian species representatives of the families Didelphidae, Dasypodidae, Canidae, Felidae, Mustelidae, Procyonidae, Ursidae, Suidae, Tayassuidae, Cervidae, Bovidae, Antilocapridae, Aplodontidae, Sciuridae, Castoridae, Erethiziontidae, Myocastoridae, Ochotonidae, and Leporidae. To determine species richness for each park, I added up all of the presence records in the reserve.

The questionnaire also asked managers to list the different habitat types included within the reserve boundaries. Although many different levels of habitat description were received, habitat types were grouped according to mammalian habitat definitions. I chose this method because the different habitat requirements for mammals would serve as criteria for different groupings of mammals. Habitat types were defined as coniferous

Figure 1. Distribution of national parks, national wildlife refuges, and national forests with useable data.


L. Superior
L. Michigan
L. Huron
L. Ontario
L. Erie
■ National Park
● National Wildlife Refuge
▲ National Forest

forest, deciduous forest, mixed coniferous-deciduous forest, forest ecotone or edge, grasslands, marshes, desert, desert shrub, aquatic, agricultural or non-agricultural human disturbance. The reserves were then divided into different groups based on how many habitat types they had inside their boundaries. Group 1 had one to three habitat types, group 2 had four to six habitat types, and group 3 had seven to nine habitat types.

The questionnaires sent to reserve managers also asked them to classify the reserves as isolated by agriculture, non-agricultural human disturbance, e.g., cities and development, a different matrix other than the reserve, homogeneous with the surrounding area, or a combination of any of these. To classify a reserve as truly isolated, the surrounding matrix had to be completely different than the habitat found within the reserve or the reserve must be surrounded by agricultural or non-agricultural human disturbance. I used this information to test the differences in species assemblage and richness based on land use outside the reserve. The reserves were divided into four groups: 1) “frag-ag” was an area surrounded by agriculture, 2) “frag-h” was an area surrounded by non-agricultural human disturbance, 3) “frag-hag” was an area surrounded by both agricultural and non-agricultural human disturbance, and 4) “non-frag” was an area homogeneous to the surrounding land types.

To test differences in species assemblage, I classified each mammalian species into groups based on habitat requirements and life histories. A species was classified as a disturbed site species (*d*) if its habitat description included any human structures or agricultural fields (e.g., buildings, row crops, fence rows.). A species was categorized as an undisturbed site species (*u*) if its habitat description included interior areas or pristine habitats undisturbed by humans. In the taxa used for my study, there were 53 *d* species and 61 *u* species (Appendix B).

To acquire habitat descriptions and life histories, I used guides for mammals from all over the United States (Burt 1957; Olin 1961; Ingles 1965; Godin 1977; Jones et al. 1985; Jones 1988) and Mammalian Species Accounts when available. The classification of some mammals into these categories was difficult. Some species could go into either classification based on human tolerance of the species and some species fell in between the categories. However, with most of these species, the classification was based on human tolerance of the particular species, e.g., Ursus americanus. The majority of the species were obviously either *d* or *u* and easily classified.

Hypotheses tested

To test the influence of different habitat types on species richness, I used an analysis of covariance (ANCOVA) with size of the reserve as a covariate. ANCOVA uses a combination of regression and analysis of variance (ANOVA) techniques to remove the influence of reserve size from the groups. Since size of the reserve should have a large influence on species richness, the ANCOVA uses regression to determine the average size and then performs an ANOVA on different groups as if they were all in the same sized area. Here, the ANCOVA tested the H_o: group 1 = group 2 = group 3 regarding overall species richness, *d* species richness, and *u* species richness. I also used simple linear regression to assess any relationship between habitat types and richness. I used curvilinear regression to asses the shape of the distribution of my data and to explain relationship between species richness and size of a reserve according to my data.

I used the Arrhenius equation (Equation 2; Preston 1962) and simple linear regression to determine the *c* and *z* values for my species area curve. Then I transformed the equation (Equation 3) to obtain species-area curve equations for overall, disturbed, and undisturbed species richness. When comparing the influence of size of a reserve on *d* species richness and *u* species richness, I compared the *z* values for the Arrhenius equations since curves have no slope to test.

I used ANCOVA with size as the covariate to test the effect of agricultural and non-agricultural human disturbance outside reserve boundaries on species richness within the reserve. The H_0: frag-ag = frag-h = frag-hag = non-frag was used regarding overall species richness, *d* species richness, and *u* species richness. All the statistical tests were conducted using the SAS computer program.

Results

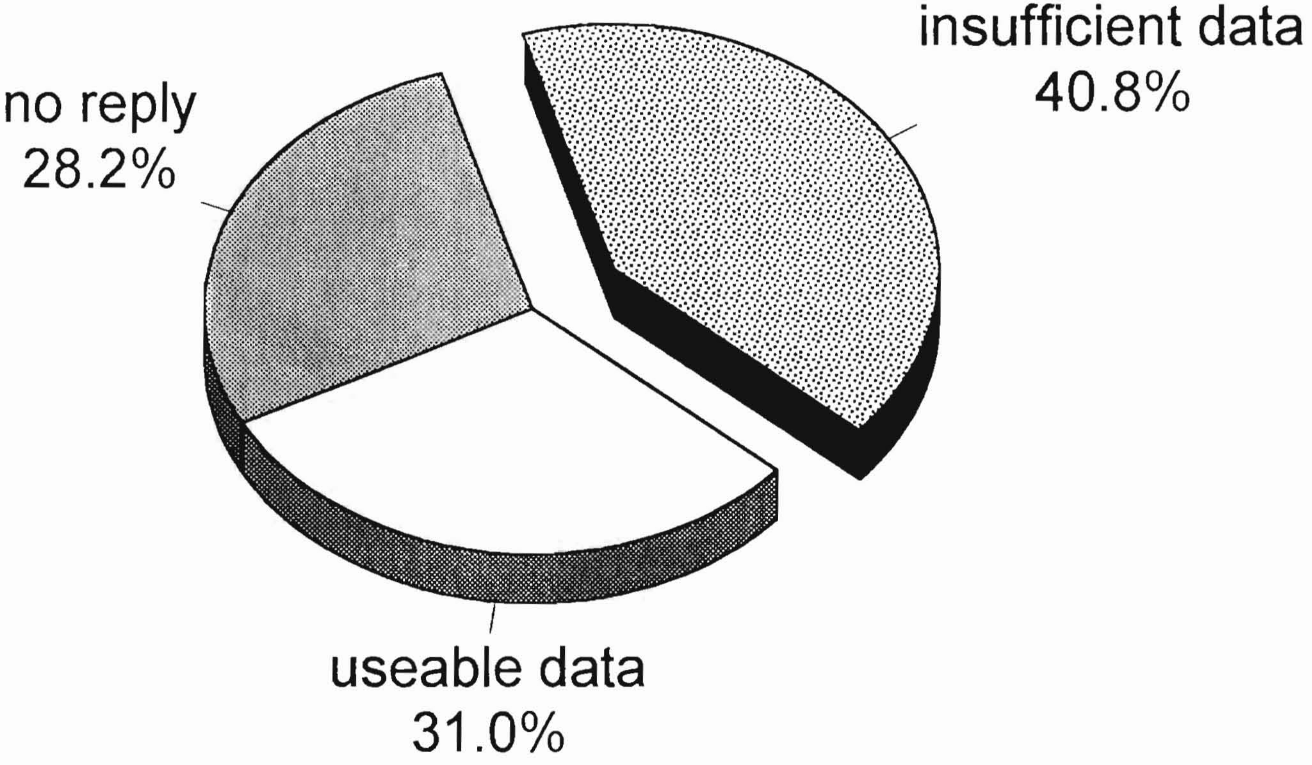
Of the 429 requests for mammal lists I sent out, 120 did not reply (28%). Of the 309 that did reply, 133 (31%) had data useable for my study (Figure 2). Of the 176 (41%) that were insufficient for use, most of the reserves had either no list of mammals, low confidence that the list accurately represented the mammalian species assemblage on the reserve (<4), an outdated list, or the list did not include large groups of mammals (usually small rodents, insectivores, and bats). Although the families I used did not include these taxa of mammals, I felt the complete omission of such large groups of mammals, like bats and small rodents, indicated possible misrepresentation of other species. The data I did use went through a rigorous screening process and I am confident they represented the mammalian species of the reserves reasonably accurately (Appendix C).

A trend was present between species richness and size in fragmented areas ($P < 0.0001$; $R^2 = 0.49$; Figure 3). The species-area curve equation for overall species richness is

$$S = 5.75A^{0.12} . \qquad (4)$$

When plotting the relationships between disturbed site species and undisturbed site species against reserve size, there was a noticeable difference between the R^2 of these two groups. The disturbed site species had a significant slope, however, the R^2 value was only 0.27 (Figure 4). For undisturbed site species, the R^2 value was 0.55 (Figure 5). Although the R^2 for *u* species is not large, the increase in R^2 from the *d* species should be noted. The species-area curve equation for *d* species (Figure 4) is

Figure 2. Percentage of questionnaire responses considered useable, insufficient, and those with no reply[a].



a) 429 total questionnaires sent

Figure 3. Overall species richness versus reserve size. (Regression line [dashed]:$\beta \neq 0$, $P = 0.001$; $\beta_2 = 0$, $P = 0.1385$; $R^2=0.45$. Species-area curve: Equation 4)

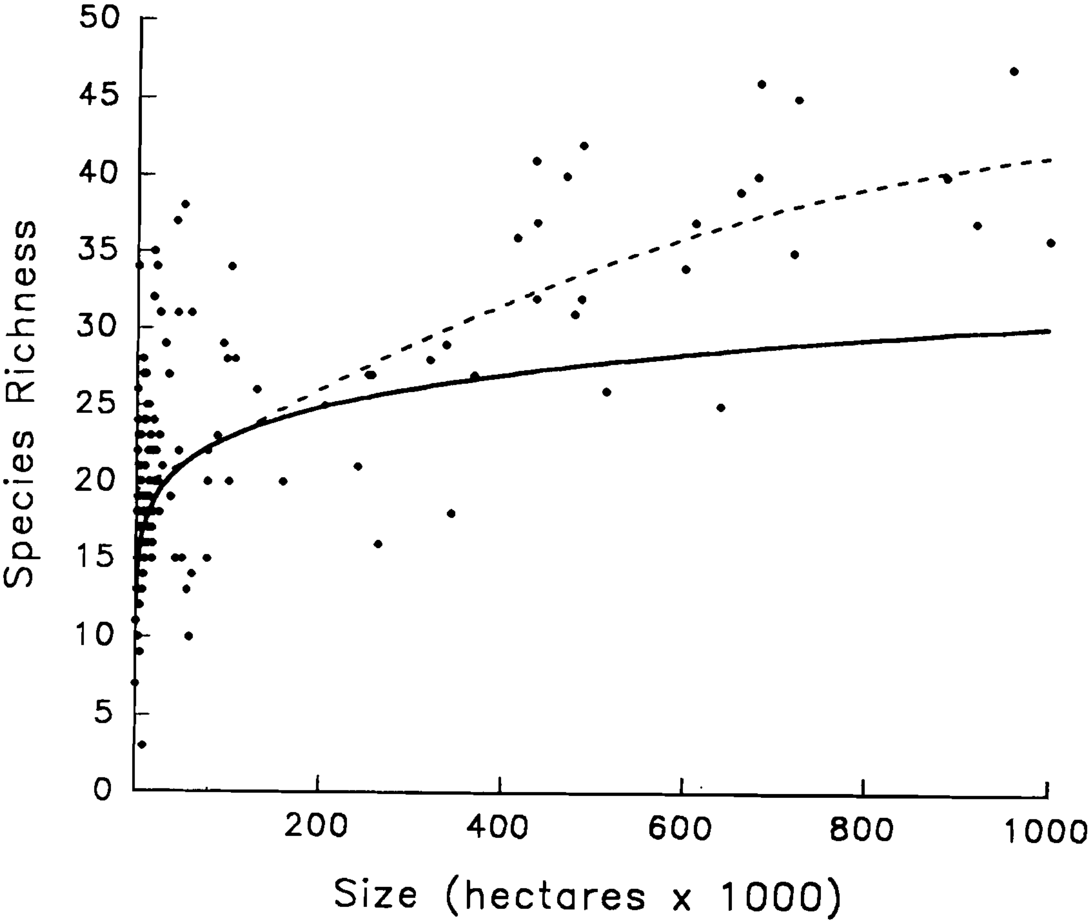

Species Richness
0
5
10
15
20
25
30
35
40
45
50
200
400
600
800
1000
Size (hectares x 1000)

Figure 4. Disturbed species richness versus reserve size.(Regression line [dashed]: $\beta \neq 0$, $P = 0.001$; $\beta_2 = 0$, $P = 0.4648$; $R^2 = 0.23$. Species-area curve [solid]: Equation 5.)

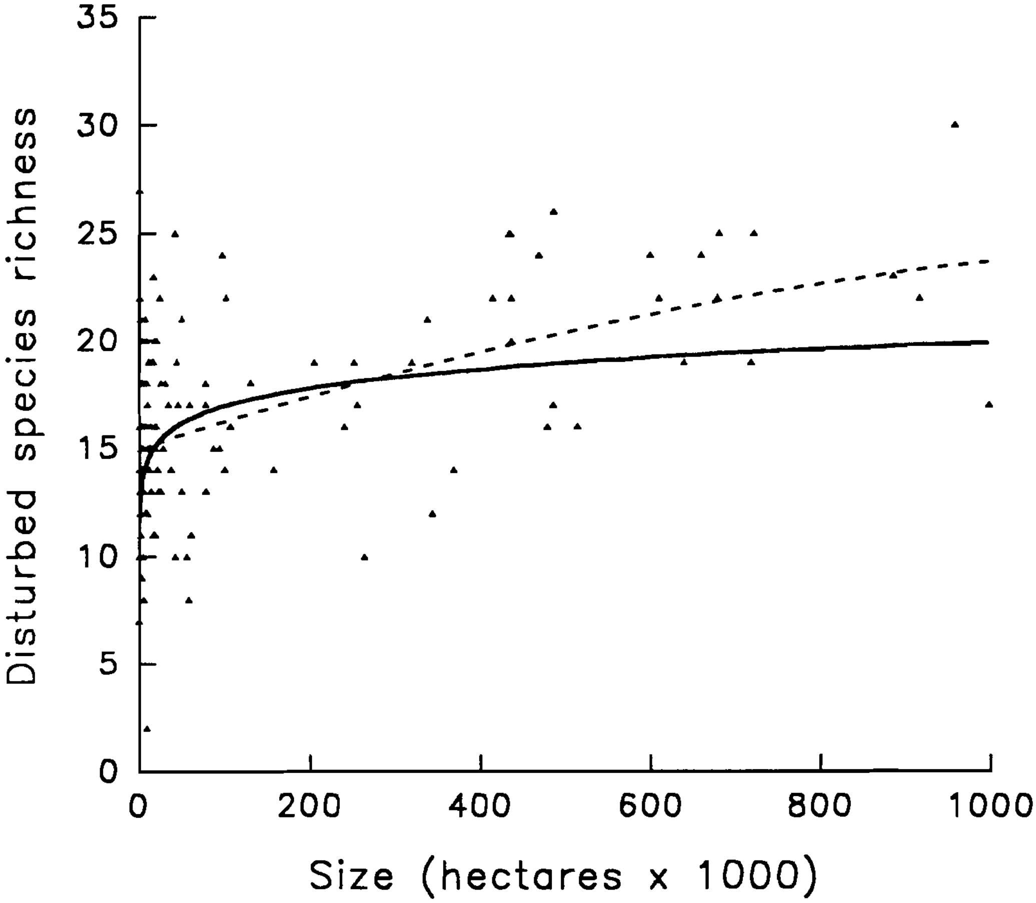
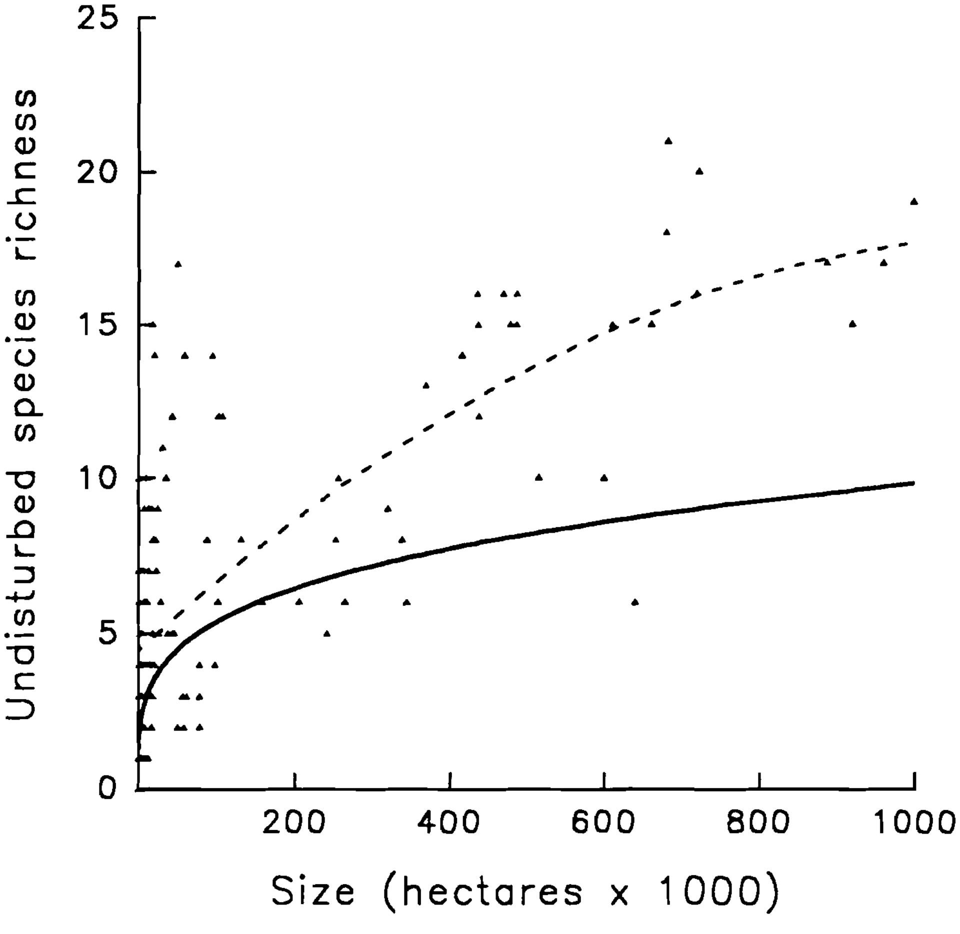

Disturbed species richness
35
30
25
20
15
10
5
0
0
200
400
600
800
1000
Size (hectares x 1000)

Figure 5. Undisturbed species richness versus reserve size. (Regression line [dashed]: $\beta_1 \neq 0$, $P = 0.001$; $\beta_2 = 0$, $P = 0.563$; $R^2 = 0.63$. Species-area curve [solid]: Equation 6.)



25
20
15
10
5
0
200
400
600
800
1000
Undisturbed species richness
Size (hectares x 1000)

$$S = 7.58A^{0.07} . \qquad (5)$$

and for *u* species (Figure 5)

$$S = 0.27A^{0.26} . \qquad (6)$$

Since there are no significance tests for differences R^2 or curves, t-tests were conducted on *z* values (slope of log-log plot; Figures 6 thru 8) to determine the influence of size on *d* and *u* species richness. There was no significant difference ($t = 0.62$; $P > 0.05$) between the *z* values. However, the *c* and *z* values can explain the effect of environmental conditions and magnitude of isolation to a particular taxa, as described below.

When plotting species richness against number of habitat types, a trend was present ($P = 0.02$) although slight ($r^2 = 0.04$; Figure 9). To test the H_o of no difference among the three groups, I used an ANCOVA with size of the reserve as the covariate. The assumptions for the ANCOVA test, e.g., normal distribution, homogeneous variance, homogeneous slopes among the groups, were satisfied ($P < 0.05$). Within each habitat type group, the undisturbed species richness was significantly ($P < 0.05$) lower than the disturbed species richness. The groups were significantly different at the 0.05 level for overall species richness ($P = 0.05$; Figure 10). Species richness in Group 3 was significantly higher than the other groups ($P < 0.02$). With disturbed species, there was no significant difference among the three groups ($P = 0.38$; Figure 11). There was a difference in the undisturbed species richness among the three groups ($P = 0.009$; Figure 11). Individual comparisons showed that, again, group 3 was significantly higher than the other two groups.

To test the difference in species richness in reserves with different land use

Figure 6. Log species richness versus log reserve size. ($\log S = 0.12 \log A + 0.76$; $P < 0.001$; $r^2 = 0.35$)

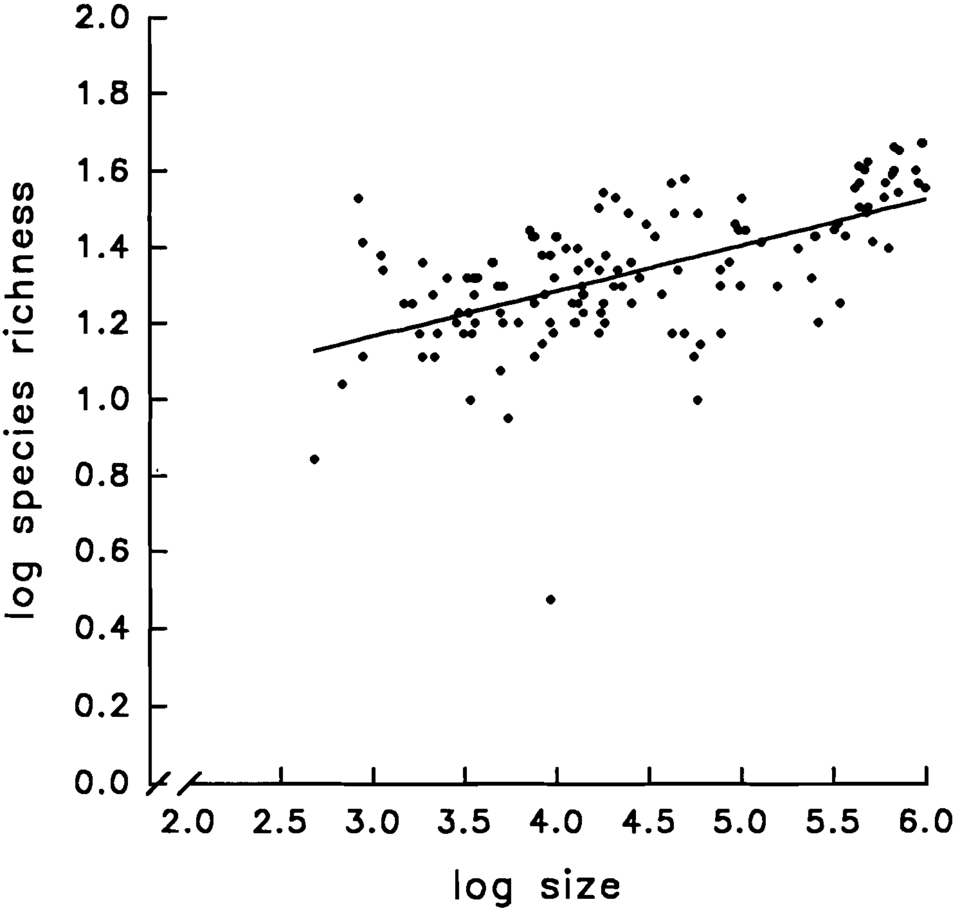

2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
log species richness
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
log size

Figure 7. Log disturbed species richness versus log reserve size. ($\log S = 0.06 \log A + 0.88$; $P < 0.001$; $r^2 = 0.16$)

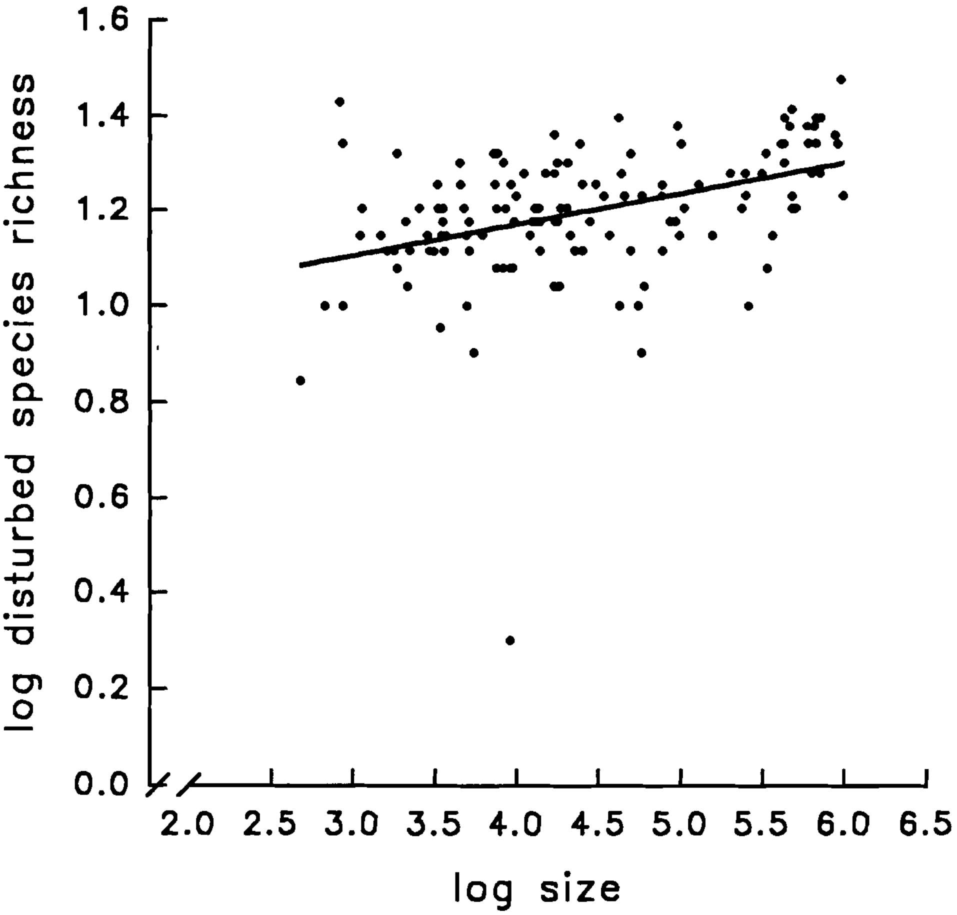

1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
log disturbed species richness
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
log size

Figure 8. Log undisturbed species richness versus log reserve size. ($\log S = 0.26 \log A - 0.56$; $P < 0.001$; $r^2 = 0.43$)

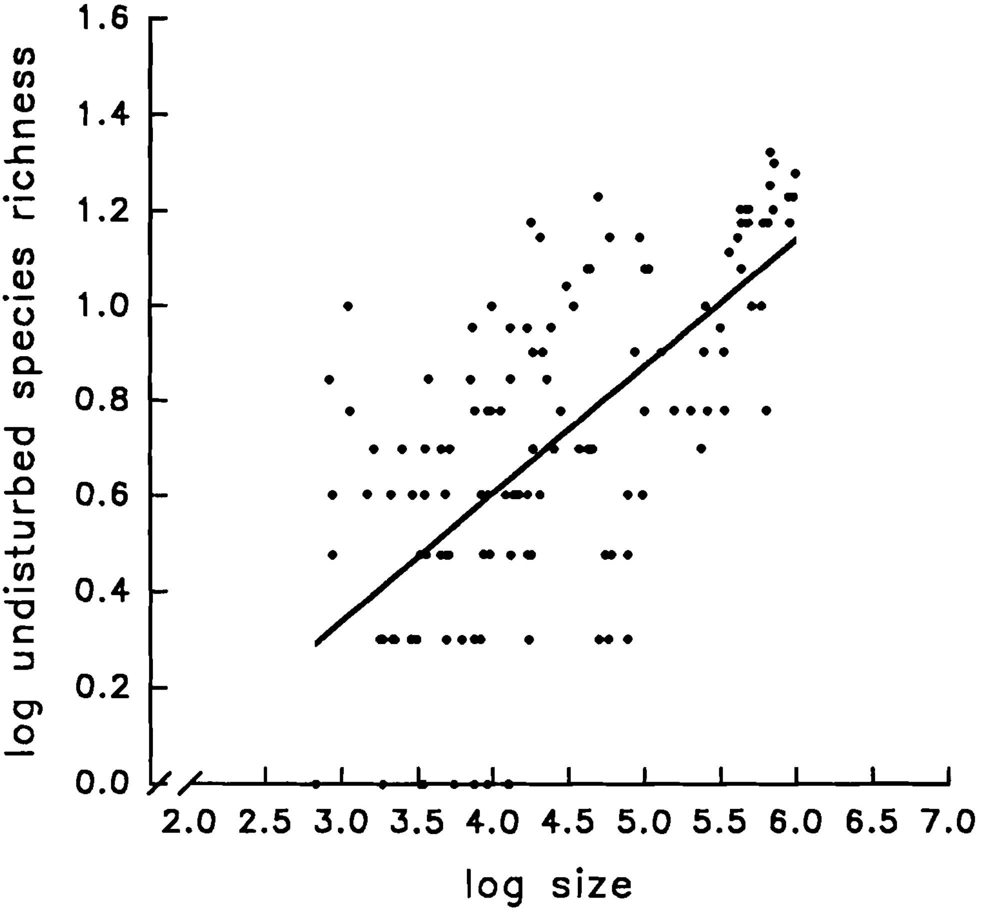

log undisturbed species richness
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
log size

Figure 9. Overall species richness versus number of habitat types. ($r^2 = 0.04$)

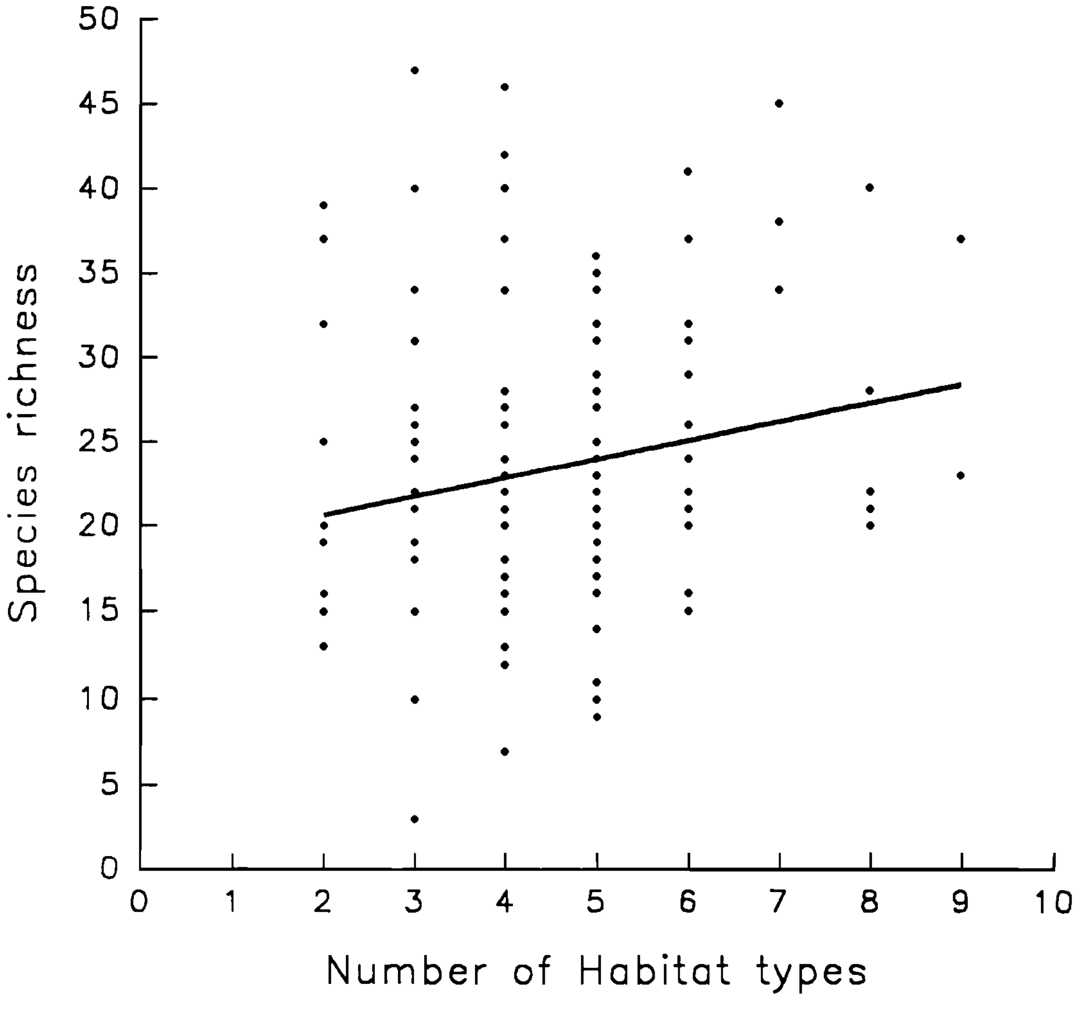

Species richness
50
45
40
35
30
25
20
15
10
5
0
0
1
2
3
4
5
6
7
8
9
10
Number of Habitat types

Figure 10. Differences in overall species richness relative to number of habitat types.(*P = 0.02)

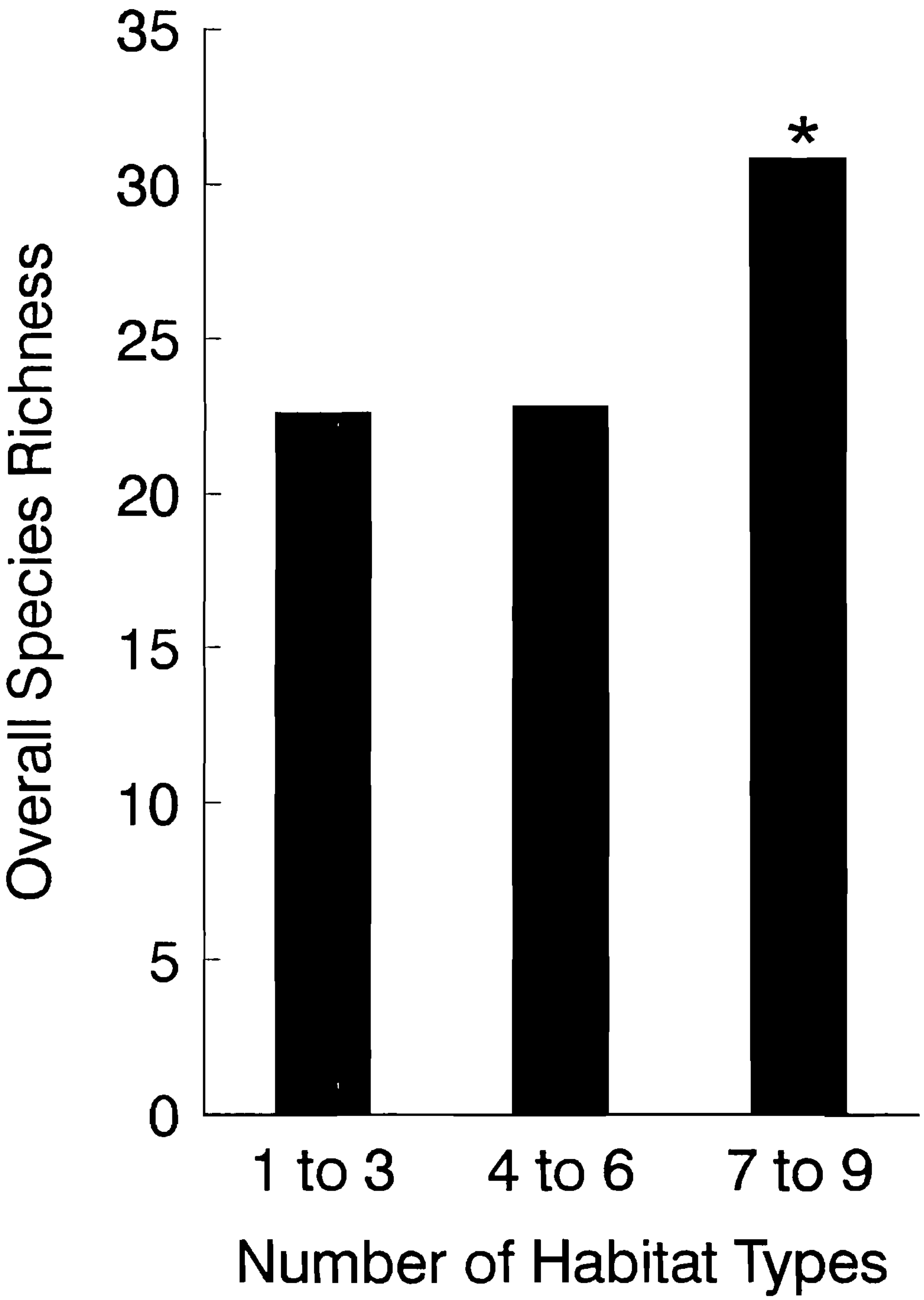
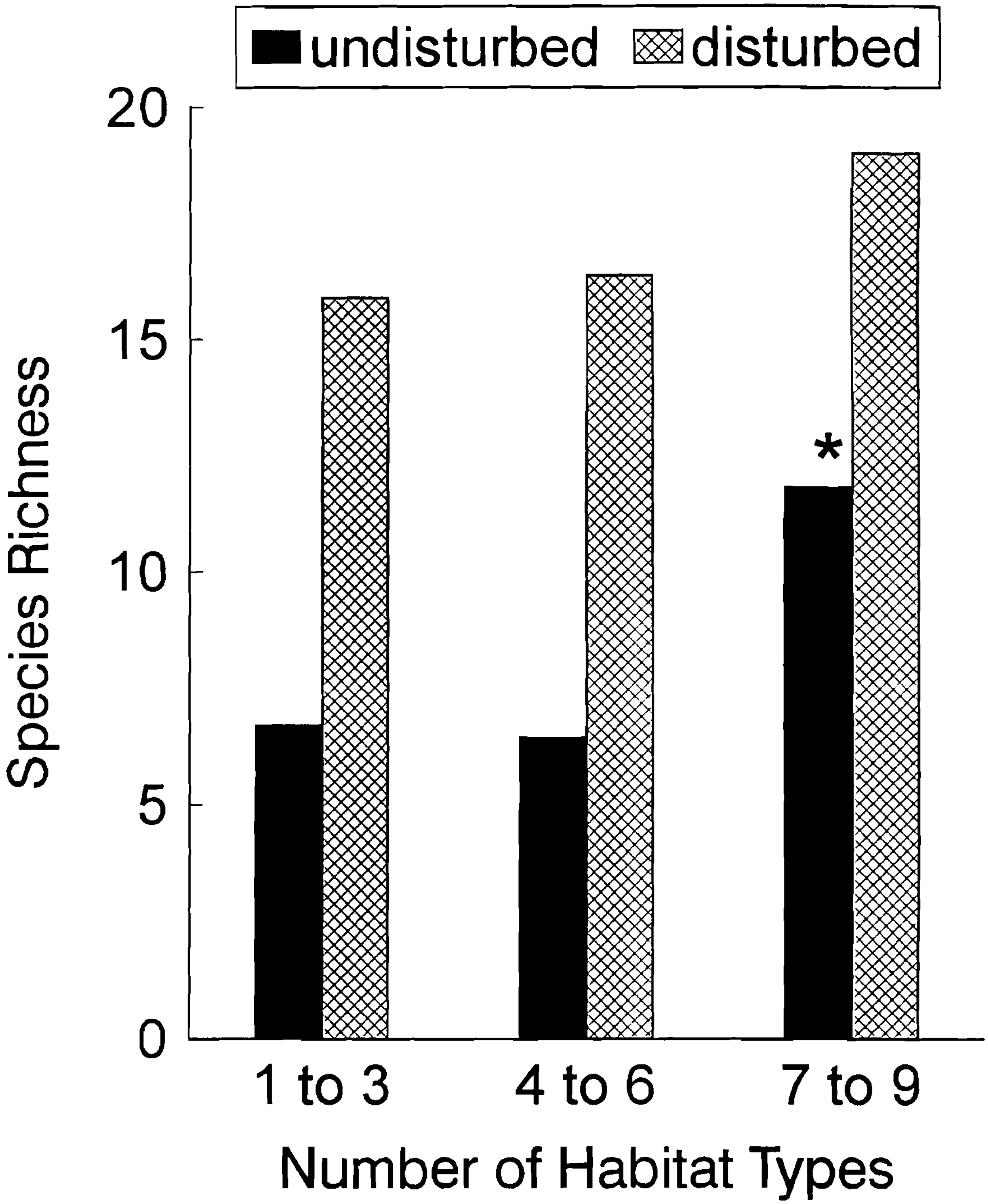

Overall Species Richness
35
30
25
20
15
10
5
0
*
1 to 3
4 to 6
7 to 9
Number of Habitat Types

Figure 11. Differences in undisturbed and disturbed species richness relative to number of habitat types.(*P = 0.0092)


undisturbed
disturbed
Species Richness
20
15
10
5
0
*
1 to 3
4 to 6
7 to 9
Number of Habitat Types

classifications (frag-ag, frag-h, frag-hag, and non-frag) I used an ANCOVA with size of the reserve as the covariate. All assumptions of the ANCOVA test were satisfied. Within each land use group, undisturbed species richness was significantly lower than disturbed species richness. There was no difference between the classifications with overall richness ($P = 0.20$; Figure 12). When testing the differences in the groups relative to *d* species richness, I failed to reject the null hypothesis ($P = 0.07$; Figure 13). Since this is a coarse study with many factors affecting the dependent variable other than those factors being tested, and the P-value was close to the α-value, individual comparisons among groups were performed. When testing each group individually, the areas surrounded by non agricultural human disturbance were, again, significantly lower than the other areas ($P = 0.02$). There was no difference between the classifications with *u* species richness ($P = 0.37$; Figure 13). In all cases, the frag-h classification (or those areas surrounded by non-agricultural human disturbance) had the lowest species richness.

Figure 12. Differences in overall species richness relative to land use outside of the reserve.

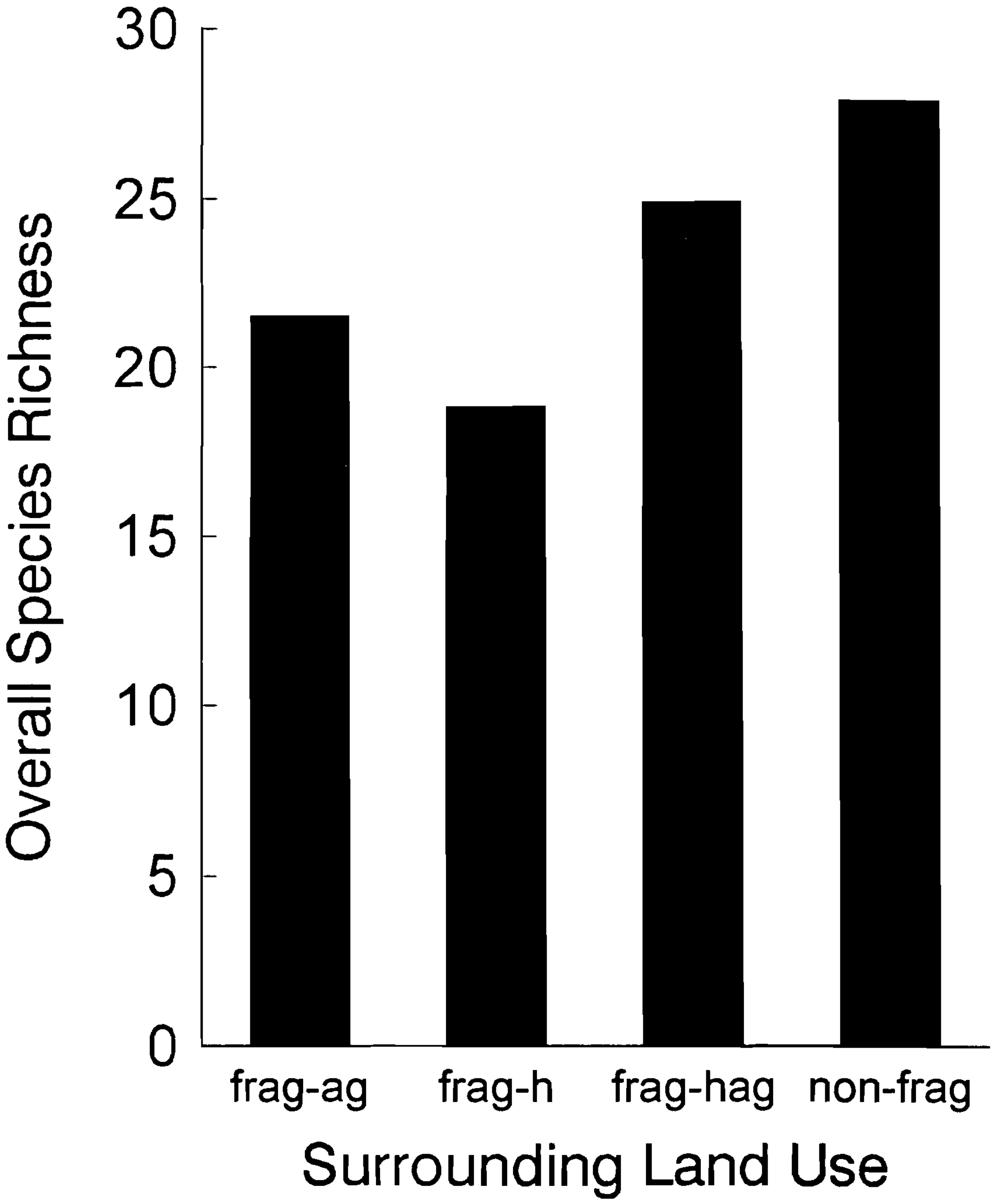
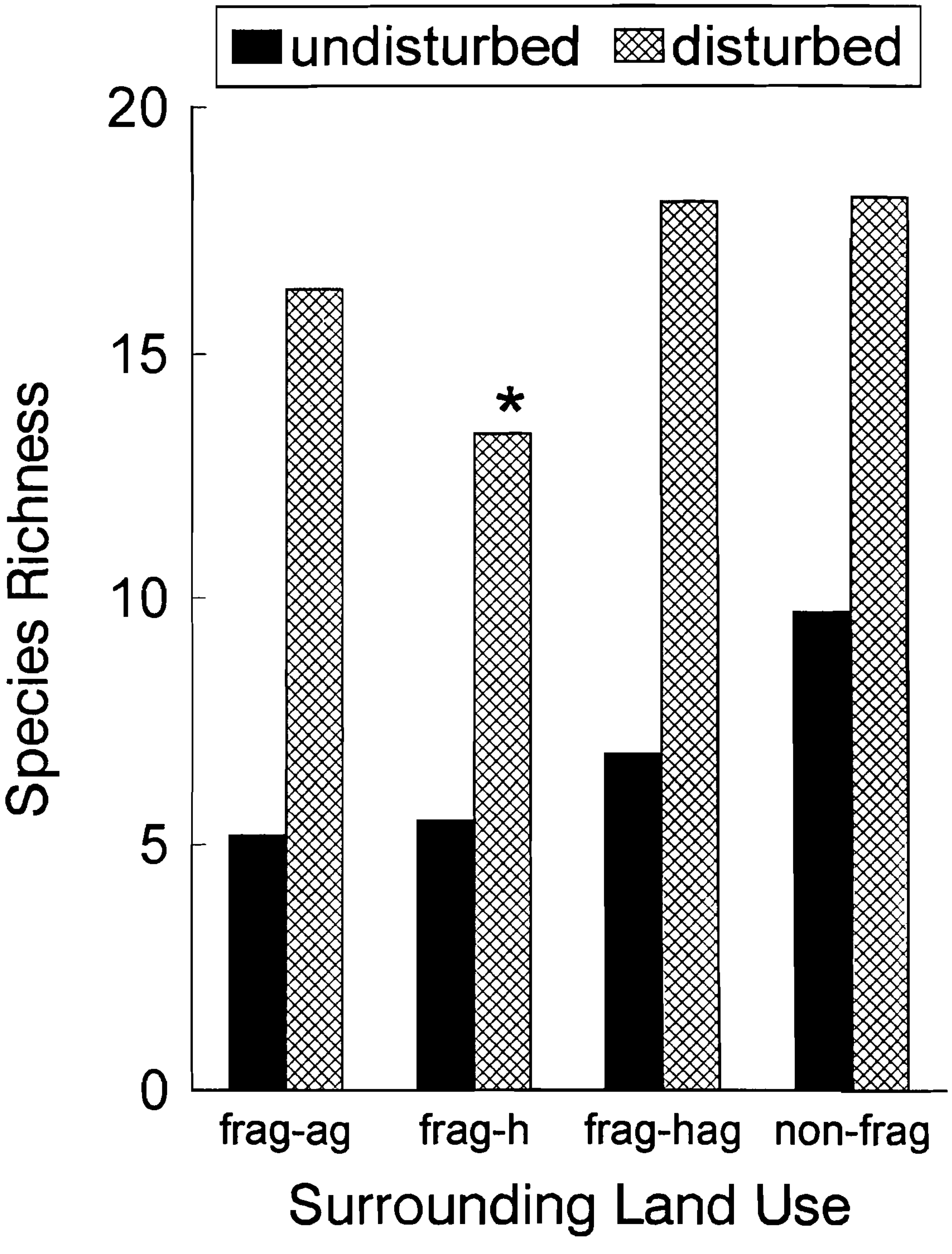

Overall Species Richness
30
25
20
15
10
5
0
frag-ag
frag-h
frag-hag
non-frag
Surrounding Land Use

Figure 13. Differences in undisturbed and disturbed species richness relative to land use outside the reserve.(*P = 0.02)


undisturbed
disturbed
20
15
10
5
0
Species Richness
*
frag-ag
frag-h
frag-hag
non-frag
Surrounding Land Use

Discussion

Many scientists believe the first step in solving the decreasing biodiversity problem is to know which species are present, extinct, or on the verge of extinction (Franklin 1988; Murphy 1988; Myers 1988; Wilson 1988). The public lands of the United States (national parks, national wildlife refuges, and national forests) serve as sanctuaries for many species in danger of extinction (Newmark 1995). Therefore, knowledge of the species in reserves and how well these reserves are protecting species is vital to understanding the biodiversity of the United States. Newmark (1995) addressed the extinction rates of mammal populations in western North American national parks and used the land-bridge island hypothesis as a possible explanation for his results. Land-bridge islands are formed when the sea level increases enough to cover up the land bridge, creating an island. When this occurs, the extinction rate increases until equilibrium is reached (MacArthur & Wilson 1967). Newmark (1995) found the number of extinctions after the establishment of national parks triples the number of colonizations. The land use outside of parks has become drastically different than the land use within parks. The change in the land use is equated to the rising sea level cutting off the species on the "island" from the "mainland". Newmark (1995) found the land-bridge island equilibrium theory consistent with the large extinction rates in the national parks. He also found the size of the park is inversely related to extinction rate, which is also another prediction of island biogeography.

Stohlgren et al. (1995) studied the reliability of species lists (plants and animals) in national parks and found some parks had an excellent inventory program. However, they felt the majority of the inventories were less complete than what is needed for accurate management. Stohlgren et al. (1995) attributed the incompleteness of the inventories to badly kept voucher specimens, a disproportionate amount of effort given to charismatic plants and animals, difficulty in achieving information on previous park studies, and differences in abundance classification, i.e., common, uncommon, rare.

In my study, the number of reserve managers with little knowledge of the species assemblage in their reserve (41%) is alarming. Of this 41%, some reserve managers had no list at all. Some managers had a list but it was too outdated to use in my study or it excluded many taxa of mammals, primarily insectivores, bats, and small rodents primarily because these are non-charismatic species. Reserve managers need to allocate more funding and energy to the inventory of the species on their reserves. The National Park Service has initiated a service wide Inventory and Monitoring Program (Ruggiero et al. 1992). One goal of the National Biological Service is to determine and monitor the status and trends of the nation's biological resources (Stohlgren et al. 1995). Knowledge of species on our public lands means a beginning to understanding biodiversity.

Since the main cause for decrease of biodiversity is growth of the human population and its increasing influence on habitats, the next step in conquering the biodiversity problem should be to assess how the human influence on habitats affect species richness and assemblage on reserves. Humans can extirpate a species by directly killing all members of that species, destroying a species' habitat, or fragmenting the habitat to a point where it is no longer viable for a species. To help solve these problems, humans have set aside parcels of land to serve as preserves for species. Many facets of human influence on these preserves and facets of the preserves themselves can affect the species richness and assemblage in the reserve. I have examined just a handful of these facets: 1) the relationship between reserve size and species richness and assemblage, 2) the relationship between number of habitat types and species richness and assemblage, and 3) the effect of the type of land use surrounding the reserve on species richness and assemblage.

Relationship of reserve size to species richness and assemblage

Inspired by the theories of island biogeography (MacArthur & Wilson 1967), investigators have studied reserve size and its relationship to species richness for many years. Since the original theories and models were developed, many authors have used these ideas to relate species richness for habitat "islands", areas of useable habitat for particular species surrounded by unsuitable habitat, (Simberloff and Abele 1982; Glenn 1990; Enoksson et al. 1995) or to debate the issue of reserve design (Diamond 1975; Gilbert 1980; Margules et al. 1982; Boecklen & Gotelli 1984).

In my study, I used mammalian species from public lands across the conterminous the United States to test the species-area relationship and to determine the effect of size of reserves on species assemblage. When plotting species richness against reserve size, a curvilinear relationship existed that was consistent with the island biogeography theory and species-area curve as it pertains to habitat "islands". Equation 4 shows that the z value of these data is 0.12, which is what is predicted by MacArthur and Wilson (1967) to be the appropriate z value for mainland habitat "islands". Data used in these analyses were only from reserves surrounded by agricultural and non-agricultural human disturbance or those surrounded by a different matrix than the reserve. The reserves that were homogeneous with the surrounding matrix were not used in these analyses because the species-area curve would not apply to those reserves not considered islands. The large variability in data points could be due to factors other than those tested in my study affecting the data, e.g., degree of isolation, distance from a species source, and latitude. However, the R^2 was 0.49, thus showed a reasonable fit. MacArthur and Wilson (1967) use equilibrium between extinction and colonization rates to explain the influence of size of a reserve on species richness. Other factors that can affect the equilibrium are degree of isolation of the island, habitat heterogeneity, distance from a species source, and proximity and shapes of the island. There are additional factors affecting species richness such as latitude, rate of productivity, disturbance, and if the area is near seismic activity (Rosenzweig 1995). Since size of the reserve is the only data available for my study, assumptions can be made that the other 0.51 ($1-R^2$) of the variation in species richness is explained by these other factors. Since these results follow the species-area curve as expected on mainlands ($z = 0.12$), further analyses were performed with confidence these data fit the models of island biogeography.

To test the effect of size of a reserve on species assemblage (number of *d* and *u* species), the null hypothesis was that the size of the reserve did not affect the species assemblage found in a reserve. Size of the reserve explained 27% of the variation in the *d* species richness and 56% of the variation in the *u* species. When comparing slopes of the Arrhenius equation (Equation 2), there was no significant difference, although the *u* species slope was slightly larger. According to my data, size of the reserve influenced undisturbed species richness nearly twice as much as disturbed species richness. When considering species that require habitats undisturbed by humans, this makes sense. Consider first, the concept that the larger a reserve, the more undisturbed land available for *u* species. Therefore, the number of *u* species would increase because more suitable habitat would be available. Many of these species require large home ranges. For example, the home range of a wolf (Canis lupus) or a grizzly bear (Ursus arctos) is 26 to 259 km^2 (Jones 1988), a mountain lion (Puma concolor) home range is 39 to 90 km^2 (Ingles 1965), and a fisher (Martes pennanti) can wander 90 km in one day (Ingles 1965). Therefore, one would expect as the size of a reserve increases, so does the number of many *u* species because large, continuous habitats are available for these species' range. Consider also the number of *u* species that require large areas to satisfy food requirements, either to hunt for a large number of prey or graze in a large area e.g., C. lupus, U. arctos, Cervus elaphus, and Bos bison. The larger reserve size should allow for adequate amounts of food required to support such species.

The difference between my species-area curves and the curvilinear regression line the regression line shows the relationship with the variance of my data and the species area curve is the expected relationship. According to my data, the species area curve underestimates species richness. Therefore, conclusions about extinction rates and number of species an area can hold given that species area curves to calculate the rates (Wilson 1992) are conservative.

Relationship of habitat heterogeneity to species richness and assemblage

MacArthur and Wilson (1967) stated that size of a reserve is not the only determining factor of species richness. Other biologists (Margules et al. 1982; Forman & Godron 1986; Rosenzweig 1995) discussed habitat heterogeneity as a strong influence on species richness. As the boundaries of the reserve enlarge, they will most likely include more habitat types. This increase in number of habitat types will cause more species to be present.

In plotting species richness against number of habitat types, a slight trend was present. The r^2 is low, possibly because high variability of the data and habitat types are discrete groups. Therefore, it is difficult to draw conclusions about the relationship of these variables from my analyses. However, the simple regression technique was instrumental in determining a trend. When using ANCOVA to compare habitat types, overall species richness increased significantly with number of habitat types. This is expected when considering habitat diversity and species diversity have evolved together (Rosenzweig 1995). All species cannot live in the same place nor consume the same resources. Therefore, each species has evolved in a different habitat that will fulfill its own requirements for survival while not greatly overlapping another species requirements for survival. Where there are many different habitats, several different species will have evolved over time to utilize these habitats. Thus, when there is great habitat diversity, there will be great species diversity.

With disturbed species richness, there was no significant difference between the habitat type groups. Many of these species live under many different conditions and in many different types of habitats, e.g., Didelphis virginiana, Spermophilus lateralis, Procyon lotor, Canis latrans, Odocoileus virginianus, and Sylvilagus floridanus.

Therefore, increasing number of habitat types would not affect disturbed species richness. Rosenzweig (1995) states that in order for habitat diversity to affect species richness, species in question should have evolved to be specialists within those habitats. The disturbed species are habitat generalists. When comparing differences in undisturbed species richness, habitat types did have an influence. Undisturbed species richness was significantly higher in reserves with seven to nine habitat types (Figure 8). Many undisturbed species are specialists, e.g., Martes pennanti, Lynx lynx, Alces alces, Ovis canadensis, Marmota flaviventris, and Sylvilagus aquaticus. Therefore, many different kinds of habitat types would increase the numbers of these species.

Since the number of disturbed and undisturbed species used in my study were approximately equal, one would expect the two groups of species to be equally represented in each group. However, within each habitat type group, the number of undisturbed species was statistically significantly lower, which suggests undisturbed species are under represented in the United States reserve system.

Relationship of surrounding land use to species richness and assemblage

Many people look to reserves as a refuge for species whose habitat has declined or has been altered some way by human impact. Granted, within the reserve, there is preservation of habitats. However, the type of land use outside of these reserves and how it affects the species inside the reserve should be examined. For example, logging, grazing, hunting, and trapping are permitted along the boundaries of many western national parks, but not within the parks themselves (Newmark 1995). This may have an effect on the mammals within the parks. Rudis (1995) explored how land use outside the reserves affects bottomland plant communities in the southeastern United States and found that land use outside the reserves did affect the type of plant communities included within the reserve boundaries.

In my study, reserves were divided into four different groups based on the type of land use surrounding the reserve (agricultural human disturbance, non-agricultural human disturbance, both agricultural and non-agricultural human disturbance, or homogeneous with the surrounding areas). Overall species richness was not influenced by external land use. There was a decrease, although not statistically significantly, in the number of species in areas surrounded by non-agricultural human disturbance. Therefore, non-agricultural human disturbance surrounding reserves has the greatest negative influence on overall species richness. The highest species richness was in non-fragmented areas. The data show a trend toward non-fragmented reserves supporting the greatest number of species. This is expected because areas with undisturbed, continuous habitats will contain both *d* and *u* species causing the overall species richness to be greater.

Relative to *d* species richness, I failed to reject the null hypothesis (no difference between land use groups) at the 0.07 level. However, since variance is high and the P-value for this test is close to the chosen alpha level (0.05), further analyses were performed on individual comparisons. In these further investigations, areas surrounded by non-agricultural human disturbance have a significantly lower number of *d* species. Non-agricultural human disturbance should have no effect on disturbed species since these species can tolerate these types of habitats. However, since non-agricultural human disturbance (cities) so intensely alters the habitat, it could have an effect on all types of species, no matter their tolerance for human disturbance.

Relative to *u* species richness, again, there were no significant differences between the land use groups. However, there were more *u* species in reserves surrounded by non-fragmented areas. Since *u* species have very little tolerance of any type of human disturbance, it is expected that there are more in areas of continuous habitat undisturbed by humans.

My results are inconsistent with other studies in which land use outside a reserve had a significant effect on the species richness and assemblage, e.g., Rudis 1995 and Newmark 1995, for two possible reasons. First, land use outside reserves used in my study could have no effect on the mammalian species richness within the reserve. Second, reserves could have been classified incorrectly into land use groups. A couple of methods by which classifications could be made more accurate are: 1) use of satellite images to correctly determine the land use outside the reserves, and 2) determine whether the reserves are true "islands" or whether there were areas along reserve borders homogeneous with the surrounding matrix to allow mammals to move in and out of the reserve. Within each land use group, the undisturbed species were significantly underrepresented. In all tests concerning external land use, reserves surrounded by non-agricultural human disturbance had the lowest species richness that concurs with the numerous statements by conservationists across the globe that human development and influence have severe negative influences on biodiversity.

Species-area curve equations: what they can tell us

The *c* and *z* values of species-area curve equations can show the influence of external land use and environmental conditions on species within a reserve. The *z* value for the overall species-area relationship (Equation 4) was 0.12, which is consistent with mainland habitat "islands" (MacArthur & Wilson 1967). The *z* value for the undisturbed species-area relationship (Equation 6) was consistent with true, oceanic islands (MacArthur & Wilson 1967). Therefore, the disturbance surrounding the reserves in the United States has a isolating effect to undisturbed species as water does to mammals on islands. The isolation of undisturbed species can lead to breakdown of metapopulation connectivity (Bright 1993), decreased dispersal, and genetic inbreeding (Noss & Cooperrider 1994). Relative to *c* values, MacArthur and Wilson (1967) note that a lower *c* value means poorer environmental conditions and a low representation for the species in the taxa being tested. The *c* value for disturbed species is 7.58 (Equation 5), whereas the *c* value for undisturbed species is 0.27 (Equation 6). The small *c* value for undisturbed species means in the reserves where these species live, the conditions are sub-optimal and they are under represented.

Conclusion

An important result of my study is the demonstrated lack of knowledge within the United States about biodiversity on its public lands. Such lands serve as refuges for many species, therefore, we should set goals to have accurate and thorough inventories of all public lands. The first step in solving the decreasing biodiversity problem, understanding biodiversity, cannot be taken until efforts are made to accomplish these goals.

Many factors influence species richness and assemblage. Latitude, degree of isolation, precipitation, reserve size, habitat diversity, rate of disturbance, productivity, and land use outside the reserve are only a few. I have tested only three of these factors: size of the reserve, habitat heterogeneity, and land use outside the reserve. Size of the reserve and habitat diversity have a profound effect on species richness. The larger an area in size, the more species are present that is consistent with the well known concept of the species-area curve. The more habitat types in a reserve, the higher the species richness, as well. However, these two factors are highly correlated, as size of an area increases, so does the number of habitat types within its boundaries (Rosenzweig 1995). Therefore, future empirical studies determining the effect of reserve size on species richness should keep habitat heterogeneity in mind when making conclusions.

In my study, land use outside the reserve did not affect species richness and that result does not agree with other studies (see Rudis 1995; Newmark 1995). In reserves sharing boundaries with non-agricultural human disturbance, the species richness was less, although not statistically significantly. Reserves sharing boundaries with agriculture, either row crop or grazing, had more species than reserves surrounded by non-agricultural human disturbance, but less than those reserves homogeneous with the surrounding area. I predict more reliable assessment of land use outside the reserves with satellite images would give a more accurate test of the external land use hypothesis. Since undisturbed species are under represented in the United States reserve system, conservation efforts should concentrate on these types of species. Undisturbed species should have large undisturbed areas representative of all habitat types. In order to reduce the influence of human disturbance on species richness within the reserves of the United States, buffer zones around the reserves could be created where human disturbance is less intense than what is currently surrounding the reserves (Noss & Cooperrider 1994). This may not be possible in some areas, however, legislators, reserve managers, and the public should keep in mind the isolating influence of external land use on species richness and assemblage inside the reserve when making decisions about management practices on reserves.

Future Research

Research needs to be done on the inventories of not only mammals, but of amphibians, reptiles, birds, plants, insects, and other invertebrates on public lands of the United States. In doing this, we can start to understand biodiversity. Testing the effect of latitude on species richness with my data (or data from other parts of the world) would be an interesting study. Satellite images could be used to assess accurately the intensity of different land uses outside the reserve and to determine if external land use does influence species richness and assemblage. The influence of land administration (Department of Agriculture versus Department of Interior) on species richness could be tested, as well. Another study that could be done would be to conduct a field study encompassing the degree of land use, habitat diversity, and size influence on species diversity and assemblage. A combination of all of these would have important conclusions and would add to our knowledge of biodiversity and the factors that affect it.

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Appendices

Appendix A. Example of questionnaire sent to reserve managers who provided mammal lists.

Katie M. McGrath
Division of Biological Sciences
Emporia State University
Emporia, KS 66801
email: mcgrathk@esuvm1.emporia.edu

United States National Park
Ms. Jane Doe
100 Jefferson Ave.
Max, NE 75632

Dear Ms. Doe,

Thank you for your quick response to my request for mammal and herp lists for your area. In order to better complete my project, I need a little more information. Could you please fill out this short survey? Thank you for your time and effort.

1. What is the total acreage for your area? ________________________

2. What are the different habitat types found in your area? List in order from most to least dominant types.

3. How would you classify the habitat of your area (circle all that apply)?

    a. a different habitat from the surrounding matrix
    b. fragmented within the area
    c. homogeneous with the surrounding areas
    d. surrounded by agriculture
    e. surrounded by human development

4. On a 1-5 scale (one being least confident and 5 being most confident), how confident are you that your mammal lists adequately represent the mammalian species that are found in your reserve? ______

Thank you again,

Katie M. McGrath

Appendix B. Classification of mammalian species based on habitat descriptions[a].

Species	Classification
Family Didelphidae	
Didelphis virginiana[b]	d
Family Dasypodidae	
Dasypus novemcinctus	d
Family Canidae	
Canis latrans	d
C. lupus	u
C. rufus	u
Urocyon cinereoargenteus	d
Vulpes velox	d
V. vulpes	d
Family Felidae	
Herpailurus yagouaroundi	u
Lynx lynx	u
L. rufus	u
Puma concolor	u
Family Mustelidae	
Conepatus leuconotus	u
C. mesoleucus	u
Enhydra lutris	u
Gulo gulo	u
Lontra canadensis	u
Martes americana	u
M. pennanti	u
Mephitis macroura	d
M. mephitis	d
Mustela erminea	d
M. frenata	d
M. nivalis	d
M. vison	d
Spilogale gracilis	d
S. putorious	d
Taxidea taxus	d
Family Procyonidae	
Bassariscus astutus	u
Procyon lotor	d

Appendix B (continued).

Species	Classification
Family Ursidae	
Ursus americanus	u
U. arctos	u
Family Suidae	
Sus scrofa	d
Family Tassysuidae	
Pecari tajacu	u
Family Cervidae	
Alces alces	u
Cervus elaphus	u
Odocoileus hemionus	d
O. virginianus	d
Rangifer tarandus	u
Family Antilocapridae	
Antilocapra americana	u
Family Bovidae	
Bos bison	u
Oreamnos americanus	u
Ovis canadensis	u
Family Aplodontidae	
Aplodontia rufa	u
Family Sciuridae	
Ammospermophilus harrisii	u
A. interpres	u
A. leucurus	u
A. nelsoni	u
Cynomys gunnisoni	u
C. leucurus	u
C. ludovicianus	u
C. parvidens	u
Glaucomys sabrinus	u
G. volans	u
Marmota caligata	u
M. flaviventris	u
M. monax	d
M. olympus	u
Sciurus aberti	u

Appendix B (continued).

Species	Classification	
Family Sciuridae (cont.)		
Sciurus aberti	u	
S. arizonensis	u	
S. carolinensis		d
S. griseus	d	
S. niger	d	
Spermophilus beecheyi	d	
S. beldingi	d	
S. coumbianus	d	
S. elegans	d	
S. franklinii	u	
S. lateralis	d	
S. mexicanus	u	
S. richardsonii		d
S. saturatus	u	
S. spilosoma	u	
S. tereticaudus	u	
S. townsendii	u	
S. tridecemlineatus	d	
S. variegatus	u	
S. washingtoni	d	
Tamias alpinus	u	
T. amoenus	d	
T. cinereicollis	u	
T. dorsalis	d	
T. merriami	u	
T. minimus	d	
T. quadrivittatus	u	
T. rufus	u	
T. senex	u	
T. siskiyou	d	
T. sonomae	d	
T. speciosus	d	
T. striatus	d	
T. townsendii	d	

Appendix B (continued).

Species	Classification
Family Sciuridae (cont.)	
T. umbrinus	d
Tamiasciurus douglasii	d
T. hudsonicus	d
Family Castoridae	
Castor canadensis	u
Family Erethizontidae	
Erethizon dorsatum	d
Family Myocastoridae	
Myocastor coypus	d
Family Ochotonidae	
Ochotona collaris	u
O. princeps	u
Family Leporidae	
Brachylagus idahoensis	d
Lepus alleni	d
L. americanus	d
L. californicus	d
L. callotis	d
L. townsendii	d
Sylvilagus aquaticus	u
S. audubonii	d
S. bachmani	u
S. floridana	d
S. nuttallii	u
S. palustris	u
S. transitionalis	u

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[a] d = disturbed site species, u = undisturbed site species.

[b] scientific and family names follow Wilson and reeder (1993).

Appendix C. Listing of location, size, and species richness of national parks, national wildlife refuges, and national forests.

Location	Size (hectares)	*d* species richness	*u* species richness	total richness
Acadia NP, ME	13200.0	15	7	22
Agassiz NWR, MN	61500.0	22	9	31
Allegheney NWR, PA	205200.0	19	6	25
Alligator NWR, NC	60898.4	11	3	14
Aransas NWR, TN	460001.0	7	5	22
Arapahoe NWR, CO	9306.8	18	6	24
Arapahoe NF, CO	515600.0	16	10	26
Badlands NP, SD	97600.0	24	4	28
Benton Lake NWR, MT	4953.2	14	3	17
Big Bend NP, TX	320000.0	19	9	28
Big Stone NWR, MN	4510.0	20	3	23
Blackwater NWR, MD	8366.4	12	2	14
Bosque del Apache NWR, NM	22876.4	13	7	20
Bowdoin NWR, MT	6220.4	14	2	16
Brazoria NWR, TX	28320.8	15	6	21
Cabeza Prieta NWR, AZ	344000.0	12	6	18
Capitol Reef NP, AZ	101747.2	22	12	34
Carolina Sandhills NWR, SC	18400.0	11	5	16
Caribou NF, ID	437690.4	22	15	37
Carlsbad Caverns NP, NM	18701.2	16	8	24
Catahoula NWR, LA	2123.2	15	4	19
Chassohowitazka NWR, FL	12200.0	14	4	18

Appendix C (continued).

Location	Size (hectares)	*d* species richness	*u* species richness	total richness
Chataqua NWR, IL	1795.2	13	2	15
Chequamegon NWR, WI	337841.6	21	8	29
Cherokee NWR, TN	252000.0	19	8	27
Chincoteague NWR, VA	5472.8	8	1	9
Chippewa NWR, MN	600000.0	24	10	34
Coconino NF, AZ	720000.0	19	16	35
Columbia NWR, WA	9280.0	12	4	16
Crab Orchard NWR, IL	17420.0	15	2	17
Cross Creeks NWR, TN	3544.8	15	4	19
Cypress Creek NWR, IL	14128.0	15	4	19
J.N. “Ding” Darling NWR, FL	2161.6	11	2	13
De Soto NWR, IA	3129.2	13	2	15
Dismal Swamp NWR, VA	42800.0	10	5	15
Eastern Shore of VA NWR, VA	680.0	10	1	11
Frances Marion NWR, SC	100376.8	14	6	20
Ft. Niobra NWR, NE	7652.4	21	6	27
Gallatin NF, MT	680000.0	22	18	40
Gifford Pinchot NF, WA	611080.0	22	15	37
Grand Canyon NP, AZ	487350.2	17	15	32
Grand Teton NP, WY	50000.0	21	17	38
Gray’s Lake NWR, ID	13120.0	16	9	25
Great Basin NP, NV	30840.0	18	11	29

Appendix C (continued).

Location	Size (hectares)	*d* species richness	*u* species richness	total richness
Great Meadows NWR, MA	3547.1	16	5	21
Green Mountain NF, VT	130160.0	18	8	26
Guadalupe Mountains NP, TX	34566.4	17	10	27
Hagerman NWR, TX	4528.018	18	5	23
Holla Bend NWR, AR	1633.2	13	5	18
Hoosier NF, IN	78000.0	17	3	20
Humbolt Bay NWR, CA	880.0	10	3	13
Idaho Panhandle NF, ID	1000000.0	17	19	36
Iroquois NWR, NY	7600.0	16	2	18
J. Heinz NWR, PA	480.0	7	0	7
Kisatchie NWR, LA	241200.0	16	5	21
Kofa NWR, AZ	264000.0	10	6	16
Konza Prairie Research Area, KS	3487.0	14	1	15
Kootenai NF, ID	1109.6	14	10	24
Lacassine NWR, LA	13188.0	15	3	18
Laguana Acosta NWR, TX	18074.8	15	3	18
Lassen Volcanic NP, CA	42400.0	25	12	37
Little River NWR, OK	4811.6	16	4	20
Lostwood NWR, ND	10760.0	19	3	22
Loxahatchee NWR, FL	58266.4	8	2	10
Minnesota Valley NWR, MN	880.0	22	4	26
MacKay Island NWR, NC	3426.0	9	1	10

Appendix C (continued).

Location	Size (hectares)	*d* species richness	*u* species richness	total richness
Maxwell NWR, NM	1480.0	14	4	18
Medicine Lake NWR, MT	12582.8	15	1	16
Merritt Island NWR, FL	56000.0	10	3	13
Mesa Verde NP, CO	20800.0	20	14	34
Mingo NWR, MO	8669.2	16	3	19
Missisquoi NWR, VT	2535.2	16	5	21
Modoc NF, CA	660652.0	24	15	39
Moosehorn NWR, ME	9778.4	15	6	21
Mt. Rainier NP, WA	92444.8	15	14	29
National Bison Range, MT	7416.4	18	9	27
National Deer Key Refuge, FL	9200.0	2	1	3
National Elk Refuge, WY	10000.0	17	10	27
Nisqually NWR, WA	1140.0	16	6	22
Okanogan NWR, WA	682400.0	25	21	46
Okefenokee NWR, GA	158400.0	14	6	20
Olympic NP, WA	368800.0	14	13	27
Ottawa NWR, OH	3327.2	16	1	17
Ouichita NF, AR	640000.0	19	6	25
Parker River NWR, MA	1864.8	12	1	13
Patuxent NWR, MD	5120.0	13	3	16
Pawnee National Grassland, CO	77912.0	13	2	15
Petrified Forest NP, AZ	37413.2	14	5	19

Appendix C (continued).

Location	[illegible]	*d* species richness	*u* species richness	total richness
Piedmont NWR, GA	[illegible]	13	4	17
Prescott NF, AZ	[illegible]	16	15	31
Red Rock NWR, MT	[illegible]	20	15	35
Redwood NP, CA	[illegible]	19	12	31
Reelfoot NWR, TN	[illegible]	15	4	19
Rice Lake NWR, MN	[illegible]	21	7	28
Rio Grande NWR, TX	[illegible]	18	5	23
Rocky Mountain NP, CO	[illegible]	16	12	28
Ruby Lake NWR, NV	[illegible]	19	4	23
Sabine NWR, LA	[illegible]	13	2	15
Sacramento NWR, CA	[illegible]	12	3	15
Salt Plains NWR, OK	12800.0	15	1	16
Santa Ana NWR, UT	835.2	27	7	34
Seedskadee NWR,WY	8400.0	20	4	24
Shiawassee NWR, MI	3620.8	13	3	16
Siskiyou NF, OR	437861.6	20	12	32
Siuslaw NF, OR	256000	17	10	27
Squaw Creek NWR, MO	2871.2	14	2	16
St. Vincent NWR, FL	4943.2	10	2	12
Stanislau NF, CA	436217.2	25	16	41
Sunkhaze NWR, ME	3734.8	14	7	21
Great Swamp NWR, NJ	2950.0	13	4	17

Appendix C (continued).

Location	Size (hectares)	*d* species richness	*u* species richness	total richness
Swanquarter NWR, NC	17090.0	11	4	15
Tahoe NF, CA	470214.0	24	16	40
Tamarac NWR, MN	17089.6	23	9	32
Targhee NF, ID	723014.8	25	20	45
Tenessee NWR, TN	20543.2	16	4	20
Tensas River NWR, LA	25569.9	13	5	18
Tremplealau NWR, WI	2246.8	13	2	15
Upper Mississippi River NWR, IL	78000.0	18	4	22
Voyageurs NP, MN	87221.6	15	8	23
Wallowa-Whitman NF, OR	960000.0	30	17	47
Wasatch-Cache NWR, UT	487899.2	26	16	42
Washita NWR, OK	3280.0	18	3	21
Waubay NWR, SD	1860.0	21	2	23
Wheeler NWR, AL	13800.0	16	4	20
White River NF, CO	920000.0	22	15	37
Willipa NWR, WA	21606.2	14	8	22
Wind Cave NP, SD	11316.8	19	6	25
Winema NF, OR	415594.4	22	14	36
Woodruff NWR, FL	7600.0	12	1	13
Yazoo NWR, MS	5176.4	15	5	20
Yellowstone NP, WY	887929.2	23	17	40
Zion NP, UT	59020.0	17	14	31

Katie M. McGrath

Signature of Graduate Student

Elmer J. Finck

Signature of Major Advisor

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5/16/96

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July 25, 1996

Date Received