AN ABSTRACT OF THE THESIS OF

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

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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

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

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.

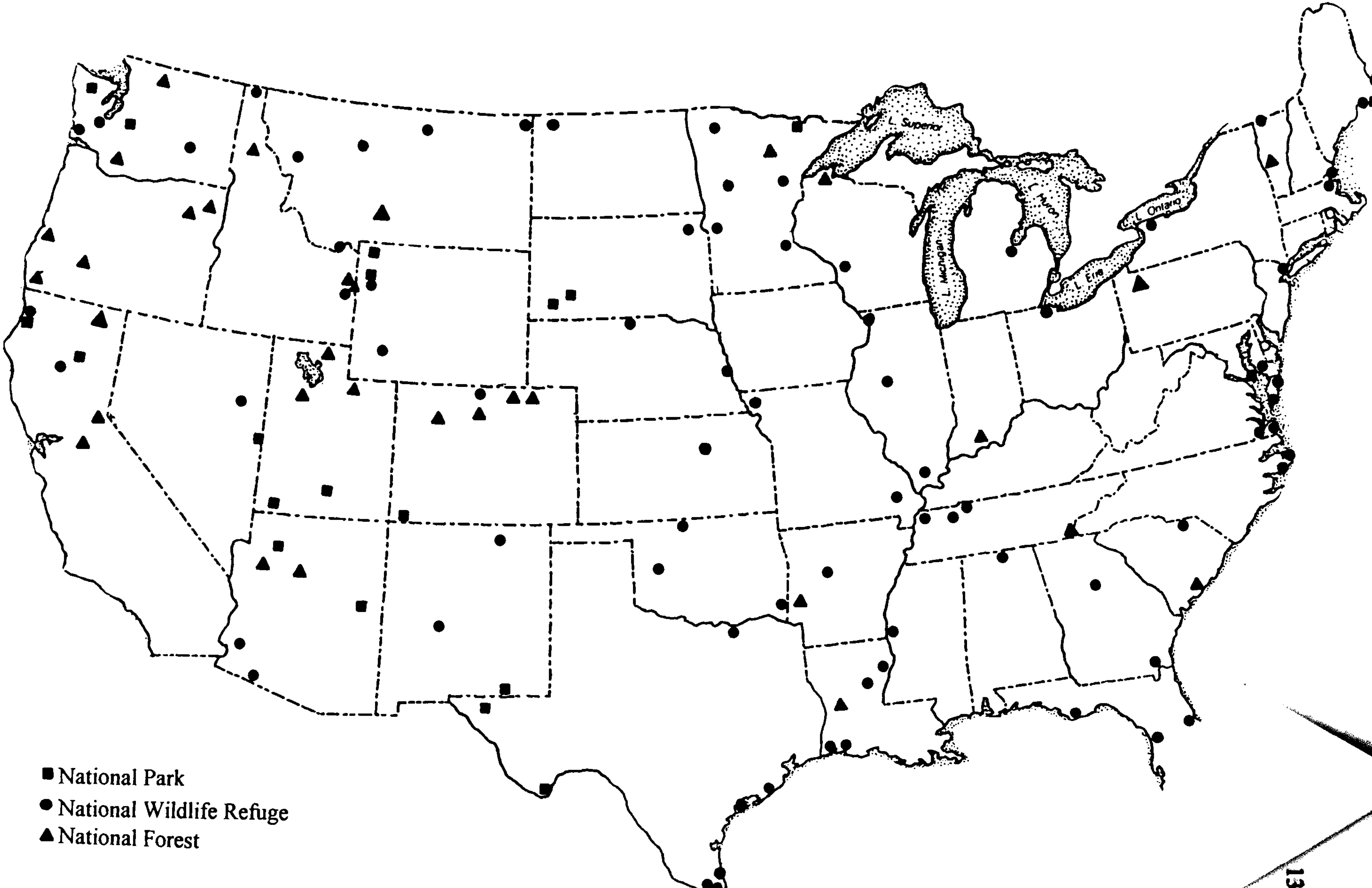
Materials and Methods

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 useab
data.



■ 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

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

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].